# PETITION TO LIST THE GREATER SAGE-GROUSE *Centrocercus urophasianus* UNDER THE SOUTH DAKOTA ENDANGERED SPECIES ACT

Presented by


Erik Molvar
Western Watersheds Project
P.O. Box 1770
Hailey, Idaho 83333
(307) 399-7910
emolvar@westernwatersheds.org

Nancy Hilding
Prairie Hills Audubon Society
P.O. Box 788
Black Hawk, South Dakota 57718
(605) 787-6466
nhilshat@rapidnet.com

Erik Molvar
319 S. 6th Street
Laramie, WY 82070

Nancy Hilding
6300 W Elm Street
Black Hawk, South Dakota 57718


**Presented to:**

Game, Fish and Parks Commission
Joe Foss Building
523 East Capitol
Pierre, SD 57501
C/o Jon Kotilnek <Jon.Kotilnek@state.sd.us>

August 27, 2020

## PETITION FOR RULEMAKING

This petition for rulemaking is submitted pursuant to SDCL 1-26-13.

Western Watersheds Project, Prairie Hills Audubon Society of western South Dakota, Erik Molvar, and Nancy Hilding submit this petition. Nancy Hilding is a resident of Meade County, South Dakota. Erik Molvar is a resident of Laramie, Wyoming. Prairie Hills Audubon Society is a non-profit corporation registered in South Dakota. Western Watersheds Project is a nonprofit corporation registered in Hailey, Idaho. As such, both organizations are persons by South Dakota law and Federal Supreme Court decisions.

We request that the South Dakota Game, Fish and Parks Commission amend South Dakota administrative rule 41:10:02:02 to add the greater sage grouse to South Dakota's list of threatened bird species. Below find the rule with the proposed amendment inserted as item number (4):

**41:10:02:02. List of threatened birds.** Birds classified as threatened in the state are as follows:

(1) Osprey, ***Pandion haliaetus***;

(2) Piping plover, ***Charadrius melodus***;

(3) American dipper, ***Cinclus mexicanus.***

(4) Greater Sage Grouse, ***Centrocercus urophasianus***

## STATEMENT OF REASONS

Western Watersheds Project and Prairie Hills Audubon Society hereby petition the South Dakota Game, Fish, and Parks Commission to list the greater sage-grouse (*Centrocercus urophasianus*) as an endangered species under the South Dakota Endangered Species Law. (Chapter 34A-8 of South Dakota codified laws). SDCL 34A-8-4 gives the authority to list species to the Commission.

The greater sage-grouse has been declining in numbers for many years and is in imminent danger of extirpation across its entire range in South Dakota. Sage-grouse may be already extirpated in southwestern South Dakota, although there is reason to believe that birds may still occur in this part of the state. Current conservation measures currently in place are failing to address the causes of the decline or to compensate for habitat degradation by habitat improvement elsewhere, as evidenced by the continued decline of the species.

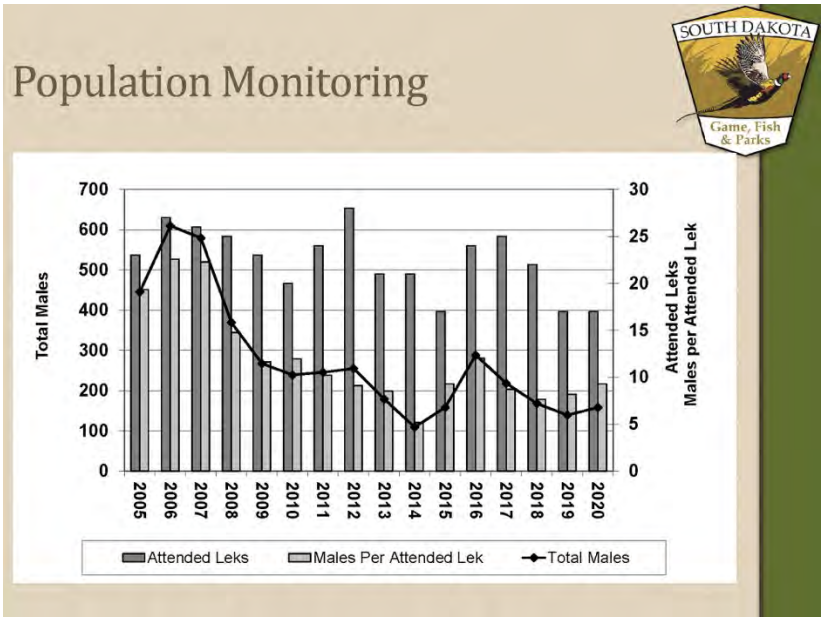
### POPULATION STATUS

South Dakota's statewide cumulative count of sage-grouse descended to a historic low in 2019, down to 139 strutting males. This represents a 77.2% decline from the male count at the last major peak, in 2006. In 2020, the cumulative number of strutting males stood at 158. Lek count trends, based on South Dakota Fish, Wildlife, and Parks data, follow:

| | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2019 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Total Males** | 233 | 445 | 609 | 579 | 369 | 267 | 239 | 245 | 255 | 179 | 109 | 158 | 288 | 218 | 168 | 139 |
| **Males per Attended Lek** | 15.5 | 19.3 | 22.6 | 22.3 | 14.8 | 11.6 | 12.0 | 10.2 | 9.1 | 8.5 | 5.2 | 9.3 | 12.0 | 8.7 | 7.6 | 8.2 |

Conservatively assuming a sex ratio of two females per male (*sensu* Braun et al. 2015), and a conservative census success rate for strutting males of 75 percent (as demonstrated by Fremgen et al. 2016 and Coates et al. 2019, high male counts represent between 77% and 93% of males in each population) to yield the largest scientifically defensible figure, 158 strutting males can be extrapolated to a total population size of 632 birds.

The minimum viable population threshold for species generally is 5,000 individuals (Traill et al. 2010), and the 5,000-bird minimum viable population threshold has been established for sage-grouse in particular (Aldridge and Brigham 2003). Because the sage-grouse is a lekking species, in which one or two males typically do all of the breeding at a given lek, the genetic contributions of the sexes are skewed. Between the low total population, its danger of isolation from sage-grouse populations in other states, and this skewed ratio of breeding birds, the current total sage-grouse population in South Dakota is too small to prevent inbreeding and the genetic problems (birth defects, inbreeding depression reducing the number of viable offspring) that go with it.




Garton (2015) performed the most current population viability analysis for the Dakotas population (encompassing North and South Dakota and small portions of Montana and Wyoming), and found a 72.5% probability that the overall multi-state population would decline below 50 strutting males for this population in 100 years, and a 21.5% chance of declining below

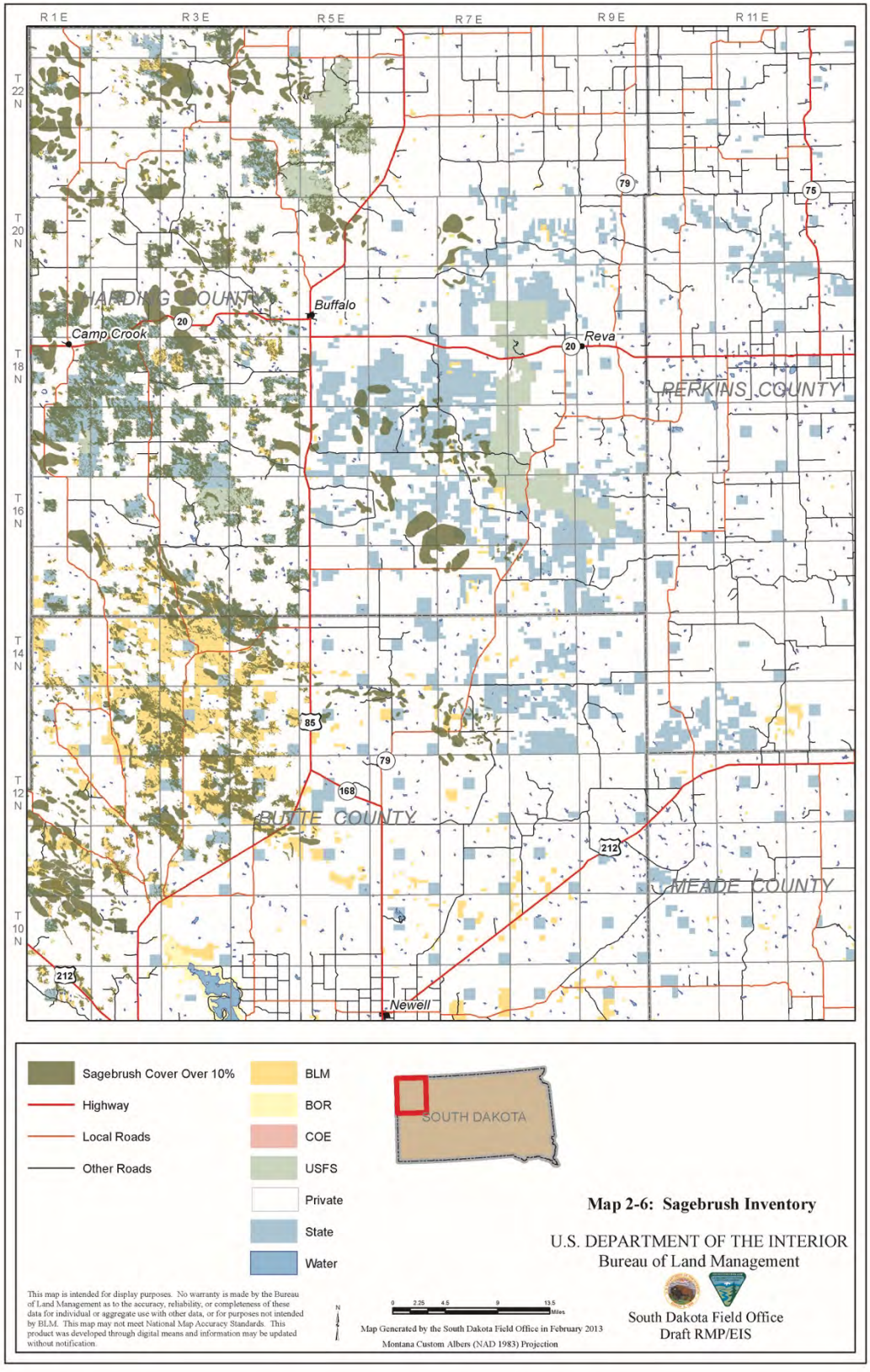
20 males by 2045. In effect, the South Dakota sage-grouse population may already be trapped within an extinction vortex.

According to the 2014 South Dakota Sage Grouse Plan (SDGFP 2014), greater sage-grouse habitat is currently found predominantly on private lands:

Table 1. South Dakota sage-grouse core area surface ownership acreage.

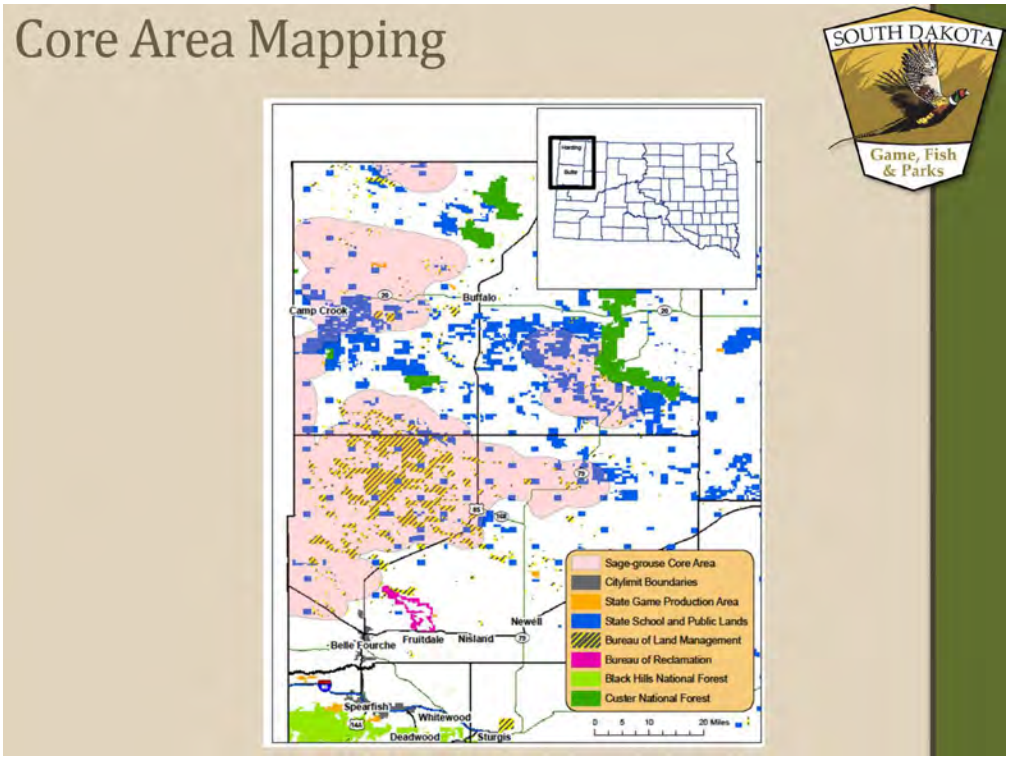
| | Acres | % of Total |
|---|---|---|
| **State** | | |
| School and Public Lands | 126,347 | 12.86% |
| Game, Fish and Parks | 408 | 0.04% |
| Total | 126,755 | 12.90% |
| **Federal** | | |
| Bureau of Land Management | 116,354 | 11.84% |
| Forest Service | 1,383 | 0.14% |
| Total | 117,737 | 11.98% |
| **Private** | | |
| Total | 738,342 | 75.12% |
| **Grand Total** | 982,834 | |

The Bureau of Land Management mapped sage-grouse habitats in northwestern South Dakota only, in the following map from their 2013 Greater Sage-grouse Resource Management Plan Amendment Draft EIS.


R1E
R3E
R5E
R7E
R9E
R11E
T 22 N
T 20 N
T 18 N
T 16 N
T 14 N
T 12 N
T 10 N
HARDING COUNTY
Buffalo
Camp Crook
Reva
PERKINS COUNTY
BUTTE COUNTY
MEADE COUNTY
Newell
20
79
75
85
168
212
Sagebrush Cover Over 10%
Highway
Local Roads
Other Roads
BLM
BOR
COE
USFS
Private
State
Water
SOUTH DAKOTA
Map 2-6: Sagebrush Inventory
U.S. DEPARTMENT OF THE INTERIOR
Bureau of Land Management
South Dakota Field Office
Draft RMP/EIS
This map is intended for display purposes. No warranty is made by the Bureau of Land Management as to the accuracy, reliability, or completeness of these data for individual or aggregate use with other data, or for purposes not intended by BLM. This map may not meet National Map Accuracy Standards. This product was developed through digital means and information may be updated without notification.
0 2.25 4.5 9 13.5 Miles
Map Generated by the South Dakota Field Office in February 2013
Montana Custom Albers (NAD 1983) Projection

## THREATS TO THE SURVIVAL OF THE SPECIES

South Dakota's surviving sage-grouse population in South Dakota occupies the northwestern corner of the state, a sparsely populated area with limited industrial and residential development. Nonetheless, human activity has rendered habitat changes sufficient to initiate unnatural declines of sage-grouse in South Dakota which continue to the present day. The following is a brief summary of known causes of sage-grouse habitat degradation that have been linked to population declines based on the best available scientific information.




Sagebrush buds and leaves are the dominant proportion of their diets, and they use sagebrush shrubs as cover to site their nests. Crop farming (including operations producing hay and alfalfa for livestock) directly converts the sagebrush/grassland habitats that sage-grouse require to survive and reproduce into sagebrush-free non-habitat. In addition, the common pesticides commonly aerially sprayed on cropfields can directly poison sage-grouse directly (Blus et al. 1989).

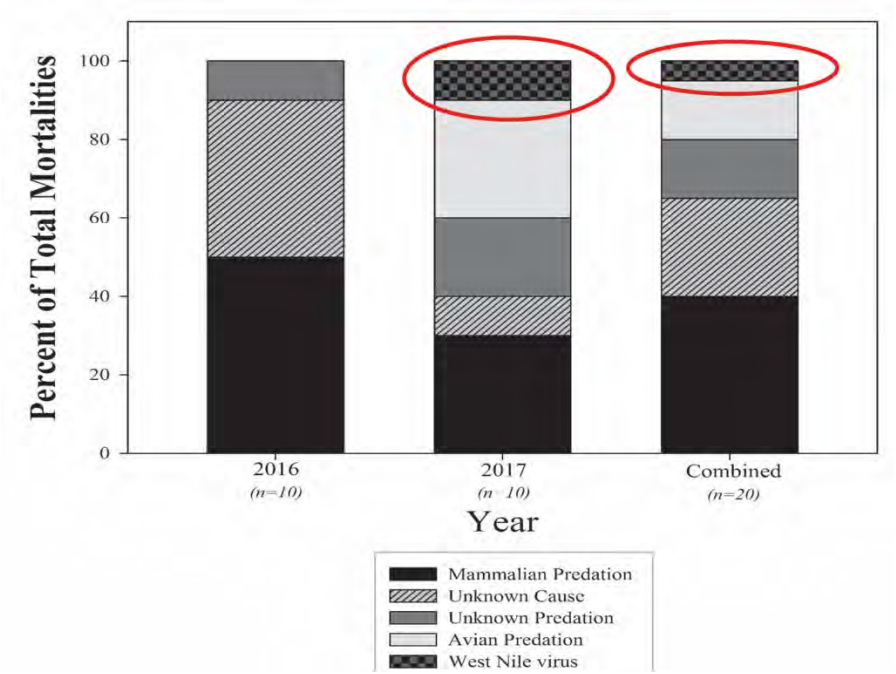
Livestock grazing is the most widespread, and likely most significant, threat to sage-grouse survival in South Dakota. The best available science has established that at least 7 inches (18 cm) of residual stubble height needs to be provided in nesting and brood-rearing habitats throughout their season of use. According to Gregg et al. (1994: 165), "Land management practices that decrease tall grass and medium height shrub cover at potential nest sites may be detrimental to sage-grouse populations because of increased nest predation.... Grazing of tall grasses to <18 cm [7 inches] would decrease their value for nest concealment.... Management activities should allow for maintenance of tall, residual grasses or, where necessary, restoration of grass cover within these stands." Hagen et al. (2007) analyzed all extant scientific datasets up to that time

and concluded that the 7-inch threshold was the threshold below which significant impacts to sage-grouse occurred (*see also* Herman-Brunson et al. 2009). The exception to this 7-inch rule is found in the mixed-grass prairies of the Dakotas, where sparser cover from sagebrush and greater potential for tall grass have led to a recognition that a 26-cm (10.2-inch) stubble height standard is warranted (Kaczor 2008, Kaczor et al. 2011). Foster et al. (2014) found that livestock grazing could be compatible with maintaining sage-grouse populations, but notably stubble heights they observed averaged more than 18 cm (7 inches) during all three years of their study, and averaged more than 10.2 inches in two of the three years of the study.

Doherty et al. (2014) found a similar relationship between grass height and nest success in northeast Wyoming and south-central Montana but did not prescribe a recommended grass height. While there are those who have attempted to cast doubt on the necessity of maintaining grass heights to provide sage-grouse hiding cover, based on timing differences in grass height measurements between failed nests and successful nests, these concerns have been refuted for Wyoming. The significance of the Doherty et al. (2014) study was explicitly tested by Smith et al. (2018a), who confirmed that grass height **continued to have a significant effect** on nest success for this Wyoming study after correction factors were applied to the data. Smith et al. (2018b) found little effect of livestock grazing on sage-grouse nest success in Montana, but the grass heights in grazed pastures differed little from ungrazed controls in this study, indicating an unusually light level of livestock grazing in sage-grouse habitat. This outcome supports management for very light livestock grazing. As yet, there has been no mechanism in South Dakota to require that at least 10.2 inches of residual grass behind to provide adequate hiding cover for sage-grouse, and this lack is likely the primary reason that these birds have been declining, and continue to decline.

Barbed-wire fencing presents multiple serious impacts for sage-grouse. Stevens et al. (2013) found that fence collisions are a significant cause of grouse mortality, with fences on flat areas near leks posing a particularly high risk for causing sage-grouse fatalities (*see also* Van Lanen et al. 2017). Christiansen (2009) documented 146 sage-grouse fence collisions and mortalities along a 4.7-mile length of barbed-wire fence in western Wyoming over a 2½-year period, and found that marking fences reduced collisions by only 61%, such that 39% of the collision rate on unmarked fences continues to occur on marked fence sections. All three of these studies documented that fence markers could reduce collision mortality, but marked fences were still the cause of major amounts of collision mortality under all three studies. Unused fences should be removed, and their rights-of-way (as applicable) withdrawn. Removal of this existing fencing would decrease potential raptor perching and subsequently the indirect impacts of raptors preying on grouse as and other prey species. The removal of fencing could also eliminate any direct mortality due to grouse colliding with problem fences. However, there is currently an absence of regulations that require or even incentivize the removal of the fences that are collision hazards for grouse.

Stock watering reservoirs and coalbed methane retention ponds provide breeding habitat for mosquitoes that carry West Nile virus. West Nile virus mortalities have been confirmed in South Dakota (Kaczor 2008), as recently as 2017 (T. Runia, SDFWP, pers. comm.). Documented West Nile deaths in South Dakota are as follows:




Source: Travis Runia presentation, August 20, 2020.[1] West Nile has been implicated in major sage-grouse population declines in the Powder River Basin (Doherty 2007, Walker et al. 2007a, Walker and Naugle 2011), and presents an ongoing threat to sage-grouse (Taylor et al. 2012), which have demonstrated little to no ability to develop a natural immunity to this non-native disease (Walker et al. 2007b). Accordingly, new stock watering and fluid mineral production reservoirs should be prohibited in Core Areas (BLM Priority Habitat Management Areas), and existing manmade reservoirs should be breached and eliminated to the extent possible.

There is a limited history of past oil and gas development in northwest South Dakota, although there currently are few active oil and gas wells in this area.[2] Holloran (2005) conducted the seminal study (funded by the oil and gas industry), and it found significant negative impacts from both access roads (even when shielded from the lek by intervening topography) and individual producing (post-drilling) oil and gas wells within 1.9 miles from active leks (Holloran 2005). Measurable impacts on sage-grouse from coalbed methane development in northeast Wyoming were found to extend out to 4 miles (Walker 2008), and subsequent research has recorded effects as far away as 12.4 miles from leks (Taylor et al. 2012). Holloran et al. (2007) found that yearling sage-grouse avoided otherwise suitable nesting habitat within 930m (almost 0.6 mile) of oil and gas-related infrastructure. This means that individual wellsites, and their access roads and other related facilities, will be surrounded by a 0.6-mile band of habitat that has substantially lost its habitat capability for use by nesting grouse. The consequences of industrial development in the context of inadequate lek buffers are reductions in population size and persistence. State researchers, using lek buffers of 0.25 mile, 0.5 mile, 0.6 mile, 1.0 mile, and 2.0

[1] Online at https://gfp.sd.gov/management-plans/

[2] See map, https://denr.sd.gov/des/og/maps/New%20Maps%2001.22.2020/State_wide_oil_gas_wells.pdf

mile, estimated lek persistence of 4, 5, 6, 10, and 28 percent, respectively (Apa et al. 2008). Standard energy development within 2 miles of a lek is projected to reduce the probability of lek persistence from 87% to 5% (Walker et al. 2007a). Manier et al. (2014) placed the range of appropriate lek buffer distances for industrial projects at 3.1 to 5 miles.

Advances in science make it increasingly clear that noise from roads or industrial facilities is having a major negative effect on sage-grouse and their ability to make use of otherwise suitable habitats. Noise can mask the breeding vocalizations of sage-grouse (Blickley and Patricelli 2012), displaces grouse from leks (Blickley et al. 2012a), and causes stress to the birds that remain (Blickley et al. 2012b). According to Blickley et al. (2010), "The cumulative impacts of noise on individuals can manifest at the population level in various ways that can potentially range from population declines up to regional extinction. If species already threatened or endangered due to habitat loss avoid noisy areas and abandon otherwise suitable habitat because of a particular sensitivity to noise, their status becomes even more critical." Noise must be limited to a maximum of 10 A-weighted decibels (dBA) above the ambient natural noise level after the recommendations of Patricelli et al. (2012); the ambient noise level in central Wyoming was found to be 22 dBA (Patricelli et al. 2012) and in western Wyoming it was found to be 15 dBA (Ambrose and Florian 2014, 2015; Ambrose et al. 2015). Sage-grouse lek population declines once noise levels exceed the 25 dBA level. With this in mind, ambient noise levels should be defined as 15 dBA and cumulative noise should be limited to 25 dBA in occupied breeding, nesting, brood-rearing, and wintering habitats, which equates to 10 dBA above the scientifically-derived ambient threshold.

Federal sage-grouse plans have applied a 3% limit on surface disturbance (per Knick et al. 2013), and a site density standard limiting sites to one per square mile. However, these densities are calculated across a project analysis area, which can exceed 225 square miles based on the real-world example of BLM analysis of the Lost Creek uranium project in the Red Desert of Wyoming. Knick et al. (2013) measured disturbance across an area much smaller (a 3-mile buffer around leks) than a project analysis area. Therefore, 3% surface disturbance as measured across a project area is an even higher percentage of surface disturbance when calculated using the Knick et al. (2013) protocol. According to the BLM's expert team (National Technical Team 2011) both site density and disturbance percentage should be calculated per square-mile section of land.

Currently, important sage-grouse wintering habitats have not been spatially identified in South Dakota, and even if they were, there is an absence of measurable, enforceable standards to prevent degradation of wintering habitats at the federal, state, and local levels, across all land ownerships. Doherty et al. (2008) demonstrated that Greater Sage-Grouse in the Powder River Basin avoided otherwise suitable wintering habitats once they have been developed for energy production, even after timing and lek buffer stipulations had been applied. In addition, Carpenter et al. (2010) found that wintering sage-grouse avoided otherwise suitable habitats within a 1.2-mile radius of wellsites. Dzialek et al. (2012: 12) confirmed these relationships for wintering sage-grouse in Wyoming, and concluded:

> First, we can say with increasing confidence that the winter pattern of occurrence among sage-grouse shows consistency throughout disparate portions of its

> distribution. Second, avoidance of human activity appears to be a general feature of winter occurrence among sage-grouse.

Holloran et al. (2015) determined that increasing wellpad density had a negative impact on sage-grouse winter habitat use regardless of whether liquid gathering systems were used to reduce human activity levels or not, and also found a negative impact of distance to wellsites (within 2.8 km or 1.75 miles) and distance to roads. To the extent that new road construction, mineral development, and transmission and utility lines continue to occur, they should be excluded from important wintering areas, which exclusion should also be applied to a buffer of 2 miles around any such habitats.

Transmission lines are known to negatively affect sage-grouse, due in part to the propensity of raptors and corvids to perch on them and/or concentrate their hunting activity nearby. Wisdom et al. (2011) found that lands within 3.1 miles of transmission lines and highways had an elevated rate of lek abandonment. Nonne et al. (2011) found that raven abundance increased along the Falcon-Gondor powerline corridor in Nevada both during the construction period, and long-term after powerline construction activities had ceased. Braun et al. (2002) reported that 40 leks with a power line within 0.25 mile of the lek site had significantly slower population growth rates than unaffected leks, which was attributed to increased raptor predation. Dinkins (2013) documented sage-grouse avoidance of powerlines not just during the nesting period but also during early and late brood-rearing. LeBeau et al. (2014) found that sage-grouse avoided habitats within 2.9 miles of transmission lines during the brood-rearing period. The National Technical Team (NTT 2011) recommended that Priority Habitats be exclusion areas for overhead powerlines, and that General Habitats should be avoidance areas for overheads lines. Regulations blocking transmission lines from being built across key sage-grouse habitats, and requiring existing overhead lines to be buried, do not exist at any governmental level in South Dakota.

The National Technical Team (2011) reviewed the best available science on wind energy facilities, noting the sage-grouse's avoidance of tall structures, and recommended that priority habitats be "exclusion areas" for these facilities. LeBeau (2012) found that sage-grouse experienced significant declines in nest and brood survival in proximity to wind turbines. Yet no moratorium is presently in place to prevent wind farm development in key sage-grouse habitats. Federal sage-grouse plans offer mere avoidance, which is discretionary, rather than exclusion.

Wisdom et al. (2011) found that extirpated range of sage-grouse was closer to highways (mean = 3.1 miles) than occupied range for sage-grouse, and Holloran (2005) found that "main haul roads" — gravel roads accessing 5 or more natural gas wells — had a significant negative effect up to 1.9 miles from the road on sage-grouse lek attendance compared to unaffected leks (regardless of whether the road was visible from the lek or not), and that increased traffic led to increased impact. At minimum, all roads need to be sited at least 0.8 miles from lekking and nesting habitat, and main haul roads should be sited at least 2 miles away. At minimum, all roads need to be sited at least 0.8 miles from lekking and nesting habitat. Patricelli et al. (2012) tested the impact or road and drilling noise on sage-grouse, and reached the following conclusions:

> "…we recommend that interim management strategies focus not on limiting traffic noise levels, but rather on the siting of roads or the limitation of traffic volumes during crucial

> times of the day (6 pm to 9 am) and/or season (i.e. breeding season). We estimate that noise levels will typically drop to 30 dBA at 1.3 km (0.8 mi) and to 32 dBA at 1.1 km (0.7 mi) from the road (these levels represent 10 dB over ambient using 20 or 22 dBA ambient respectively). Therefore to avoid disruptive activity in areas crucial to mating, nesting and brood-rearing activities, we recommend that roads should be sited (or traffic should be seasonally limited) within 0.7-0.8 miles from the edge of these areas. We emphasize that we are not recommending the siting of roads 0.7-0.8 miles from the edge of the lek perimeter, but rather 0.7-0.8 miles from the edge of crucial lekking, nesting and early brood-rearing areas."

There is presently no regulation blocking road construction in nesting habitats (within 5.3 miles of leks), or within two miles of leks to prevent disturbance to breeding birds, nor is there any program in place to close or re-route existing roads that presently occur within these sensitive areas.

There has been a great deal of interest in uranium mining in southwest South Dakota, and rare-earth minerals have also been the subject of mining speculation in the local region. In addition, bentonite mining is a significant problem in northwestern South Dakota, and indeed sage grouse habitat protections have been excluded in bentonite mining areas in the past. Braun (1986) also found a significant negative effect of mining haul roads on sage-grouse leks within 1.9 miles of the road. Yet there is nothing to prevent mining within sage-grouse habitats in South Dakota.

## CONCLUSIONS

It is necessary to list the greater sage-grouse under the South Dakota Endangered Species Law because of the ongoing decline of sage-grouse populations in South Dakota, and the absence of required regulatory actions to prevent new habitat impacts or to restore previously impacted sage-grouse habitats. The current state plan includes only voluntary or discretionary measures, with an absence of measurable, enforceable, and mandatory standard to protect sage-grouse and their habitats.

Listing will have the effect of preventing hunting of this species, which is of limited effect given the very few grouse taken each year. It is in the long-term best interest of hunters to increase the sage grouse population to the point where it becomes huntable once again, and listing offers the best path to achieve this result. While hunting is typically not considered a principle cause of sage-grouse population declines, when populations get as small as South Dakota's, the taking of even a few could make the difference between survival and extirpation of an individual lek population.

Various federal, state or local agencies may require environmental impact reviews prior to permitting or approving various development activities. The greater sage grouse is rated as a species of greatest conservation need in the South Dakota Wildlife Action Plan. As such, it may be reviewed in some environmental impact statements. However, some may just require review of federal species and some just federal and state species. Being listed as a state listed species may improve the quality of environmental review allocated to it and potentially result in protection by agencies of government during permitting and approval processes.

We appreciate your diligence and consideration of applying science-based state-level protections to this bird.

## Literature Cited


Ambrose, S., and C. Florian. 2014. Sound levels at greater sage-grouse leks, Pinedale Anticline Project Area, Wyoming, April 2013. Unpublished report prepared for the Wyoming Game and Fish Department, 133 pp. Available online at http://www.wy.blm.gov/jio-papo/papo/wildlife/reports/sage-grouse/2013GSGacoustic-rpt.pdf.

Ambrose, S., C. Florian, and J. MacDonald. 2014. Sound levels at greater sage-grouse leks in the Pinedale Anticline Project Area, WY, April 2013-2014. Unpublished report prepared for the Wyoming Game and Fish Department, 79 pp.

Ambrose, S., C. Florian, and J. MacDonald. 2015. Sound levels at greater sage-grouse leks in the Pinedale Anticline Project Area, WY, April 2013-2015. Unpublished report prepared for the Wyoming Game and Fish Department, 113 pp.

Apa, T., J. Bohne, T. Christiansen, J. Herbert, B. James, R. Northrup, D. Olsen, A. Robinson, P. Schnurr, T.O. Smith, and B. Walker. 2008. Using the Best Available Science to Coordinate Conservation Actions that Benefit Greater Sage-grouse Across States Affected by Oil & Gas Development in Management Zones I-II (Colorado, Montana, North Dakota, South Dakota, Utah, and Wyoming). Unpublished multi-state report of game and fish agencies, 10 pp. Online at http://www.ourpubliclands.org/files/upload/ti-State_ScienceGroupDocument_FINAL_01-28-08.pdf.

Blickley, J. L. and Patricelli, G. L. 2010. Impacts of Anthropogenic Noise on Wildlife: Research Priorities for the Development of Standards and Mitigation. Journal of International Wildlife Law & Policy, 13: 4, 274 — 292. http://dx.doi.org/10.1080/13880292.2010.524564.

Blickley, J.L., and G.L. Patricelli. 2012. Potential acoustic masking of greater sage-grouse (*Centrocercus urophasianus*) display components by chronic industrial noise. Ornith. Monogr. 74: 23-35.

Blickley, J.L., D. Blackwood, and G.L. Patricelli. 2012a. Experimental Evidence for the Effects of Chronic Anthropogenic Noise on Abundance of Greater Sage-Grouse at Leks. Conserv. Biol. 26:461-471.

Blickley J.L., Word K.R., Krakauer A.H., Phillips J.L., Sells S.N., et al. 2012b. Experimental Chronic Noise Is Related to Elevated Fecal Corticosteroid Metabolites in Lekking Male Greater Sage-Grouse (*Centrocercus urophasianus*). PLoS ONE 7(11): e50462. doi:10.1371/journal.pone.0050462.

Blus, L.J., C.S. Staley, G.W. Pendleton, T.H. Craig, E.H. Craig, and D.K. Halford. 1989. Effects of organophosphorus insecticides on sage grouse in southeastern Idaho. J. Wildl. Manage. 53: 1139-1146.

Braun, C.E. 1986. Changes in sage grouse lek counts with advent of surface coal mining. Proc. Issues and Technology in the Management of Impacted Western Wildlife, Thorne Ecol. Inst. 2:227-231.

Braun, C.E., O.O. Oedekoven, and C.L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage grouse. In Transactions North American Wildlife and Natural Resources Conference 67:337-349.

Braun, C.E., D.A. Budeau, and M.A. Schroeder. 2015. Fall population structure of sage-grouse in Colorado and Oregon. Oregon Dept. of Fish and Wildlife Tech. Rep. 005-2015, 68 pp.

Carpenter, J., C. Aldridge, and M.S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 74:1806-1814.

Christiansen, T. 2009. Fence Marking to Reduce Greater Sage-grouse (*Centrocercus urophasianus*) Collisions and Mortality near Farson, Wyoming – Summary of Interim Results. Wyoming game and Fish Department Report, 2 pp. Online at http://wgfd.wyo.gov/web2011/Departments/Wildlife/pdfs/SG_FENCEMARKING0000671.pdf.

Coates, P. S., G. T. Wann, G. L. Gillette, M. A. Ricca, B. G. Prochazka, J. P. Severson, K. M. Andrle, S. P. Espinosa, M. L. Casazza, and D. J. Delehanty. 2019. Estimating sightability of greater sage-grouse at leks using an aerial infrared system and *N*-mixture models. Wildlife Biology 2019(1): 1–12, https://doi.org/10.2981/wlb.00552.

Dinkins, J. B., 2013. Common raven density and greater sage-grouse nesting success in southern Wyoming: Potential conservation and management implications. PhD Dissertation, Utah State Univ. http://digitalcommons.usu.edu/etd/1700.

Doherty, M.K. 2007. Mosquito populations in the Powder River Basin, Wyoming: A comparison of natural, agricultural and effluent coalbed natural gas aquatic habitats. M.S. Thesis, Montana State Univ., 95 pp.

Doherty, K.E., D.E. Naugle, J.D. Tack, B.L. Walker, J.M. Graham, and J.L Beck. 2014. Linking conservation actions to demography: Grass height explains variation in greater sage-grouse nest survival. Wildlife Biology 20:320-325.

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, and J. B. Winstead. 2012. Temporal and hierarchical spatial components of animal occurrence: conserving seasonal habitat for greater sage-grouse. Ecosphere 3:30.

Fremgen, A. L., C. P. Hansen, M. A. Rumble, R. S. Gamo, and J. J. Millspaugh. 2016. Male Greater Sage-Grouse Detectability on Leks. J. Wildl. Manage. 80: 266–274

Garton, E.O., A.G. Wells, J.A. Baumgardt, and J.W. Connelly. 2015. Greater sage-grouse population dynamics and probability of persistence. Final Report to Pew Charitable Trusts, 90 pp.

Gregg, M.A., J.A. Crawford, M.S. Drut, and A.K. DeLong. 1994. Vegetational cover and predation of sage grouse nests in Oregon. J. Wildl. Manage. 58:162-166.

Hagen, C.A., J.W. Connelly, and M.A. Schroeder. 2007. A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. Wildlife Biology 13:42–50.

Herman-Brunson, K.M., K.C. Jensen, N.W. Kaczor, C.C. Swanson, M.A. Rumble, and R.W. Klaver. 2009. Nesting ecology of greater sage-grouse *Centrocercus urophasianus* at the eastern edge of their historic distribution. Wildl. Biol. 15: 395-404.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. PhD Dissertation. University of Wyoming. Laramie, Wyoming.

Holloran, M.J., R. C. Kaiser, and W. A. Hubert. 2007. Population response of yearling greater sage-grouse to the infrastructure of natural gas fields in southwestern Wyoming. Completion report. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, WY, USA.

Holloran, M.J., B.C. Fedy, and J. Dahlke. 2015. Winter habitat use of greater sage-grouse relative to activity levels at natural gas well pads. J. Wildl. Manage. 79:630-640.

Kaczor, N. 2008. Nesting and brood-rearing success and resource selection of greater sage-grouse in northwestern South Dakota. M.S. Thesis, South Dakota State Univ., 85 pp.

Kaczor, N. W., K. C. Jensen, R. W. Klaver, M. A. Rumble, K. M. Herman-Brunson, and C. C. Swanson. 2011. Nesting success and resource selection of greater sage-grouse. Pp. 107–118 *in* B. K. Sandercock, K. Martin, and G. Segelbacher (editors). Ecology, conservation, and management of grouse. Studies in Avian Biology (no. 39), University of California Press, Berkeley, CA.

Knick, S.T., S.E. Hanser, and K.L. Preston. 2013. Modeling ecological minimum requirements for distribution of greater sage-grouse leks – Implications for population connectivity across their western range, USA. Ecology and Evolution 3: 1539-1551.

LeBeau, C.W. 2012. Evaluation of greater sage-grouse reproductive habitat and response to wind energy development in south-central Wyoming. M.S. Thesis, Univ. of Wyoming, 120 pp.

LeBeau, C. W., J. L. Beck, G. D. Johnson, and M. J. Holloran. 2014. Short-term impacts of wind energy development on greater sage-grouse fitness. J. Wildl. Manage. 78: 522-530.

Manier, D.J., Bowen, Z.H., Brooks, M.L., Casazza, M.L., Coates, P.S., Deibert, P.A., Hanser, S.E., and Johnson, D.H., 2014, Conservation buffer distance estimates for Greater Sage-Grouse—A review: U.S. Geological Survey Open-File Report 2014–1239, 14 pp., *http://dx.doi.org/10.3133/ofr20141239*.

National Technical Team (NTT). 2011. A Report on National Greater Sage-grouse Conservation Measures. Available online at www.blm.gov/pgdata/etc/medialib/blm/co/programs/wildlife.Par.73607.File.dat/GrSG%20Tech%20Team%20Report.pdf.

Nonne, D., E. Blomberg, and J. Sedinger. 2011. Dynamics of greater sage-grouse (*Centrocercus urophasianus*) populations in response to transmission lines in central Nevada. Progress Report: Year 9. Unpublished report, 55 pp.

Patricelli, G.L., J.L. Blickley, and S.L. Hooper. 2012. The impacts of noise on greater sage-grouse: A discussion of current management strategies in Wyoming with recommendations for further research and interim protections. Unpubl. report prepared for: The Bureau of Land Management, Lander Field Office and Wyoming State Office, Cheyenne and Wyoming Game and Fish Department, 25 pp.

Smith, J.T., J.D. Tack, K.E. Doherty, B.W. Allred, J.D. Maestas, L.I. Berkeley, S.J. Dettenmaier, T.A. Messmer, and D.E. Naugle. 2018a. Phenology largely explains taller grass at successful nests in greater sage-grouse. Ecol. and Evol. 8: 356-364.

Smith, J.T., J.D. Tack, L.I. Berkeley, M. Szczypinski, and D.E. Naugle. 2018b. Effects of livestock grazing on nesting sage-grouse in central Montana. J. Wildl. Manage. 82: 1503-1515.

(SDGFP) South Dakota Department of Game, Fish and Parks, Division of Wildlife. 2014a. Sage-grouse management plan for South Dakota 2014-2018. Wildlife Division Report Number 2014-02. South Dakota Department of Game, Fish and Parks, Pierre, South Dakota. https://gfp.sd.gov/UserDocs/nav/SageGrouseManagementPlan.pdf

(SDGFP) South Dakota Department of Game, Fish and Parks, Division of Wildlife. 2014b. South Dakota Wildlife Action Plan. South Dakota Department of Game, Fish and Parks, Pierre, South Dakota. https://gfp.sd.gov/wildlife-action-plan/

Stevens, B.S., D.E. Naugle, B. Dennis, J.W. Connelly, T. Griffiths, and K.P. Reese. 2013. Mapping sage-grouse fence collision risk: Spatially explicit models for targeting conservation implementation. Wildl. Soc. Bull. 37: 409-415.

Taylor, R. L., D. E. Naugle, L. S. Mills. 2012. Viability analysis for conservation of sage-grouse populations: Buffalo Field Office, Wyoming. BLM Contract 09-3225-0012; Number G09AC00013. Final Report. Prepared for Bureau of Land Management, Buffalo Field Office. Buffalo, WY.

Van Lanen, N.J., A.W. Green, T.R. Gorman, L.A. Quattrini, and D.C. Pavlacky, Jr. 2017. Evaluating efficacy of fence markers in reducing greater sage-grouse collisions with fencing. Biol. Conserv. 213: 70-83.

Walker, B. L. 2008. Greater Sage-grouse Response to Coal-bed Natural Gas Development and West Nile virus in the Powder River Basin, Montana and Wyoming, USA. Ph.D. Dissertation, Univ. Montana. Missoula, MT.

Walker, B. L., and D. E. Naugle. 2011. West Nile virus ecology in sagebrush habitat and impacts on greater sage-grouse populations. Pages 127–142 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, Vol. 38. University of California Press, Berkeley, USA.

Walker, B.L., D.E. Naugle, and K.E. Doherty. 2007a. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71(8):2644-2654.
Walker, B.L., D.E. Naugle, K.E. Dougherty, and T.E. Cornish. 2007b. West Nile virus and greater sage-grouse: Estimating infection rate in a wild bird population. Avian Diseases 51:691-696.

Wisdom, M.J., C.W. Meinke, S.T. Knick, and M.A. Schroeder. 2011. Factors associated with extirpation of sage-grouse. Studies in Avian Biology 38:451–472.

April 7, 2015

**Review of Greens Hollow Sound Study by Tetra Tech (2008)**

Skip Ambrose
Sandhill Company
393 Castle Creek Lane
HC 64 Box 2205
Castle Valley, UT 84532
Telephone: 435-259-0401
Cell: 435-220-0129
Email: skipambrose@frontiernet.net

## Summary of Findings

The Tetra Tech "Green Hollow Sound Study" has several deficiencies, including:

1. Tetra Tech sound level meters measured down to about 27 dBA, but actual sound levels in the area are often less than 15 dBA.
2. Tetra Tech measured sound levels in July; grouse typically display in late March to early May when sound levels are generally lower.
3. Tetra Tech measured from mid-morning to mid-afternoon. Grouse typically display between 1800-0800, which is generally a quieter time of day.
4. Tetra Tech did not follow protocols developed by the American National Standards Institute (ANSI) for outdoor sound level measurements.
5. Tetra Tech did not use acoustic metrics recommended by ANSI for reporting sound level information ($L_{90}$ for background ambient and $L_{50}$ for existing ambient). Tetra Tech used a metric ($L_{eq}$) that would suggest higher sound levels at leks than actually present.

The Tetra Tech Greens Hollow Sound Study (2008) concluded that average "background" sound levels in the lek areas was ±34.7 dBA. However, sound level measurements by Sandhill Company between March 29-31, 2015, found that background sound levels ($L_{90}$) were 16.3 dBA for all hours of the day, and 15.1 dBA for hours important to lekking activity (1800-0800). Using the same (incorrect) metric as Tetra Tech to establish background ($L_{eq}$), Sandhill Company reported $L_{eq}$ = 24.5 dBA, while Tetra Tech reported $L_{eq}$ = 34.7 dBA.

The existing vent fan is 4350 m from the Wildcat Knolls lek and clearly audible. The proposed vent fan would be 2680 m from the Wildcat Knolls lek, resulting in higher sound levels at the lek. Anthropogenic sounds >25 dBA have the potential to negatively impact greater sage-grouse.

For these reasons, the report by Tetra Tech and subsequent analysis of potential impacts in the DEIS and SEIS are inaccurate and misleading, and could result in harmful impacts to greater sage-grouse.

## Introduction

The purpose of this paper is to provide a review of the Greens Hollow Sound Study in 2008, conducted by Tetra Tech, Salt Lake City, UT. The purpose of the Tetra Tech study was to measure sound levels at sensitive resource locations, such as leks of greater sage-grouse (*Centrocercus urophasianus*), and determine potential acoustic impacts of a proposed coal mine vent fan on sensitive resources. Anthropogenic sounds have the potential to negatively impact greater sage-grouse (Blickley et al. 2011; Blickley and Patricelli 2012; Patricelli et al. 2013). Accurate background sound level data are essential for assessment of potential negative impacts.

## Specific Issues in the Tetra Tech Study

*Equipment*

The sound level meter used in this study was a Quest Technologies Model 2200. The manufacturer states that this model is capable of measuring sound levels between 30-140 dBA (this is the range the manufacturer guarantees, most sound level meters will measure slightly better than guaranteed, 27.5 dBA in the Tetra Tech study). The minimum sound levels reported by Tetra Tech are at or near the minimum level that can be measured by this model sound level meter. *This means that actual sound levels are lower than reported.*

Use of inappropriate equipment most often leads to false and deceptive results. Consider a study attempting to determine the average height of all individuals in Utah, and using a 36" stick as a measuring device. The results would show the average height of a person in Utah to be about 35.9" which of course is not true. The average height is about 59 inches, considering babies to adults, but if the measuring device only goes to 36" an accurate study is not possible.

Sound level meters used in any measurement should be capable of measuring the full range of sound levels at the study site. Other acoustic studies in sage habitats relative to greater sage-grouse have shown sound levels are often <10 dBA during April during early morning hours (Ambrose et al. 2014). The use of a sound level meter that measures down to only 27 dBA cannot provide accurate results if actual sound levels are lower. If background sound levels are reported as high, a new noise source would be less likely to have any influence, whereas if background sound levels are low, the potential for impacts due to a new noise source is greater.

*Metric Used to Establish "Background Sound Level"*

The Tetra Tech study used the $L_{eq}$ metric to establish the background sound level. $L_{eq}$ is an energy average (or logarithmic average), and, as such, a very short but very loud sound will greatly influence (increase) the average sound level. The American National Standards Institute (ANSI) recommends that the $L_{90}$ metric be used to establish background sound level (ANSI 1994). $L_{90}$ levels are always lower than $L_{eq}$ levels. The background sound levels reported by Tetra Tech are much higher than typical sound levels in the study area.

*Dates and Time of Day*

Greater sage-grouse typically display between about 0500-0800, or starting just before sunrise and ending 3-4 hours later. This is usually the quietest time of day, and this is why birds with audio displays are most active at this time; their songs and display sounds carry a great distance because few other sounds are present.

The Tetra Tech study measured sound levels in late July between the hours 0823 and 1433. Grouse typically display in April and May, and typically do not display after about 0800. The time of season and time of day when Tetra Tech measured are not appropriate for measuring sound levels at leks used by greater sage-grouse. One would expect sound levels to be higher in July due to the presence of more birds and insects in July as compared to April, and one would expect sound levels to be higher after 0800 due to increasing winds (which produces sound due to wind through vegetation). Further, meteorological conditions in July are substantially different from April, and as a result, sound attenuation rates would be different. One would expect sound to attenuation more in July than in April due to warmer temperatures.

Sound levels in April during the primary lekking hours (0500-0800) would almost certainly be lower than reported by Tetra Tech, and thus the potential for impacts would be greater than determined in the DEIS and SEIS.

*Measurement Duration*
Tetra Tech made 2-minute sound level measurements at several locations. A 2-minute sample may or may not be representative of actual conditions. Measurement periods need to be long enough to ensure all variability in sound levels are measured, and this usually requires several days at each measurement location.

*Microphone Height*
The Tetra Tech study placed microphones at approximately 1 meter off the ground. Grouse ear height is 0.3 m (12”), thus data collected at 1 m may not represent what the target species, greater sage-grouse in this case, experience.

**Discussion**
The current mine vent fan is 4350 m from the Wildcat Knolls lek and is clearly audible at the lek. The proposed mine vent fan is 2680 m from the Wildcat Knolls lek. One would expect the proposed vent fan to be audible and also result in higher sound levels at the lek than the current vent fan.

Analysis of anthropogenic sound levels at greater sage-grouse leks in the Pinedale Anticline Project Area sound of Pinedale, WY, relative to trends of counts of male greater sage-grouse at those leks, demonstrate that sound levels <25 dBA are not significantly associated with trends of counts, while sound levels >30 dBA are strongly and significantly associated with declining trends (7 of 9 leks with sound levels >30 dBA no longer have grouse present). These data suggest that when anthropogenic sound levels approach 25-30 dBA, negative impacts to greater sage-grouse will start to occur (S. Ambrose, unpublished data).

**Summary**
The Tetra Tech study (1) used inappropriate equipment (not sensitive enough), (2) measured at inappropriate times of year and times of day (not when greater sage-grouse are displaying), and (3) did not follow protocols developed by the American National Standards Institute (ANSI) for outdoor sound level measurements. Further, Tetra Tech did not use acoustic metrics recommended by ANSI for reporting sound level information, and metrics used by Tetra Tech

suggested higher sound levels at leks than probably occurred there during the lekking period. For these reasons, the report by Tetra Tech and subsequent analysis of potential impacts in the DEIS and SEIS are inaccurate and misleading.

**Literature Cited**


Ambrose, S., C. Florian, and J. MacDonald. 2015. Ambient sound levels in sage habitats in Wyoming, April 2014. Unpublished report to Wyoming Department of Game and Fish, Pinedale, WY.

American National Standards Institute (ANSI). 1994. ANSI S12.18-1994, Procedures for Outdoor Measurement of Sound Pressure Level. Acoustical Society of America, New York, NY.

Blickley, J. L., D. Blackwood, and G. L. Patricelli. 2011. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. Conservation Biology, Vol. 26, No. 3, 461-471.

Blickley, J. L., and G. L. Patricelli. 2012. Potential acoustic masking of greater sage-grouse (Centrocercus urophasianus) display components by chronic industrial noise. Ornithological Monographs, Vol. 2012, No. 74, 23.35.

Patricelli, G. L., J. L. Blickley, and S. L. Hooper. 2013. Recommended management strategies to limit anthropogenic noise impacts on greater sage-grouse in Wyoming. Human-Wildlife Interactions 7(2):230-249, Fall 2013.

**Summary of Sound Level Measurements at Wildcat Knolls Lek, March 29-31, 2015**

Skip Ambrose and Chris Florian
Sandhill Company
393 Castle Creek Lane
HC 64, Box 2205
Castle Valley, UT 84532

**Introduction and Methods**

Between March 29, 2014, 1400 hours, and March 31, 2015, 1430, we collected continuous 1-second dBA and 1/3 octave band data (12.5-20,000 Hz) at the Wildcat Knolls greater sage-grouse lek. The sound level meter was placed on the north side of the lek, within the boundary of the lek, at 12" above ground height (average grouse ear height). One-third octave band data are useful in determining the potential for masking sounds important to wildlife. For example, most sounds produced by greater sage-grouse during lekking activity are low frequency, typically <500 Hz. Sounds of the current mine vent fan are highest in the 250 Hz range, suggesting the potential for masking grouse sounds is high.

**Results**

The "existing ambient" ($L_{50}$) sound level at Wildcat Knolls was 19.4 dBA for all hours (0000-2400) and 17.1 dBA for greater sage-grouse lekking hours (1800-0800) (Table 1). The "background ambient" sound level ($L_{90}$) was 16.3 dBA for all hours and 15.1 dBA for lekking hours. Daily $L_{50}$ dBA patterns are shown in Figure 1, showing lower sound levels during evening and early morning, with elevated levels during daylight hours when winds are higher.

The current vent fan was audible during all hours of the day, and was clearly noticeable at 250 Hz (Figure 2). This fan sound likely has some influence on both the $L_{50}$ and $L_{90}$ levels.

The Tetra Tech sound study (2008) reported "average" ($L_{eq}$) sound levels at the Wildcat Knolls lek between 31.0-39.2 dBA. We found $L_{eq}$ = 24.5 dBA, median for all hours of the day, and 21.2 dBA for hours important to lekking greater sage-grouse.

**Discussion**

Sound level measurements from March 29-31, 2015, found that sound levels were much lower than reported by Tetra Tech. These differences were likely due to several factors, including:

- Tetra Tech used sound levels meters that were not capable of measuring as low as actual sound levels are in the area.
- Tetra Tech measured during daytime hours in July, times and months when greater sage-grouse are not displaying (and which would result in higher readings).
- Tetra Tech used inappropriate metrics to determine existing and background sound levels. Tetra Tech used the $L_{eq}$ metric, an energy average that almost always results in higher levels. ANSI recommends using the $L_{50}$ metric to determine existing ambient and the $L_{90}$ metric to determine background ambient.
- Tetra Tech collected sound levels for 2 minutes at each location, and such a short measurement can either over-estimate or under-estimate actual sound levels.

Table 1. Hourly metrics for Wildcat Knoll Greater Sage-grouse lek, March 29-31, 2015.

| Hour | NHours | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|
| 0 | 2 | 13.6 | 44.2 | 20.9 | 19.7 | 16.1 | 14.5 |
| 1 | 2 | 13.8 | 49.0 | 23.2 | 23.2 | 18.0 | 15.6 |
| 2 | 2 | 14.6 | 31.4 | 19.8 | 22.2 | 18.9 | 16.4 |
| 3 | 2 | 14.5 | 47.2 | 23.3 | 22.4 | 18.7 | 16.2 |
| 4 | 2 | 13.9 | 27.6 | 18.1 | 20.2 | 17.4 | 15.6 |
| 5 | 2 | 13.9 | 28.9 | 17.7 | 20.0 | 16.7 | 14.9 |
| 6 | 2 | 14.2 | 47.5 | 25.6 | 27.0 | 20.0 | 15.9 |
| 7 | 2 | 15.4 | 51.7 | 30.3 | 31.3 | 24.1 | 19.8 |
| 8 | 2 | 14.4 | 57.0 | 29.5 | 25.0 | 19.3 | 16.6 |
| 9 | 2 | 14.4 | 58.6 | 23.4 | 25.8 | 19.6 | 17.2 |
| 10 | 2 | 15.2 | 43.2 | 25.7 | 28.5 | 21.1 | 17.3 |
| 11 | 2 | 15.3 | 45.6 | 26.5 | 30.4 | 22.1 | 18.3 |
| 12 | 2 | 15.5 | 46.9 | 29.5 | 33.2 | 25.2 | 20.0 |
| 13 | 2 | 15.8 | 49.3 | 31.2 | 35.1 | 26.2 | 20.1 |
| 14 | 2 | 16.0 | 48.9 | 29.9 | 33.9 | 25.6 | 20.1 |
| 15 | 2 | 14.7 | 45.1 | 27.1 | 29.9 | 21.0 | 16.6 |
| 16 | 2 | 15.1 | 51.0 | 29.2 | 30.3 | 22.1 | 17.2 |
| 17 | 2 | 14.6 | 44.8 | 26.9 | 30.1 | 21.0 | 17.3 |
| 18 | 2 | 14.3 | 37.3 | 21.5 | 24.5 | 19.5 | 15.3 |
| 19 | 2 | 13.9 | 50.4 | 27.3 | 23.4 | 15.3 | 14.2 |
| 20 | 2 | 13.7 | 45.7 | 23.0 | 22.7 | 15.0 | 14.1 |
| 21 | 2 | 13.6 | 40.5 | 18.7 | 17.9 | 14.4 | 13.9 |
| 22 | 2 | 13.5 | 26.2 | 15.4 | 16.9 | 14.7 | 14.0 |
| 23 | 2 | 13.6 | 27.7 | 17.6 | 19.9 | 16.7 | 14.7 |
| GRHO001 | 0000-2400 | 13.5 | 58.6 | 24.5 | 24.8 | 19.4 | 16.3 |
| | 0800-1800 | 14.4 | 58.6 | 28.2 | 30.2 | 21.6 | 17.3 |
| | 1800-0800 | 13.5 | 51.7 | 21.2 | 22.3 | 17.1 | 15.1 |

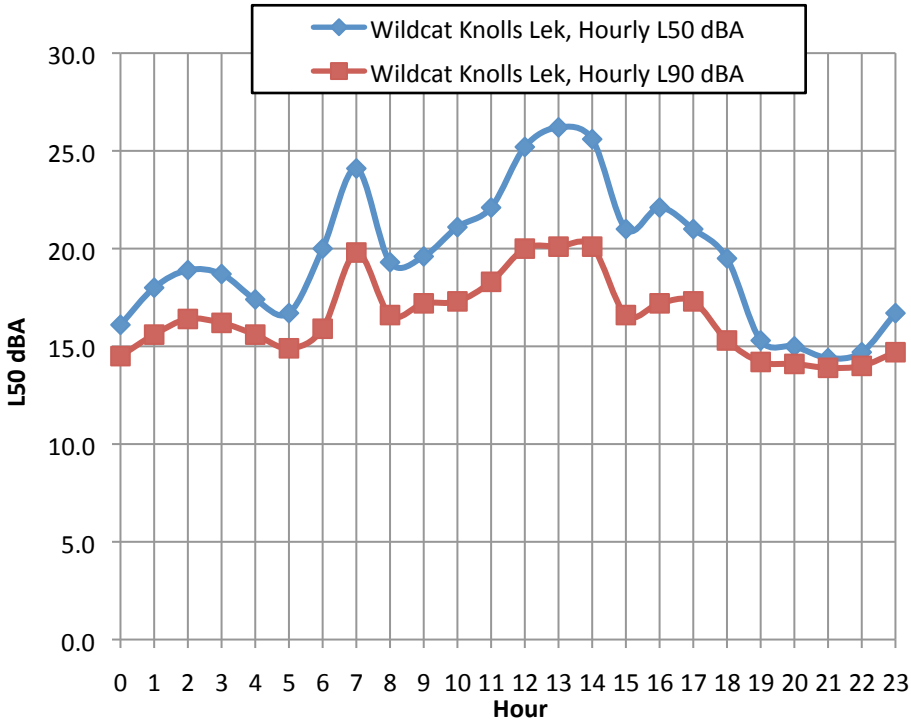



Figure 1. L50 dBA and L90 dBA, Wildcat Knolls lek, March 29-31, 2015.

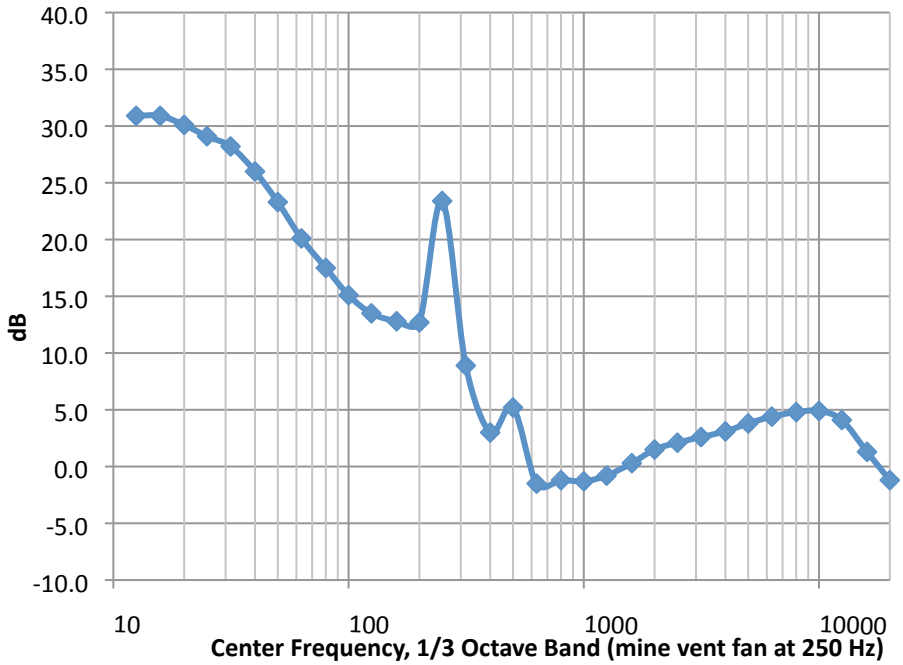



Figure 2. One-third octave band levels, Wildcat Knoll Greater Sage-grouse lek, March 29-31, 2015. Note higher levels at 250 Hz; this is noise from the mine vent fan, 4350 m from the lek.

**Review of Wildlife Section, Technical Report, Greens Hollow Coal Lease Tract**

Section 3.2.5.1.2.1 TES Birds. P. 92

> "As the drilling activities would occur year-round, breeding birds would either become habituated to the noise and disturbance or move to another location for that breeding period or permanently."

Comment: This statement implies that grouse have the option of simply moving to an alternate location. This is rarely the case for wildlife species. They are where they are for a reason.

Section 3.2.5.1.2.1 TES Birds. P. 92

> "If vent shaft construction occurred during sage-grouse lekking season, noise from the construction measured at the edge of the lek would not be allowed to exceed 10 dB above ambient sound level at sunrise."

Comment: For this assessment, it is essential to know the actual ambient sound level at sunrise. The Tetra Tech does not provide such information.

Section 3.2.5.2.4 Constant Background Sound. P. 99

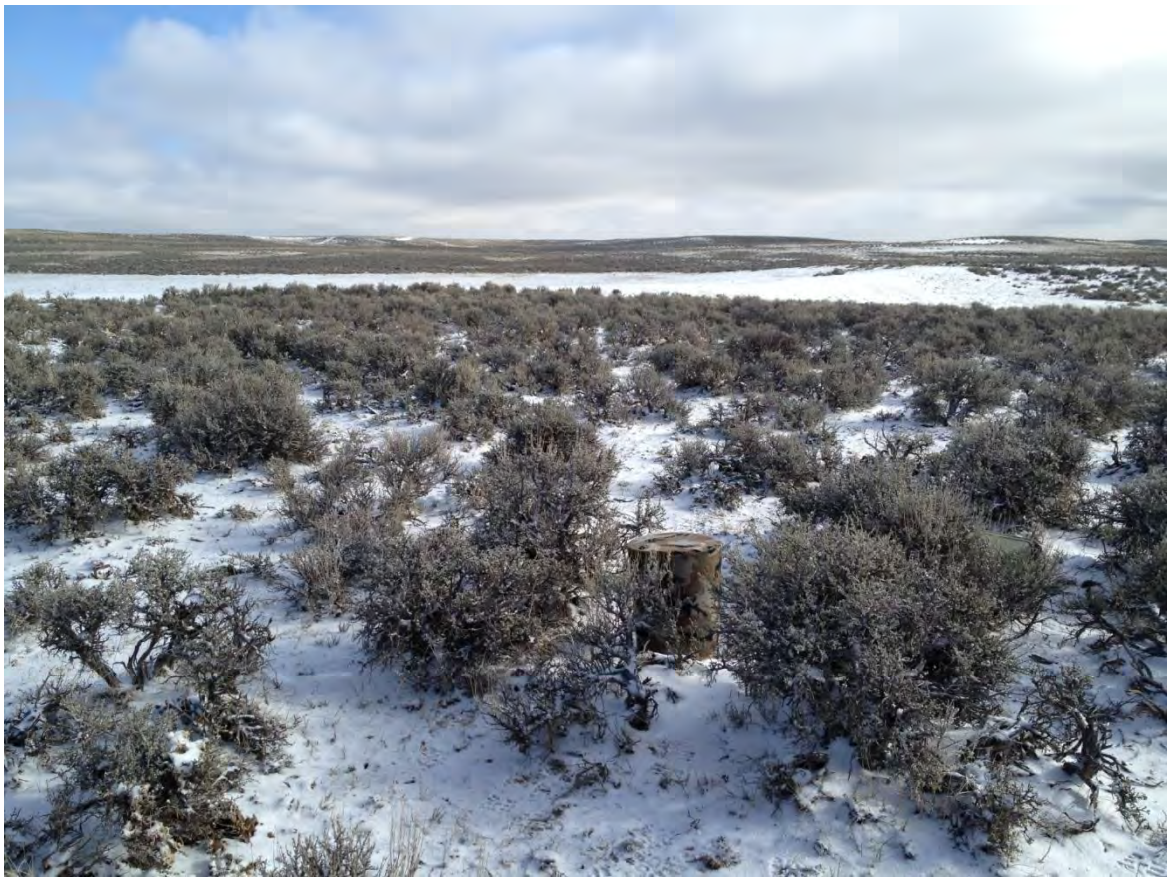
> "Sampling in the study area determined that background sound levels for the analysis area averaged 34.0 dBA. This level was recorded within the vicinity of the analysis area where the currently-operating SUFCO fan was not audible to human researchers sampling noise levels. These readings were taken at various locations throughout the analysis area to get an average baseline across the area without noise interference from passing vehicles, overhead airplanes, during calm wind conditions, quiet researchers, and as stated above, where the SUFCO mine was inaudible to researchers. This is considered to be the background noise levels for the analysis area in mid-summer (Tetra Tech 2008).
>
> "Current guidelines for limiting noise impacts on sage-grouse suggest a maximum of 10 dB above ambient measured at the edge of the lek (Morales et al 2011). Noise levels above this threshold have been shown to reduce peak male attendance at affected leks. This same study also showed intermittent noise to be more detrimental than constant noise of the same decibel level (Blickley et al 2012)."

Comment: For this assessment, it is essential to know the actual ambient sound level at sunrise during the time of grouse lekking in order to assess the 10 dBA over ambient threshold. The SEIS points out some of the shortcomings in the Tetra Tech sound study (time of year of sound study not during lekking, different meteorological conditions in April versus July), but regardless used the findings of that study to establish a "background noise" level for impact analysis.

As pointed out earlier, the Tetra Tech analysis did not use appropriate equipment or appropriate metrics to establish background ambient sound level. Tetra Tech used sound level meters that

would not capable of measuring as low as actual conditions, and also used $L_{eq}$ establish "background ambient sound level" while ANSI recommends $L_{90}$.

# Sound Levels at Greater Sage-grouse Leks, Pinedale Anticline Project Area, Wyoming, April 2013



## May 15, 2014

**Prepared by:**
Skip Ambrose and Chris Florian
Sandhill Company
HC 64 Box 2205
393 Castle Creek Land
Castle Valley, UT 84532
Email: skipambrose@frontiernet.net
Office: 435-259-0401
Cell: 435-220-0129

**This report was prepared for:**

Wyoming Game and Fish Department
5400 Bishop Blvd.
Cheyenne, WY 82006

Therese Hartman
Wildlife Biologist
Pinedale Anticline Project Office
P.O. Box 850
Pinedale, WY 82941

# Sound Levels at Greater Sage-grouse Leks, Pinedale Anticline Project Area, Wyoming, April 2013

## Executive Summary

Greater sage-grouse (*Centrocercus urophasianus*) use elaborate acoustic and visual display behaviors to attract and select mates, and depend on vocal communication between females and nestlings during brood rearing. A potential threat to greater sage-grouse is anthropogenic noise associated with human activity, including noise from oil and gas development and production. Several greater sage-grouse leks occur in and around the Pinedale Anticline Project Area (PAPA).

The objectives of this project were to:

- Monitor sound levels at 19 leks in PAPA;
- Monitor sound levels of common gas field activities near leks in PAPA; and
- Determine baseline ambient sound levels in sage land cover at reference areas outside PAPA (3 leks without influence of gas field sounds).

Acoustic data were collected at 39 locations in or near the PAPA in April 2013: 3 reference leks, 19 treatment leks, and 17 gas field sound sources near leks in PAPA. The reference leks were in the Speedway and Ryegrass complexes, and the treatment leks were in the Mesa, Duke's Triangle, and Yellowpoint complexes.

At the three reference leks, the baseline ambient sound level ($L_{90}$) was 15.8 dBA, and the existing ambient sound level ($L_{50}$) was 19.4 dBA (all hours, 0000-2400). At two of these leks, $L_{50}$ metrics (and to a lesser extent $L_{90}$ metrics) were influenced by grouse display sounds. For the time period 0000-0500, a time with few grouse display sounds yet with the same general metrological conditions (wind and temperature) as the primary display hours (0500-0900), the $L_{50}$ was 14.6 dBA and the $L_{90}$ was 14.2 dBA for the three reference leks.

The noise floor of sound level meters used at these reference leks were between 13-14 dBA (this is also described as instrument self-noise, the lowest measurement limit of the instrument). Whenever reported sound levels are near the noise floor of the instrument, there is some influence of instrument self-noise on dB data (the closer to the noise floor, the greater the influence). In such situations, actual sound levels are less than recorded by the sound level meter. In other words, actual sound levels at the three reference leks in this study were less than reported above. Results of this 2013 study suggest that future measurements in remote (pre-developed) locations should use instruments that measure down to approximately 5 dBA.

At the 19 treatment leks, the existing ambient sound level ($L_{50}$) was 26.6 dBA (all hours, 0000-2400). The $L_{50}$ sound level at treatment leks varied according to distance from and type of gas field sound source.

Of the common activities in the gas field, the sound level ($L_{50}$, 0000-2400 hours) of an active drill rig in the Duke's Triangle complex was the loudest (62 dBA @ 100 m), followed by the injection well complex (56 dBA @ 100 m) in the northern part of the Yellowpoint complex. Other gas field sound sources with $L_{50}$ >50 dBA @ 100 m were a second drill rig being disassembled the Duke's Triangle complex (54 dBA); Jonah compressor station (54 dBA); central gathering facility in the Mesa Complex with generator (52 dBA); and a well pad with 21 well heads and generator (50 dBA).

Equipment type and methods used for sound level measurements relative to greater sage-grouse in Wyoming have varied considerably. Both Type 1 and Type 2 sound level meters have been used, with noise floors ranging from less than 14 dBA to greater than 25 dBA. Microphone height has ranged from 12 inches to 96 inches. Measurement periods have ranged from one hour to more than 14 days. Such inconsistencies can produce significantly difference results. Instruments that measure down to only 25 dBA cannot describe acoustic conditions less than that. Wind pressure influence on dB data varies considerably due to microphone height. Short measurement periods can over- or under-estimate typical acoustic conditions. Collecting acoustic data with such a variety of equipment types and protocols can generate unusable and potentially misleading results. A standardized protocol for sound level measurement is needed to ensure acoustic data are accurate, useful for greater sage-grouse management, and comparable with data from other acoustic studies.

We recommend future acoustic studies follow guidelines prepared by Blickley and Patricelli (2012) "Noise monitoring recommendations for greater sage-grouse habitat in Wyoming" with slight modifications. We suggest these changes based on our experience measuring sound levels at over 150 remote locations in the western United States.

Equipment must be capable of measuring the entire the acoustic environment experienced by greater sage-grouse, and measurement periods must be long enough that natural variations in the acoustic environment are captured. The following basic standards are recommended for data collection:

- Microphone height should be 0.3 m (12") to ensure that measurements capture acoustic conditions experienced by greater sage-grouse.
- Sound level meters should be capable of capturing the full range of sounds (12.5-20,000 Hz) and sound levels (<10 dBA to >80 dBA) experienced by greater sage-grouse.
- Measurement periods should be long enough to capture normal acoustic variation due to seasonal and metrological conditions (estimated 14 days but needs further study).
- Continuous recordings should be collected during the entire measurement period to allow for source identification of all sounds.

The purpose of this study was to monitor sound levels at leks in the PAPA and to determine baseline ambient sound levels near leks outside the PAPA gas field. This study did not attempt to assess impacts of gas field sounds on greater sage-grouse, or at what levels such sounds negatively impact greater sage-grouse.

**Table of Contents**

**Executive Summary** ..... 3

**Table of Contents** ..... 5

**List of Tables** ..... 7

**List of Figures** ..... 11

**Introduction** ..... 13

**Objective** ..... 13

**Study Area** ..... 13

**Methods** ..... 13

*Definitions* ..... *13*
*Measurement Protocol* ..... *14*
*Baseline Ambient and Existing Ambient* ..... *16*
*Data Collection* ..... *19*
*Data Processing* ..... *19*
*Meteorological Data* ..... *20*
*Microphone Windscreen* ..... *21*
*Microphone and Anemometer Height* ..... *21*
*Measurement Locations* ..... *21*
*Measurement Schedule and Duration* ..... *22*

**Results** ..... 23

*Reference Leks* ..... *23*
*Treatment Leks* ..... *23*
*Gas Field Sound Sources* ..... *23*
*Wind Speed* ..... *27*

**Discussion** ..... 28

*Reference Leks* ..... *28*
*Measurements at Reference Leks and Influence of Greater Sage-Grouse Display Sounds* ..... *28*
*Use of $L_{90}$ or $L_{50}$ to Establish Baseline Ambient Sound Level* ..... *29*
*Treatment Leks* ..... *31*
*Hours Exceeding Baseline Ambient + 10 dBA* ..... *31*
*Sound Levels in 2013 and 2013 Counts of Greater Sage-grouse at Leks* ..... *31*
*Gas Field Sound Sources* ..... *31*
*Sound Levels at Treatment Leks Relative to Gas Field Activities* ..... *33*
*Sound Levels near the Instrument Self Noise (Noise Floor)* ..... *34*
*Wind Speed* ..... *35*
*Audibility and Common Sound Sources* ..... *35*

**Recommendations** ..... 36

*Establish Protocol for Measuring Sound Levels Relative to Greater Sage-grouse* ..... *36*

**Acknowledgements** ..... 38

**Literature Cited** ..... 38

**Appendix A. dBA and One-third Octave Metrics for PAPA Reference Leks.** ..... 41

**Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks.** ..... 49

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites.**..... 87
**Appendix D. Influence of Fleece Windscreen on Decibel Data.**..... 121
**Appendix E. Influence of Microphone Height, 1.5 m v. 0.3 m, on dB Data**..... 128
**Appendix F. Acoustic Primer.**..... 129
**Appendix G. Equipment component list, serial number, and calibration date**. ..... 133

**List of Tables**

Table 1. Number, complex, name, date-time start, date-time end, and number of hours of acoustic data collection sites, PAPA, April 2013. ..... 24
Table 2. Hourly existing ambient and baseline ambient sound levels at three reference leks near PAPA, April 2013. ..... 25
Table 3. $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$ dBA metrics at three reference leks, 0000-2400. ..... 26
Table 4. $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$ dBA metrics at 19 treatment leks, 0000-2400. ..... 26
Table 5. $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$ dBA metrics for all hours in three complexes. ..... 26
Table 6. $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$ dBA metrics for PAPA gas field sound sources, 0000-2400. ..... 27
Table 7. Wind speed data at five locations in 2013, three near PAPA leks and two near reference leks. ..... 27
Table 8. Estimated dBA @ 100 m of common gas field activities, PAPA, April 2013. 32
Table 9. Sound levels ($L_{50}$ dBA, 0000-2400) of gas field activities as measured at treatment leks, distance from lek to activity, and type of closest activity. ..... 34
Table 10. Percent time common sound sources were audible at PAPA103, Jewett Flat Red Reservoir, April 19, 2013, for three time periods of the day. ..... 36
Table 11. PAPA101 (Big John lek) hourly dBA metrics, April 6-21, 2013..... 41
Table 12. PAPA101 (Big John lek) dBA and one-third octave band metrics, April 6-12, 2013, 0000-2300. ..... 42
Table 13. PAPA102 (Big John lek) hourly dBA metrics, April 6-10, 2013..... 43
Table 14. PAPA102 (Big John lek) dBA and one-third octave band metrics, April 6-10, 2013, 0000-2300. ..... 44
Table 15. PAPA103 (Jewett Red Flat Reservoir lek) hourly dBA metrics, April 11-25, 2013. ..... 45
Table 16. PAPA103 (Jewett Red Flat Reservoir lek) dBA and one-third octave band metrics, April 11-25, 2013, 0000-2300. ..... 46
Table 17. PAPA104 (Onion Springs 2 lek) hourly dBA metrics, April 11-25, 2013..... 47
Table 18. PAPA104 (Onion Springs 2 lek) dBA and one-third octave band metrics, April 11-25, 2013, 0000-2300. ..... 48
Table 19. PAPA001 (Big Fred lek) hourly dBA metrics, April 5-7, 2013. ..... 49
Table 20. PAPA001 (Big Fred lek) dBA and one-third octave band metrics, April 5-7, 2013, 0000-2300. ..... 50
Table 21. PAPA002 (Little Fred lek) hourly dBA metrics, April 5-7, 2013. ..... 51
Table 22. PAPA002 (Little Fred lek) dBA and one-third octave band metrics, April 5-7, 2013, 0000-2300. ..... 52
Table 23. PAPA003 (Lower Sand Springs Draw) hourly dBA metrics, April 5-7, 2013.53
Table 24. PAPA003 (Lower Sand Springs Draw) dBA and one-third octave band metrics, April 5-7, 2013, 0000-2300. ..... 54
Table 25. PAPA004 (Two Buttes lek) hourly dBA metrics, April 18-21, 2013. ..... 55
Table 26. PAPA004 (Two Buttes lek) dBA and one-third octave band metrics, April 18-21, 2013, 0000-2300. ..... 56
Table 27. PAPA005 (Mesa Spring lek) hourly dBA metrics, April 18-21, 2013..... 57
Table 28. PAPA005 (Mesa Spring lek) dBA and one-third octave band metrics, April 18-21, 2013, 0000-2300. ..... 58

Table 29. PAPA006 (Lovatt Draw Reservoir lek) hourly dBA metrics, April 18-21, 2013. ..... 59
Table 30. PAPA006 (Lovatt Draw Reservoir lek) dBA and one-third octave band metrics, April 18-21, 2013, 0000-2300. ..... 60
Table 31. PAPA007 (Shelter Cabin Reservoir lek) hourly dBA metrics, April 10-12, 2013. ..... 61
Table 32. PAPA007 (Shelter Cabin Reservoir lek) dBA and one-third octave band metrics, April 10-12, 2013, 0000-2300. ..... 62
Table 33. PAPA008 (The Rocks lek) hourly dBA metrics, April 10-12, 2013..... 63
Table 34. PAPA008 (The Rocks lek) dBA and one-third octave band metrics, April 10-12, 2013, 0000-2300..... 64
Table 35. PAPA009 (South Rocks lek) hourly dBA metrics, April 10-12, 2013..... 65
Table 36. PAPA009 (South Rocks lek) dBA and one-third octave band metrics, April 10-12, 2013, 0000-2300..... 66
Table 37. PAPA010 (Stud Horse Butte lek) hourly dBA metrics, April 10-12, 2013. .. 67
Table 38. PAPA010 (Stud Horse Butte lek) dBA and one-third octave band metrics, April 10-12, 2013, 0000-2300. ..... 68
Table 39. PAPA011 (Little Saddle lek) hourly dBA metrics, April 12-14, 2013. ..... 69
Table 40. PAPA011 (Little Saddle lek) dBA and one-third octave band metrics, April 12-14, 2013, 0000-2300..... 70
Table 41. PAPA012 (Alkali Draw lek) hourly dBA metrics, April 12-14, 2013. ..... 71
Table 42. PAPA012 (Alkali Draw lek) dBA and one-third octave band metrics, April 12-14, 2013, 0000-2300..... 72
Table 43. PAPA013 (Sand Draw lek) hourly dBA metrics, April 12-14, 2013. ..... 73
Table 44. PAPA013 (Sand Draw lek) dBA and one-third octave band metrics, April 12-14, 2013, 0000-2300..... 74
Table 45. PAPA014 (Lovatt West lek) hourly dBA metrics, April 18-21, 2013. ..... 75
Table 46. PAPA014 (Lovatt West lek) dBA and one-third octave band metrics, April 18-21, 2013, 0000-2300..... 76
Table 47. PAPA015 (Cat lek) hourly dBA metrics, April 21-23, 2013. ..... 77
Table 48. PAPA015 (Cat lek) dBA and one-third octave band metrics, April 21-23, 2013, 0000-2300. ..... 78
Table 49. PAPA016 (Tyler Draw North lek) hourly dBA metrics, April 15-17, 2013.. 79
Table 50. PAPA016 (Tyler Draw North lek) dBA and one-third octave band metrics, April 15-17, 2013, 0000-2300. ..... 80
Table 51. PAPA017 (Oil Fork Road lek) hourly dBA metrics, April 15-17, 2013..... 81
Table 52. PAPA017 (Oil Fork Road lek) dBA and one-third octave band metrics, April 15-17, 2013, 0000-2300. ..... 82
Table 53. PAPA018 (Mesa Road 3 lek) hourly dBA metrics, April 15-17, 2013..... 83
Table 54. PAPA018 (Mesa Road 3 lek) dBA and one-third octave band metrics, April 15-17, 2013, 0000-2300..... 84
Table 55. PAPA019 (Bloom Reservoir lek) hourly dBA metrics, April 15-17, 2013. .. 85
Table 56. PAPA019 (Bloom Reservoir lek) dBA and one-third octave band metrics, April 15-17, 2013, 0000-2300. ..... 86
Table 57. PAPA201 (Injection Well 100 m) hourly dBA metrics, April 14-15, 2013... 87

Table 58. PAPA201 (Injection Well 100 m) dBA and one-third octave band metrics, April 14-15, 2013, 0000-2300. ..... 88
Table 59. PAPA202 (Injection Well 200 m) hourly dBA metrics, April 14-15, 2013... 89
Table 60. PAPA202 (Injection Well 200 m) dBA and one-third octave band metrics, April 14-15, 2013, 0000-2300. ..... 90
Table 61. PAPA203 (Well Pad, 3 wells, 50 m) hourly dBA metrics, April 15-16, 2013.91
Table 62. PAPA203 (Well Pad, 3 wells, 50 m) dBA and one-third octave band metrics, April 15-16, 2013, 0000-2300. ..... 92
Table 63. PAPA204 (Well Pad, 3 wells, 100 m) hourly dBA metrics, April 15-16, 2013. ..... 93
Table 64. PAPA204 (Well Pad, 3 wells, 100 m) dBA and one-third octave band metrics, April 15-16, 2013, 0000-2300. ..... 94
Table 65. PAPA205 (Central Gathering Facility, with generator, 255 m) hourly dBA metrics, April 16-17, 2013. ..... 95
Table 66. PAPA205 (Central Gathering Facility, with generator, 255 m) dBA and one-third octave band metrics, April 16-17, 2013, 0000-2300. ..... 96
Table 67. PAPA206 (Central Gathering Facility, with generator, 555 m) hourly dBA metrics, April 16-17, 2013. ..... 97
Table 68. PAPA206 (Central Gathering Facility, with generator, 555 m) dBA and one-third octave band metrics, April 16-17, 2013, 0000-2300. ..... 98
Table 69. PAPA207 (Drill Rig, pad 9-24, 2300 m) hourly dBA metrics, April 5-7, 2013. ..... 99
Table 70. PAPA207 (Drill Rig, pad 9-24, 2300 m) dBA and one-third octave band metrics, April 5-7, 2013, 0000-2300. ..... 100
Table 71. PAPA208 (Drill Rig, pad 9-24, 300 m) hourly dBA metrics, April 5-7, 2013.101
Table 72. PAPA208 (Drill Rig, pad 9-24, 300 m) dBA and one-third octave band metrics, April 5-7, 2013, 0000-2300. ..... 102
Table 73. PAPA209 (Highway 191, 100 m) hourly dBA metrics, April 17-18, 2013. 103
Table 74. PAPA209 (Highway 191, 100 m) dBA and one-third octave band metrics, April 17-18, 2013, 0000-2300. ..... 104
Table 75. PAPA210 (Highway 191, 200 m) hourly dBA metrics, April 17-18, 2013. 105
Table 76. PAPA210 (Highway 191, 200 m) dBA and one-third octave band metrics, April 17-18, 2013, 0000-2300. ..... 106
Table 77. PAPA211 (Well heads, 3, and injection well, with generator, 100 m) hourly dBA metrics, April 18-21, 2013. ..... 107
Table 78. PAPA211 (Well heads, 3, and injection well, with generator, 200 m) dBA and one-third octave band metrics, April 18-21, 2013, 0000-2300. ..... 108
Table 79. PAPA212 (Well heads, 3, and injection well, with generator, 200 m) hourly dBA metrics, April 18-21, 2013. ..... 109
Table 80. PAPA212 (Well heads, 3, and injection well, with generator, 200 m) dBA and one-third octave band metrics, April 18-21, 2013, 0000-2300. ..... 110
Table 81. PAPA213 (Gobbler's Knob, north side, liquid stabilizing facility and central gathering facility, 150 m) hourly dBA metrics, April 22-24, 2013. ..... 111
Table 82. PAPA213 (Gobbler's Knob, north side, liquid stabilizing facility and central gathering facility, 150 m) dBA and one-third octave band metrics, April 22-24, 2013. ..... 112

Table 83. PAPA214 (North Anticline Road, east side, 50 m from centerline) hourly dBA metrics, April 22-23, 2013. ..... 113
Table 84. PAPA214 (North Anticline Road, east side, 50 m from centerline) dBA and one-third octave band metrics, April 22-23, 2013. ..... 114
Table 85. PAPA215 (Mesa pad 3-27, 21 wells, with intermittent generator, 200 m) hourly dBA metrics, April 23-24, 2013. ..... 115
Table 86. PAPA215 (Mesa pad 3-27, 21 wells, with intermittent generator, 200 m) dBA and one-third octave band metrics, April 23-24, 2013. ..... 116
Table 87. PAPA216 (Drill rig, pad 5-19, 435 m) hourly dBA metrics, April 23-24, 2013. ..... 117
Table 88. PAPA216 (Drill rig, pad 5-19, 435 m) dBA and one-third octave band metrics, April 23-24, 2013. ..... 118
Table 89. PAPA217 (Johan compressor station, 140 m ESE) hourly dBA metrics, April 23-24, 2013. ..... 119
Table 90. PAPA217 (Johan compressor station, 140 m ESE) dBA and one-third octave band metrics, April 23-24, 2013. ..... 120
Table 91. PAPA101 (foam only windscreen) and PAPA102 (foam/fleece windscreen) $L_{10}$, $L_{50}$, $L_{90}$, and $L_{eq}$ dBA metrics, April 7-10, 2013, 0000-2400. ..... 124
Table 92. PAPA101 (foam only windscreen), dBA and one-third octave band levels, April 7-10, 2013. ..... 125
Table 93. PAPA102 (foam/fleece windscreen), dBA and one-third octave band levels, April 7-10, 2013. ..... 126
Table 94. Influence of microphone height (1.5 m versus 0.3 m) on dBA metrics, March 13, 2013, 1200 hour. ..... 128
Table 95. Equipment component list, serial number, and calibration date. ..... 133

**List of Figures**

Figure 1. PAPA greater sage-grouse noise monitoring project area and lek complexes. 17
Figure 2. Typical acoustic equipment deployment. ..... 18
Figure 3. One-third octave band $L_{50}$ levels for all hours at three reference leks, Big John lek, Jewett Flat Red Flat Reservoir lek, and Onion Springs 2 lek, April 2013. ..... 28
Figure 4. $L_{50}$ dBA at three reference leks, PAPA101, PAPA103, and PAPA104..... 30
Figure 5. $L_{90}$ dBA at three reference leks, PAPA101, PAPA103, and PAPA104..... 30
Figure 6. $L_{eq}$ (median, all hours) one-third octave band frequency levels for three measurement sites: PAPA103 (Jewett Red Flat Reservoir reference lek); PAPA201 (Yellowpoint injection wells); and PAPA208 (Drill rig at pad 9-24). 33
Figure 7. Windscreen made of fleece material placed over a 0.4 m (15 in) high and 0.3 m (12 in) wide wire cylindrical cage. ..... 122
Figure 8. Data collection with LD 831 systems using two different types of windscreens, foam only and foam/fleece, both microphones 0.3 m high, 2.0 m apart. ..... 123
Figure 9. Difference in $L_{50}$ dB levels, 20-20,000 Hz, PAPA101, foam windscreen (reference) and PAPA102, foam/fleece windscreen, April 7-10, 2014 (93 hours). ..... 127
Figure 10. Difference in $L_{eq}$ dB levels, 20-20,000 Hz, PAPA101, foam windscreen (reference) and PAPA102, foam/fleece windscreen, April 7-10, 2014 (93 hours). ..... 127
Figure 11. Sound level thresholds by frequency in hearing of humans and bird species. 130
Figure 12. Spectrogram of sounds at PAPA017 (Oil Road Fork lek), with Greater Sage-grouse sounds (20-5,000 Hz), coyote sounds (500-2,000 Hz), and mechanical sounds (<500 Hz). ..... 131
Figure 13. 1-second snapshot sounds at PAPA017 (Oil Road Fork lek), with mechanical sounds, Greater Sage-grouse sounds, and coyote sounds, but with less detail than narrow band analysis. ..... 132
Figure 14. 1-second snapshot of sounds at PAPA017. This view shows a narrower band frequency analysis, with finer detail for each frequency. Mechanical sounds at about 70 Hz, Greater Sage-grouse sounds at 300-500 Hz, and coyote sounds at about 600 Hz and 1300 Hz. ..... 132

## Introduction

Greater sage-grouse (*Centrocercus urophasianus*) use elaborate audio and visual display behaviors to attract and select mates, and depend on audio communication between females and nestlings during brood rearing. A potential threat to greater sage-grouse is anthropogenic noise associated with human activity, including noise from oil and gas development and production (BLM 2008, Patricelli et al. 2013).

## Objective

The primary objectives of this project were to:

- Monitor sound levels at 19 leks in PAPA;
- Monitor sound levels of common gas field activities near leks in PAPA; and
- Determine baseline ambient sound levels in sage land cover at reference areas outside PAPA (3 leks without influence of gas field sounds).

## Study Area

The study area for this project was south and west of Pinedale, WY, primarily in the Pinedale Anticline Project Area (Figure 1). The 6 lek complexes studied were East Fork, Ryegrass, Speedway, Mesa, Duke's Triangle, and Yellowpoint.

## Methods

*Definitions*

The following are definitions of acoustic terms used in this report (NPS 2005). A brief introduction to acoustics is presented in Appendix F.

*Audibility*: Audibility is the ability of animals with normal hearing, including humans, to hear a given sound. Audibility is affected by the hearing ability of the animal, other simultaneous interfering sounds or stimuli, and by the frequency content and amplitude of the sound.

*A-Weighting (dBA)*: A-weighting is used to account for differences in human hearing sensitivity as a function of frequency. A-weighting de-emphasizes the high (6.3 kHz and above) and low (below 1 kHz) frequencies, and emphasizes the frequencies between 1 kHz and 6.3 kHz, in an effort to simulate the relative response of human hearing.

*Decibel (dB)*: A logarithmic measure commonly used in the measurement of sound. The decibel provides the possibility of representing a large span of signal levels in a simple manner as opposed to using the basic pressure unit Pascal. The difference between the sound pressure of silence versus a loud sound is a factor of 1,000,000:1 or more, therefore it is less cumbersome to use a small range of equivalent values: 0 to 130 decibels.

*Frequency*: The number of times per second that the sine wave of sound repeats itself. It can be expressed in cycles per second, or Hertz (Hz). Frequency equals Speed of Sound / Wavelength.

$L_{eq}$ (Equivalent Sound Level): The logarithmic average (i.e., on an energy basis) of sound pressure levels over a specific time period. "Energy averaged" sound levels are logarithmic values, and as such are generally much higher than arithmetic averages. $L_{eq}$ values are typically calculated for a specific time period (1-hour and 12-hour time periods are often used). $L_{eq}$ values are computed from

all of the 1-second $L_{eq}$ values for the specific time period. $L_{eq}$ must be used carefully in quantifying natural ambient sound levels because occasional loud sound levels may heavily influence (increase) the $L_{eq}$ value, even though sound levels for that period of time are typically lower.

*$L_{max}$*: The maximum sound pressure level for a given period.

*$L_{min}$*: The minimum sound pressure level for a given period.

*$L_x$ (Exceedance Percentile)*: This metric is the sound pressure level (L), in decibels, exceeded *x* percent of the time for the specified measurement period. $L_{50}$ is the sound pressure level exceeded 50 percent of the time ($L_{50}$ is the same as the median).

*Noise Floor*: The lower measurement limit of a sound level meter, also referred to as self-noise or electrical noise of all components of a sound level meter (meter, microphone, and preamplifier).

*Sound Level*: Generally, *sound level* refers to the *weighted* sound pressure level obtained by frequency weighting, usually A- or C-weighted.

*Sound Level, Baseline Ambient*: The sound level in a given location including all sounds of nature but absent most human-caused sounds. $L_{90}$ is the sound pressure level exceeded 90 percent of the time, and is commonly used to establish the baseline ambient sound level.

*Sound Level, Existing Ambient*: The sound level of all sounds in a given area, including all natural sounds as well as all mechanical, electrical and other human-caused sounds. The existing ambient sound level is generally characterized by the $L_{50}$ exceedance level (i.e., the median).

*Sound Pressure*: Sound pressure is the instantaneous difference between the actual pressure produced by a sound wave and the average barometric pressure at a given point in space. Not all pressure fluctuations detected by a microphone are sound (e.g., wind over the microphone). Sound pressure is measured in Pascals (Pa), Newtons per square meter, which is the metric equivalent of pounds per square inch.

*Sound Pressure Level (SPL)*: The logarithmic form of sound pressure. Generally, sound pressure level refers to unweighted sound pressure levels of one-third octave bands.

*Time Weighting*: The response speed of a sound level meter. Fast and slow time response were developed primarily to slow needle movement in analog meters so investigators could read and record sound levels. This is not needed with modern digital sound level meters. Both fast and slow time response add a decay factor. Decay factors can induce some error, although over time there is little difference in fast, slow, or actual sound levels.

*Measurement Protocol*

The Wyoming Game and Fish Department's Request for Proposals (RFP) for this project included acoustic measurement protocols developed for the Pinedale Anticline Project Office by Blickley and Patricelli (2012), "Noise monitoring recommendations for Greater Sage Grouse habitat in Wyoming." Methodology for this project followed the requirements and recommendations provided in the RFP and those of Blickley and Patricelli (2013), and expanded those protocols in a few situations.

In brief, Blickley and Patricelli (2013) recommended the following:

- Measurements should be made with a high quality, calibrated Type I (noise floor < 25 dB) sound level meter (SLM) with a microphone windscreen and environmental housing.
- Measurements should be collected during times when noise exposure is most likely to affect greater sage-grouse— nights and mornings (i.e. 6 pm – 9 am) and should be taken for >1 hour at each site, ideally over multiple days with suitable climactic conditions. To capture typical variability in noise level at the site of interest, deployment of SLM units for multiple days is preferred. If measurements are made on or near a lek, measurements made while birds are present on the lek period (for approximately four hours after sunrise) should be excluded from ambient or noise level calculations.
- Measurements should be made at multiple locations between each noise source and the edge of the protected area. On-lek measurements should exclude time periods when birds are lekking. If measurements are made off-lek to avoid measuring the sound produced by grouse, they should be at an equivalent location with similar topography and relative distance to noise sources in the area.
- Metrics collected should include $L_{10}$ $L_{50}$, $L_{90}$, $L_{eq}$, and $L_{max}$. All measurements should be collected in A-weighted decibels (dBA) and, if possible, also collected in unweighted (dBF) and C-weighted (dBC) decibels. SLM should log 1/3-octave band levels throughout the measurement period.
- To determine baseline ambient levels, the use of A-weighted $L_{90}$ metric is recommended. As a measure of median noise exposure, the use of A-weighted $L_{50}$ metric is recommended.
- Collect acoustic data with microphone height matching the height of a greater sage-grouse ear, approximately 0.3 m (12 in).

In addition to the protocols above recommended by Blickley and Patricelli (2013), we considered protocols used in other studies in remote areas. In 2000, the National Parks Air Tour Management Act was enacted. This Act required the National Park Service (NPS) and Federal Aviation Administration (FAA) to cooperatively develop air tour management plans for all parks that had commercial air tours (over 100 parks). This process required field measurements to establish baseline ambient sound levels in these parks which were used to assess potential impacts of noise from air tour aircraft via modeling. The NPS and FAA jointly developed protocols for measuring sound levels in remote areas such as national parks. These protocols are discussed in NPS 2005 and 2013, Lee et al. 2006, Lynch et al. 2011, Hari 2005, and Rapoza et al. 2008.

The NPS/FAA protocols are similar to those of Blickley and Patricelli (2013) but differ in a few areas, primarily microphone height, measurement duration, and collection of digital recordings. The NPS/FAA protocol calls for a microphone height of 1.5 m which is generally used for assessing noise impacts to people, while Blickley and Patricelli (2013) recommend a microphone height of 0.3 m, the height of a greater sage-grouse ear. We placed our microphones at 0.3 m.

Blickley and Patricelli (2013) recommended that measurements be for >1 hour at each site, ideally over multiple days. The NPS/FAA protocol calls for baseline ambient sound level measurements of 25 days/season (summer/winter) to ensure that dB data are no more than ±3 dB from actual levels, or 14 days to ensure ±5 dB of actual levels. The NPS/FAA recommendations were based on a statistical review of several long-term (>12 months) data sets (Hari 2005). This review found that sound levels in nature vary considerably, both seasonally and daily. This variation is due to several factors, including seasonal sound differences (birds, insects) and meteorological differences, primarily wind. Short measurement periods of only a few hours could significantly over- or under-estimate real levels. While the sounds of nature vary considerably, some human-caused sounds and patterns do not. In this study, several gas field sounds were remarkably consistent. For some sources, such as injection wells, drill rigs, and compressor stations, primary metrics such as $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$, were all within 2 dBA of each other. With such consistency, very short measurement periods, 24 hours or less, may be adequate. In consideration of both Blickley and Patricelli (2013) and NPS/FAA experience, we measured more than14 days at reference leks (where human-caused sounds were infrequent and sounds of nature dominated), and more than 24 hours at treatment leks and gas field sources (where human-caused sounds dominated).

NPS/FAA protocol calls for collecting continuous digital recordings with all measurements. This allows researchers to review and identify all sound sources, as well as review any unusual sound level data. Additionally, recordings allow researchers to determine the most common sources of sounds in a study area and to determine the percent of time that each is audible. When assessing potential impacts of noise on wildlife, it is important to know the duration that noise was audible as well as the amplitude of the noise. We collected continuous digital recordings at all measurement locations.

*Baseline Ambient and Existing Ambient*

The objectives of this study were to determine baseline ambient sound levels in sage land cover similar to that in the PAPA (but without gas field sounds), and to determine existing ambient sound levels at leks in the PAPA area. An explanation of the use of the $L_{90}$ and $L_{50}$ metrics follow.

The $L_{90}$ sound level is the sound level exceeded 90 percent of the time. In computing the $L_{90}$, most common human-caused sounds such as vehicles, aircraft, and other mechanical and electrical sounds are generally excluded. Such events may have high sound levels but many are relatively short in duration. In computing the $L_{90}$ sound level, these loud but short events are excluded and allow an estimate of the "baseline" sound level without such intrusions. Federal, state, and local governments generally use the $L_{90}$ metric to establish baseline ambient sound levels for use in environmental reviews and for assessing acoustic impacts of proposed projects or activities (EPA 1971). Blickley and Patricelli (2013) recommend the use of $L_{90}$ to establish baseline ambient sound levels. The $L_{50}$ sound level is the sound level exceeded 50% of the time, or the median, half of the levels are above this level and half are below. The $L_{50}$ metric is used to determine existing ambient sound levels, and includes all sounds in a given area (natural and non-natural) (EPA 1971).

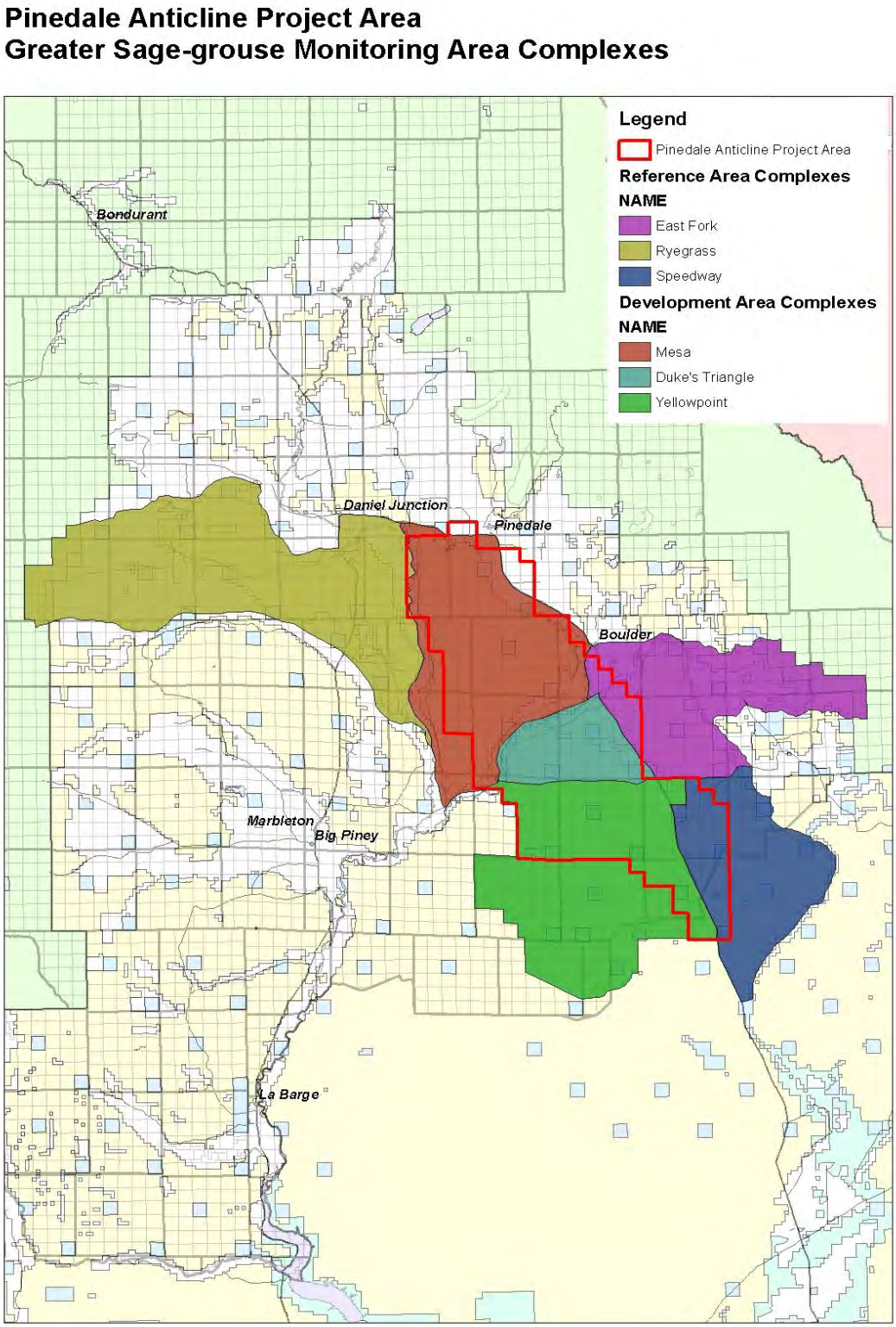



Figure 1. PAPA greater sage-grouse noise monitoring project area and lek complexes.

*Sound Level Meters*

Acoustic equipment used for data collection (sound level meters, microphones, and preamplifiers) met or exceeded ANSI S1.4-1983 Type 1 standards. One-third octave band analyzers and dBA analyzers met ANSI S1.11-2004 and ANSI S1.42-2001, respectively. All acoustic equipment and field calibrators were calibrated to meet ANSI S1.40-2006 (typically by manufacturer, Larson-Davis or B&K) prior to deployment. All systems and calibrators were factory calibrated as recommended by the manufacturer (Appendix G), and all systems were field calibrated at the beginning and end of each measurement period at each location using a field calibrator that met ANSI S1.40-1984 standards. We also collected continuous digital recordings at all measurement locations. Figure 2 shows a typical deployment (PAPA019, Bloom Reservoir Satellite lek) showing equipment case, microphone with fleece cage cover, and anemometer.

We used nine acoustic systems, each with the following components:

- Sound level meter: Larson-Davis LD831
- Microphone: PCB 377B20 or PCB377B02
- Preamplifier: Larson-Davis PRM831
- Environmental Shroud: Larson-Davis EPS2106 (case, 90 mm foam windscreen)
- Fleece windscreen over 90 mm foam (cylindrical, 0.4 m high and 0.3 m wide)
- Roland R05 digital recorder (to make continuous digital recordings)

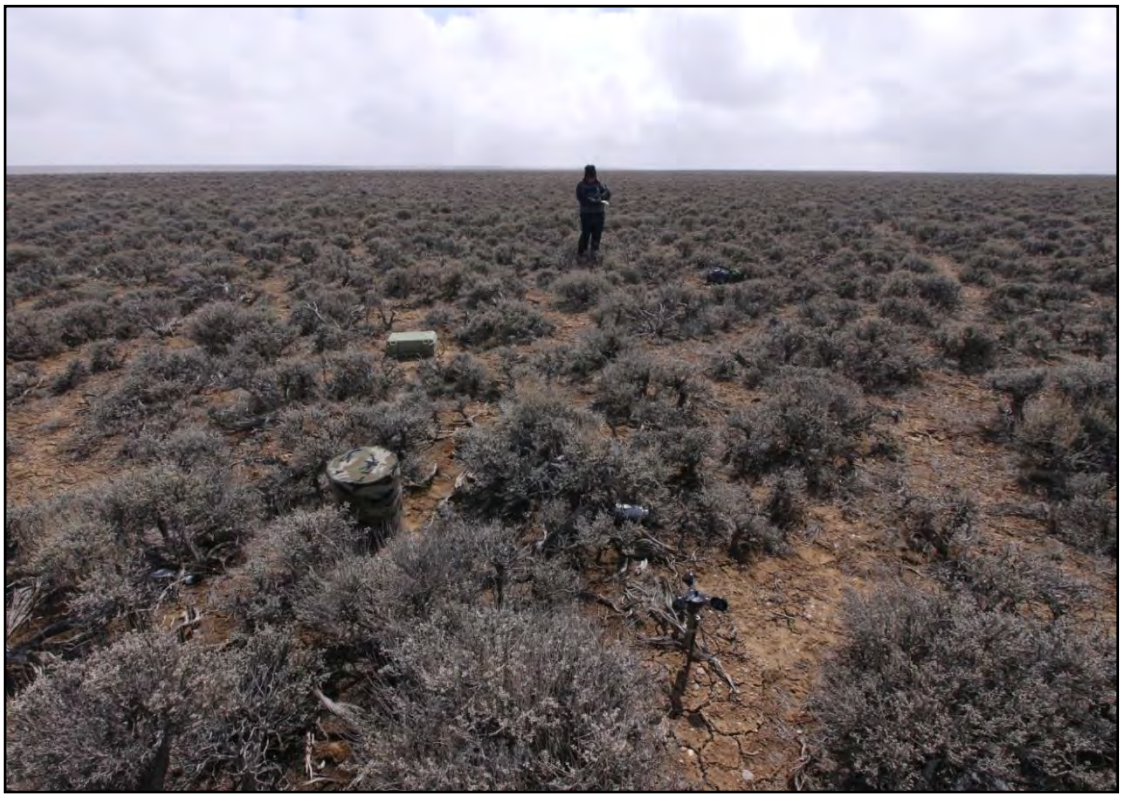


Figure 2. Typical acoustic equipment deployment.

All system components (SLM, digital recorder, and anemometer) were synchronized with GPS time, and differences at the end of the measurement period noted. We used a Bruel and Kjaer (B&K) Acoustic Calibrator Type 4231 for field calibration. In this calibrator, the reference microphone response is independent and does not change with barometric pressure. As a result, there is no need to correct calibration for the effect of elevation above sea level.

The sound level meters used in this study could measure down to approximately 13-14 dBA. This lower measurement limit is referred as the “noise floor” or "instrument self noise." The noise floor of any instrument is essentially the electrical noise of the instrument. Most ANSI Type 1 sound level meters, microphones, and preamplifiers have a noise floor, or instrument self noise, of less than 20 dBA. Manufacturers such as Larson-Davis provide general noise floor data for each of their sound level meter models and components. Although such data are provided for each model, actual noise floor levels can vary by 1-2 dBA per individual instrument. Very sensitive, low-noise microphones and preamplifiers have much lower self noise, and some can measure down to 0 dBA.

*Data Collection*

All acoustic data were collected continuously at 1-second intervals. Sound level meters were set to collect 1-second dBA, dBF, and dBC, as well as unweighted one-third octave band data, 12.5-20,000 Hz. Because we expected sound levels at some locations to be very low (<20 dBA), sound level meters were set to "low-range" with a gain of +20 dB. These settings ensured meters would collect data at the lowest measurement limit for these systems. Time response was set to “fast.”

*Data Processing*

Acoustic metrics required by the Request for Proposals and recommended by Blickley and Patricelli (2013) were computed for each measurement location, including dBA $L_{10}$, $L_{50}$, $L_{90}$, $L_{eq}$, $L_{min}$, and $L_{max}$. One-third octave data, 20-20,000 Hz, unweighted, were collected at each measurement location. $L_{min}$ and $L_{max}$ values are just that, minimum and maximum values; exceedance metrics, $L_{10}$, $L_{50}$, and $L_{90}$, are the percent time sound levels exceeded 10%, 50%, and 90% of the time; and $L_{eq}$ metrics are energy-averaged from 1-second $L_{eq}$ data. As recommended by Blickley and Patricelli (2012), the $L_{90}$ metric at reference lek locations was considered the “baseline ambient” sound level for native sage land cover in the PAPA. Times during which investigators were present were not included in analysis. Hours with <2700 seconds (75% of an hour) were not included. This ensured that any hour with only a few samples did not bias the analysis

In acoustic studies, it is common to report results in hourly statistics, $L_{eq}$, $L_{10}$, $L_{50}$, $L_{90}$, etc., over one-hour periods. Two different methods have generally been used to compute acoustic metrics. The first is referred to as the “unpooled” approach, and the second as the “pooled” approach. Both approaches report hourly statistics, but the computational methods differ. The “unpooled” approach computes hourly metrics ($L_{eq}$, $L_{10}$, $L_{50}$, $L_{90}$, etc.) for each individual hour. For long-term measurements over many days, medians, variances, etc., are computed from hourly data sets. For a 30-day data set, for example, summary hourly metrics for each hour of the day are computed from 30 data points.

Metrics are reported as a function of time of day, for each hour. The "pooled" approach combines all 1-second data from each hour or all hourly data into a single data set, and averages, medians, variances, etc., are computed from the pooled data. As with the "unpooled" approach, metrics are reported as a function of time of day.

Although prior studies (Plotkin 2002) have shown that results for pooled analyses are generally more conservative (i.e., lower) than results for an hourly analysis, analyzing ambient data by hour helps to ensure hour-to-hour and day-to-day variation is addressed. Additionally, many management decisions are based on hour of day. In the case of greater sage-grouse, for example, "lekking" hours may receive special consideration. For these reasons, analysis in this report used "unpooled" data.

We were not able to collect acoustic data for common sources in the gas field at the same distance due to different situations at each source (other nearby sound sources, terrain, land cover, security, etc.). However, it is possible to estimate sound levels at specific distances based on inverse square law and using sound levels measured at known distances. This computation assumes a loss of 6 dB per doubling of distance. Although loss of 6 dB per doubling of distance is commonly used to estimate sound attenuation, several factors influence this rate of loss, including frequency content of the sound, terrain, meteorological conditions, and others. It is important to keep in mind that these calculations are estimates, and we present the results for comparative purposes only. We used 100 meters as a common distance to present the relative (estimated) sound level of common sound sources in the gas field.

*Meteorological Data*

Meteorological data (wind speed, wind direction, temperature, and humidity) can improve the utility of acoustic data. Previous acoustic studies have established a strong correlation between land cover, wind speed, and ambient sound levels (Lee et al. 2006). Sound levels also attenuate differently in cold or hot temperatures. In general, ambient sound levels tend to increase with increasing wind speeds. Depending primarily upon the vegetative characteristics of the measurement site, a substantial change in sound level can occur as wind speeds increase. For example, ambient sound level data measured at a site containing dense foliage will be influenced by wind, primarily due to the wind interacting with leaves.

Jakobsen and Andersen (1983) described three types of wind sounds: natural wind sounds (sounds of turbulence in the air); vegetation wind sounds (sounds of vegetation being blown by wind): and microphone sounds (sounds of air flow turbulence against windscreen foam or over the microphone, generally considered "distorted" or "contaminated" sound). The first two types of wind sounds listed above are considered natural; the third type of wind sound is considered non-natural.

We used two types of anemometers during measurements. At two of the reference leks, we used Davis anemometers (Model 07911) that input data to the Larson-Davis 831 every second. At three locations in the PAPA gas field area, we use Onset HOBO anemometers (Model S-WSA-M003) that logged 1-second wind speed data to a data logger independent

of the Larson-Davis 831. All anemometers were placed 1.5-2.0 m from the microphone at that site. Anemometers were placed at 0.3 m height to match the height of the microphones.

*Microphone Windscreen*
In the PAPA area, high winds, animals, and human activity are common. In order to minimize the influence of wind on the decibel data and to protect the equipment, we used a second windscreen in addition to the standard 90 mm foam windscreen. The additional windscreen was made of thin fleece material placed over a 0.4 m (15 in) high and 0.3 m (12 in) wide wire cylindrical cage (Appendix D; Figures 7-8). This approach is similar to the dual-stage windscreen used in noise measurement systems in remote and windy areas of national parks (Miller et al. 1997, Lee et al. 2006). In order to test the influence of the fleece windscreen on decibel data, we collected data simultaneously using two LD 831 sound level meters at the Big John lek from April 7-10, 2013. One system had the standard 90 mm foam windscreen only and the other system had the 90 mm foam windscreen plus the fleece and wire cage windscreen. We tested the influence of the additional windscreen on dBA and one-third octave band decibel data, both daily and for all days, and found the influence to be minimal, generally less than the measurement precision of the instruments. Details on the windscreen test are presented in Appendix D. During the course of this study and data analysis, we determined that we did not have wind, security, or animal issues with our microphones or systems. Therefore, we believe the addition of the fleece windscreen is not required.

*Microphone and Anemometer Height*
Microphones and anemometers were placed 0.3 m (12 in) above the ground. This placement matched the approximate height of a greater sage-grouse ear and thus provided sound levels experienced by greater sage-grouse (Pater et al. 2009, Blickley and Patricelli 2012).

In order to test the influence of microphone height on decibel data, we collected data simultaneously using two LD 831 sound level meters. One system had the microphone at 1.5 m and the other system had the microphone at 0.3 m. We compared the $L_{eq}$, $L_{10}$, $L_{50}$, $L_{90}$, $L_{min}$ and $L_{max}$ dBA metrics for 1 hour on March 13, 2013 (prior to deployment in Wyoming). All metrics of the 1.5 m microphone were slightly greater than the 0.3 m microphone, but the differences were small (<1.5 dBA for $L_{10}$, $L_{50}$, and $L_{90}$). Test results are presented in Appendix E.

*Measurement Locations*
We collected acoustic data at 39 different locations in the PAPA in April 2013 (Table 1). We collected data at three reference leks, 19 treatment leks, and 17 gas field sound sources. The reference leks were in the Speedway and Ryegrass complexes, and the treatment leks were in the Mesa, Duke's Triangle, and Yellowpoint complexes. Exact measurement locations for reference and treatment leks are not provided due to security concerns. Most of the measurement locations for gas field sound sources were near leks, and exact locations are not provided due to security concerns. We collected data at the

Jonah compressor station because the compressor station near the South Rocks and Rocks leks was not operational during April 2013.

We placed sound level meters 100-200 meters from the edge of the leks to minimize the potential of grouse display sounds contaminating measurements data. This proved to be a subjective judgment as lekking grouse used a large area in and around the lek area, and grouse sounds were audible at some measurement locations.

We followed recommendations of Blickley and Patricelli (2013), citing Mueller (2002), for placement of sound level meters relative to gas field sound sources near leks. These recommendations included placing sound level meters two source widths away from the source. In most cases, gas field sound sources had several different sound sources within that activity, and these different individual sources were spread throughout the area of the source. For example, a drill rig might be on a pad 150 m across, with drilling, generators, vehicles, and other activities occurring simultaneously on the pad. In this situation, we placed the sound level meter 300 m from the drill pad (150 m x 2 = 300 m). This was not always possible due to interference from other near-by sound sources in the gas field. We placed multiple sound level meters at different distances from gas field sources, and, whenever possible, we doubled the distance between source and each meter. We used a Leica LRF 1200 laser rangefinder to determine distance from sound source to sound level meter.

*Measurement Schedule and Duration*

All acoustic data were collected during April 2013. At reference leks, data were collected more than14 days, while at treatment leks and gas field sound sources, data were collected for at least 24 hours at most locations.

**Results**

Acoustic data were collected at 39 different locations (3 reference leks, 19 treatment leks, and 17 gas field sound sources). 2,549 hours of data were collected, 1,001 hours at reference leks, 999 hours at treatment leks, and 549 hours at gas field sound sources (Table 1). Complete dBA and one-third octave band metrics are presented in Appendix A (reference leks); Appendix B (treatment leks); and Appendix C (gas field sound sources).

*Reference Leks*

At the three reference leks, the $L_{90}$ levels for all hours (0000-2400) ranged from 14.5 dBA to 17.0 dBA, and the $L_{50}$ levels ranged from 16.8 dBA to 20.4 dBA (Table 2). At reference lek PAPA101, distance highway sounds influenced decibel data, while at reference lek PAPA104, grouse display sounds influenced decibel data. Reference lek PAPA103 was least influenced by vehicle sounds or grouse display sounds ($L_{90}$ = 14.5 dBA; $L_{50}$ = 16.8 dBA). $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$ dBA levels for reference leks are shown in Table 3. Hourly dBA metrics and one-third octave band metrics for all reference leks are shown in Appendix A.

*Treatment Leks*

At the 19 treatment leks, the median sound level ($L_{50}$) (0000-2400) for all 999 hours was 26.6 dBA. $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$ dBA levels for all treatment leks are shown in Table 4. The Duke's Triangle Complex had the highest sound levels for all metrics of the three complexes, and the Mesa Complex had the lowest (Table 5). Sounds levels at leks were correlated with the type and distance to gas field activities. The Big Fred lek in Duke's Triangle was close to an active drill rig (1055 m) and had the highest sound levels (35.9 dBA), while the Cat lek was far from current gas field activity and had a median sound level of 17.5 dBA.. Hourly dBA metrics and one-third octave band metrics for all treatment leks are shown in Appendix B.

*Gas Field Sound Sources*

Sound levels of common PAPA gas field activities are shown in Table 6. Of the common activities in the gas field, the median sound level ($L_{50}$) of active drill rig in the Duke's Triangle complex was the loudest (est. 62 dBA @ 100 m), followed by the injection well complex (56 dBA @ 100 m) in the northern part of the Yellowpoint complex. Other gas field sound sources with $L_{50}$ >50 dBA @ 100 m were a second drill rig being disassembled in the Duke's Triangle complex (54 dBA); Jonah compressor station (54 dBA); central gathering facility in the Mesa Complex with generator (52 dBA); and a well pad with 21 well heads and generator (50 dBA). Hourly dBA metrics and one-third octave band metrics for gas field sound sources are shown in Appendix C.

Table 1. Number, complex, name, date-time start, date-time end, and number of hours of acoustic data collection sites, PAPA, April 2013.

| Site Num. | Complex | Lek Name | Date_Time Start | Date_Time End | Hours |
|---|---|---|---|---|---|
| Reference Leks | | | | | |
| PAPA101 | Speedway | Big John | 20130406_1045 | 20120421_0850 | 346 |
| PAPA103 | Rye Grass | Jewett Red Flat Res. | 20130411_1320 | 20130425_0738 | 329 |
| PAPA104 | Rye Grass | Onion Springs 2 | 20130411_1445 | 20130425_0650 | 326 |
| Treatment Leks | | | | | |
| PAPA001 | Duke's Triangle | Big Fred | 20130405_1450 | 20130407_1520 | 47 |
| PAPA002 | Duke's Triangle | Little Fred | 20130405_1150 | 20130407_1235 | 47 |
| PAPA003 | Duke's Triangle | Lower Sand Springs Draw | 20130405_1305 | 20130407_1645 | 50 |
| PAPA004 | Mesa | Two Buttes | 20130418_0910 | 20120421_1345 | 75 |
| PAPA005 | Mesa | Mesa Spring | 20130418_0950 | 20130421_1410 | 75 |
| PAPA006 | Mesa | Lovatt Draw Res. | 20130418_1025 | 20130421_1433 | 59 |
| PAPA007 | Yellowpoint | Shelter Cabin Res. | 20130410_0855 | 20130412_1145 | 49 |
| PAPA008 | Yellowpoint | The Rocks | 20130410_1015 | 20130412_1330 | 50 |
| PAPA009 | Yellowpoint | South Rocks | 20130410_1115 | 20130412_1404 | 50 |
| PAPA010 | Yellowpoint | Stud Horse Butte | 20130410_1200 | 20130412_1434 | 49 |
| PAPA011 | Yellowpoint | Little Saddle | 20130412_0910 | 20130414_0910 | 47 |
| PAPA012 | Yellowpoint | Alkali Draw | 20130412_1100 | 20130414_1020 | 46 |
| PAPA013 | Yellowpoint | Sand Draw | 20130412_1245 | 20130414_1135 | 46 |
| PAPA014 | Mesa | Lovatt West | 20130418_1105 | 20130421_1456 | 75 |
| PAPA015 | Mesa | Cat | 20130421_1100 | 20130423_1300 | 49 |
| PAPA016 | Mesa | Tyler Draw North | 20130415_1000 | 20130417_0920 | 46 |
| PAPA017 | Mesa | Oil Fork Road | 20130415_1100 | 20130417_1005 | 46 |
| PAPA018 | Mesa | Mesa Road 3 | 20130415_1145 | 20130417_1115 | 47 |
| PAPA019 | Mesa | Bloom Res. Sat. | 20130415_1230 | 20130417_1134 | 46 |
| PAPA Sound Sources | | | | | |
| PAPA201 | Yellowpoint | Injection well 100 m | 20130414_0810 | 20130415_1355 | 28 |
| PAPA202 | Yellowpoint | Injection well 200 m | 20130414_0810 | 20130415_1355 | 28 |
| PAPA203 | Yellowpoint | Well (3) pad 50 m | 20130415_1520 | 20130416_1420 | 22 |
| PAPA204 | Yellowpoint | Well (3) pad 100 m | 20130415_1520 | 20130416_1420 | 22 |
| PAPA205 | Mesa | CGF (with gen.) 555 m | 20130416_1640 | 20130417_1035 | 17 |
| PAPA206 | Mesa | CGF (with gen.) 255 m | 20130416_1715 | 20130417_1045 | 16 |
| PAPA207 | Duke's Triangle | Drill rig (pad 9-24) 2300 m | 20130405_1600 | 20130407_1605 | 47 |
| PAPA208 | Duke's Triangle | Drill rig (pad 9-24) 300 m | 20130405_1730 | 20130407_1440 | 44 |
| PAPA209 | Speedway | Hwy 191 100 m | 20130417_1325 | 20130418_1335 | 23 |
| PAPA210 | Speedway | Hwy 191 200 m | 20130417_1335 | 20130418_1338 | 23 |
| PAPA211 | Mesa | Well pad ICI 100 m | 20130418_1440 | 20130421_1510 | 72 |
| PAPA212 | Mesa | Well pad ICI-30 200 m | 20130415_1455 | 20130421_1510 | 65 |
| PAPA213 | Mesa | Gobbler's Knob, North, 150 m | 20130422_0820 | 20130424_0925 | 48 |
| PAPA214 | Mesa | N. Anticline Road, 50 m | 20130422_0850 | 20130423_0905 | 24 |
| PAPA215 | Mesa | Well heads, 21 (pad 3-27), 200 m | 20130423_0840 | 20130424_0910 | 24 |
| PAPA216 | Duke's Triangle | Drill rig (pad 5-19), 435 m | 20130423_1020 | 20130424_1020 | 23 |
| PAPA217 | Jonah | Jonah Compressor Sta., 140 m | 20130423_1128 | 20130424_1105 | 23 |

Table 2. Hourly existing ambient and baseline ambient sound levels at three reference leks near PAPA, April 2013.

| | L50 | | | | L90 | | |
|---|---|---|---|---|---|---|---|
| Hour | PAPA101 | PAPA103 | PAPA104 | | PAPA101 | PAPA103 | PAPA104 |
| 0 | 16.6 | 13.7 | 15.5 | | 15.7 | 13.5 | 14.2 |
| 1 | 17.6 | 13.7 | 14.8 | | 15.8 | 13.5 | 14.2 |
| 2 | 16.4 | 13.7 | 14.4 | | 15.5 | 13.5 | 14.1 |
| 3 | 16.6 | 13.6 | 14.5 | | 15.7 | 13.4 | 14.1 |
| 4 | 16.3 | 13.6 | 14.6 | | 15.5 | 13.5 | 14.3 |
| 5 | 21.5 | 16.6 | 34.2 | | 16.8 | 13.6 | 16.8 |
| 6 | 23.3 | 17.0 | 28.8 | | 18.6 | 15.3 | 16.9 |
| 7 | 19.4 | 16.2 | 18.0 | | 17.1 | 14.4 | 15.0 |
| 8 | 18.0 | 15.6 | 16.5 | | 16.3 | 14.8 | 14.8 |
| 9 | 19.4 | 19.6 | 19.1 | | 16.6 | 14.5 | 15.5 |
| 10 | 20.6 | 20.4 | 19.0 | | 18.1 | 15.9 | 15.3 |
| 11 | 18.5 | 22.5 | 20.8 | | 17.2 | 15.4 | 17.0 |
| 12 | 21.3 | 24.0 | 23.8 | | 17.8 | 18.4 | 18.1 |
| 13 | 23.2 | 24.3 | 25.7 | | 18.0 | 18.0 | 18.2 |
| 14 | 24.2 | 26.6 | 26.5 | | 19.1 | 20.0 | 20.3 |
| 15 | 24.2 | 25.1 | 24.3 | | 19.0 | 17.6 | 19.0 |
| 16 | 25.7 | 26.1 | 24.6 | | 19.3 | 18.6 | 18.7 |
| 17 | 26.6 | 24.3 | 22.5 | | 20.6 | 17.2 | 15.8 |
| 18 | 25.0 | 21.4 | 21.3 | | 19.6 | 16.4 | 16.5 |
| 19 | 23.5 | 17.2 | 17.2 | | 16.7 | 14.0 | 14.4 |
| 20 | 21.4 | 15.1 | 19.6 | | 17.6 | 13.7 | 14.5 |
| 21 | 20.2 | 15.4 | 23.5 | | 16.8 | 13.7 | 15.3 |
| 22 | 16.7 | 14.3 | 16.1 | | 15.7 | 13.5 | 14.3 |
| 23 | 16.8 | 13.7 | 15.6 | | 15.6 | 13.5 | 14.1 |

| | L50 | | | | L90 | | |
|---|---|---|---|---|---|---|---|
| Time Period | PAPA101 | PAPA103 | PAPA104 | | PAPA101 | PAPA103 | PAPA104 |
| 0000-2400 | 20.4 | 16.8 | 19.4 | | 17.0 | 14.5 | 15.3 |
| 1800-0900 | 18.0 | 15.1 | 16.5 | | 16.3 | 13.6 | 14.4 |
| 0500-0900 | 20.5 | 16.4 | 23.4 | | 17.0 | 14.6 | 15.9 |
| 0000-0500 | 16.6 | 13.7 | 14.6 | | 15.7 | 13.5 | 14.2 |

| Time Period | L50 All Sites | | L90 All Sites |
|---|---|---|---|
| 0000-2400 | 19.4 | | 15.8 |
| 1800-0900 | 16.6 | | 14.8 |
| 0500-0900 | 18.0 | | 15.8 |
| 0000-0500 | 14.6 | | 14.2 |

Table 3. $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$ dBA metrics at three reference leks, 0000-2400.

| | Lek Name | Hours | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|
| PAPA101 | Big John | 346 | 31.0 | 25.1 | 20.4 | 17.0 |
| PAPA103 | Jewett Red Flat Res. | 329 | 28.7 | 24.2 | 16.8 | 14.5 |
| PAPA104 | Onion Springs 2 | 326 | 30.2 | 29.4 | 19.4 | 15.3 |

Table 4. $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$ dBA metrics at 19 treatment leks, 0000-2400.

| Site Number | Complex | Lek Name | Hours | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|
| PAPA001 | Duke's Triangle | Big Fred | 47 | 39.8 | 40.3 | 36.9 | 34.8 |
| PAPA002 | Duke's Triangle | Little Fred | 47 | 34.7 | 33.1 | 28.4 | 25.2 |
| PAPA003 | Duke's Triangle | Lower Sand Springs Draw | 50 | 33.3 | 32.9 | 28.4 | 24.9 |
| PAPA004 | Mesa | Two Buttes | 75 | 32.6 | 30.6 | 26.4 | 22.7 |
| PAPA005 | Mesa | Mesa Spring | 75 | 36.2 | 34.6 | 30.0 | 26.7 |
| PAPA006 | Mesa | Lovatt Draw Res. | 59 | 36.7 | 35.2 | 32.0 | 29.7 |
| PAPA007 | Yellowpoint | Shelter Cabin Res. | 49 | 32.7 | 29.6 | 26.0 | 24.1 |
| PAPA008 | Yellowpoint | The Rocks | 50 | 32.0 | 29.5 | 26.2 | 24.0 |
| PAPA009 | Yellowpoint | South Rocks | 50 | 31.2 | 30.0 | 26.2 | 24.0 |
| PAPA010 | Yellowpoint | Stud Horse Butte | 49 | 32.2 | 31.6 | 27.3 | 25.4 |
| PAPA011 | Yellowpoint | Little Saddle | 47 | 30.2 | 29.3 | 22.3 | 18.8 |
| PAPA012 | Yellowpoint | Alkali Draw | 46 | 31.4 | 28.7 | 23.3 | 20.4 |
| PAPA013 | Yellowpoint | Sand Draw | 46 | 36.1 | 32.0 | 27.3 | 23.1 |
| PAPA014 | Mesa | Lovatt West | 75 | 33.5 | 33.7 | 29.6 | 27.0 |
| PAPA015 | Mesa | Cat | 49 | 28.5 | 24.8 | 17.5 | 16.0 |
| PAPA016 | Mesa | Tyler Draw North | 46 | 27.7 | 26.5 | 21.8 | 18.5 |
| PAPA017 | Mesa | Oil Road Fork | 46 | 29.2 | 28.6 | 24.9 | 22.2 |
| PAPA018 | Mesa | Mesa Road 3 | 47 | 30.2 | 29.3 | 24.1 | 20.1 |
| PAPA019 | Mesa | Bloom Res. Satellite | 46 | 28.6 | 26.6 | 22.0 | 18.3 |

Table 5. $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$ dBA metrics for all hours in three complexes.

| Complex | Hours | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|
| Duke's Triangle | 144 | 34.7 | 33.1 | 28.4 | 25.2 |
| Mesa | 518 | 30.2 | 29.3 | 24.9 | 22.2 |
| Yellowpoint | 337 | 32.0 | 29.6 | 26.2 | 24.0 |

Table 6. $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$ dBA metrics for PAPA gas field sound sources, 0000-2400.

| Site Number | Complex | Lek Name and Distance | Hours | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|
| PAPA201 | Yellowpoint | Injection well 100 m | 28 | 55.6 | 56.5 | 55.8 | 54.9 |
| PAPA202 | Yellowpoint | Injection well 200 m | 28 | 48.2 | 49.5 | 48.5 | 47.7 |
| PAPA203 | Yellowpoint | Well (3) pad 50 m | 22 | 38.4 | 39.8 | 37.5 | 35.4 |
| PAPA204 | Yellowpoint | Well (3) pad 100 m | 22 | 34.8 | 35.4 | 31.3 | 29.3 |
| PAPA205 | Mesa | CGF (with gen.) 555 m | 17 | 36.6 | 37.8 | 35.7 | 34.2 |
| PAPA206 | Mesa | CGF (with gen.) 255 m | 47 | 39.1 | 39.5 | 37.4 | 35.9 |
| PAPA207 | Duke's Triangle | Drill rig (pad 9-24), 2300 m | 47 | 34.9 | 34.8 | 30.4 | 27.2 |
| PAPA208 | Duke's Triangle | Drill rig (pad 9-24), 300 m | 44 | 53.7 | 54.2 | 52.5 | 51.0 |
| PAPA209 | Speedway | Hwy 191 100 m | 23 | 40.7 | 34.9 | 25.8 | 21.0 |
| PAPA210 | Speedway | Hwy 191 200 m | 23 | 36.1 | 32.6 | 24.9 | 21.0 |
| PAPA211 | Mesa | Well pad ICI 100 m | 72 | 46.9 | 46.7 | 45.5 | 44.3 |
| PAPA212 | Mesa | Well pad ICI-30 200 m | 65 | 40.2 | 41.4 | 38.6 | 37.0 |
| PAPA213 | Mesa | Gobbler's Knob, North, 150 m | 48 | 46.0 | 46.9 | 43.8 | 40.3 |
| PAPA214 | Mesa | N. Anticline Road, 50 m | 24 | 43.6 | 39.9 | 26.9 | 24.1 |
| PAPA215 | Mesa | Pad 3-27 (21 wells), 200 m | 24 | 45.4 | 47.3 | 44.4 | 40.4 |
| PAPA216 | Duke's Triangle | Drill rig (pad 5-19), 435 m | 23 | 42.2 | 42.5 | 41.2 | 38.8 |
| PAPA217 | Jonah | Jonah Compressor Sta., 140 m | 23 | 51.9 | 51.8 | 50.9 | 50.1 |

*Wind Speed*

Wind speed data were collected at five locations in 2013. Wind speed at 0.3 m height rarely exceeded 5 m/s (11 mph) (average 0.022% of the time at five locations) (Table 7). This was due to surrounding sage plants being higher than the anemometers and thus acting as an effective windscreen. As a result, metrics with and without wind >5 m/s did not differ and metrics reported in this report include all 1-second data.

Table 7. Wind speed data at five locations in 2013, three near PAPA leks and two near reference leks.

| Wind Speed (m/s) | PAPA011 | PAPA019 | PAPA207 | PAPA101 | PAPA103 |
|---|---|---|---|---|---|
| Mean | 0.5 | 0.4 | 0.3 | 0.7 | 0.2 |
| Min | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Max | 5.7 | 5.0 | 6.1 | 7.2 | 6.4 |
| Percent >5.0 m/s | 0.004% | 0.000% | 0.003% | 0.045% | 0.060% |

**Discussion**

*Reference Leks*

Sound levels at the three reference leks were similar (75% of $L_{50}$ and $L_{90}$ levels <20 dBA). Both PAPA103 (Jewett Red Flat Reservoir) and PAPA104 (Onion Springs 2) were slightly quieter, on average, than PAPA101 (Big John lek), probably due to distant highway noise at PAPA101 (Highway 191 was 7.8 km or 4.5 mi from PAPA101). One-third octave band data were also similar, with higher levels in lower frequencies at Big John lek probably due to distance highway sounds (Figure 3).

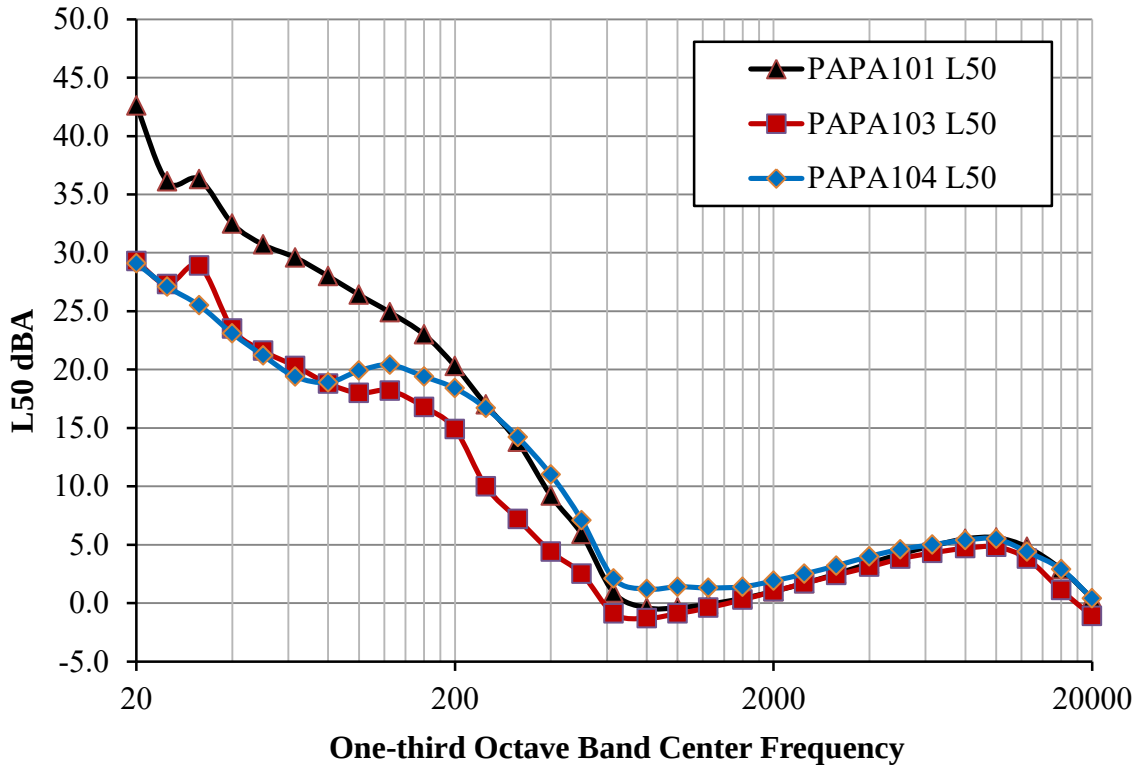



Figure 3. One-third octave band $L_{50}$ levels for all hours at three reference leks, Big John lek, Jewett Flat Red Flat Reservoir lek, and Onion Springs 2 lek, April 2013.

*Measurements at Reference Leks and Influence of Greater Sage-Grouse Display Sounds*

Sound level meters at the three reference leks were placed 100-200 m from the edge of the lek in an effort to minimize the influence of greater sage-grouse display sounds on the dB data. We assumed this distance would be adequate to minimize such influence but this was not always the case. Both the $L_{50}$ metric, and to a less degree the $L_{90}$ metric, were influenced by grouse sounds (apparent in dB data and verified by playback of recordings). In Figures 4 and 5, it is clear that grouse sounds influenced $L_{50}$ and $L_{90}$ levels during the primary lekking hours, 0500-0900. This was most evident at PAPA104, and to a lesser degree at PAPA101 and PAPA103. Decibel levels from 0000 to 0500 were very low, as was the 0900 hour after lekking activity ended for the day. Review of decibel data and recordings suggest that sound levels during the hours 0500-0900 would be similar to levels during 0000-0500 if grouse were not present. General daily acoustic patterns were

evident at the three reference leks and can be seen in Figures 4 and 5. From 0000-0500, sound levels were generally low with few natural or non-natural sounds. From about 0500-0800, grouse sounds were common, declining between the 0800-0900 hours. After the 0900 hour, sound levels began to increase due to common daily sounds sources, including wind through vegetation and increased human activity (vehicle and aircraft sounds).

*Use of $L_{90}$ or $L_{50}$ to Establish Baseline Ambient Sound Level*

The appropriateness of using either the $L_{90}$ or the $L_{50}$ to establish baseline ambient sound level depends on the duration (or percent time audible) of human-caused sounds. If no human-caused sounds were present, the $L_{50}$ metric would represent the ambient sound level. However, in most locations, there is usually a great deal of human-caused sounds, often more than 50% and $L_{90}$ is the appropriate metric for establishing baseline ambient sound levels. In situations where human-caused sounds are uncommon, the $L_{90}$ metric can underestimates baseline ambient sound level, and the $L_{50}$ is a more appropriate metric for establishing baseline ambient sound levels. The appropriateness of using the $L_{90}$ or $L_{50}$ for establishing baseline ambient sound levels depends on the amount of time that anthropogenic sounds are audible.

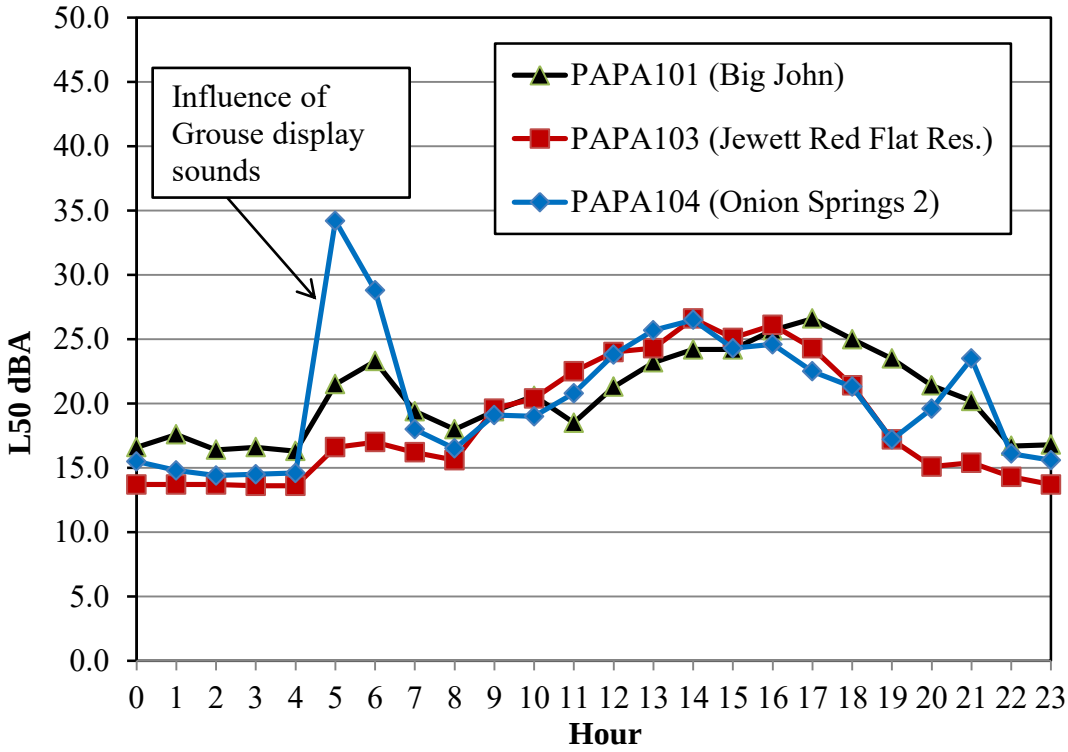



Figure 4. $L_{50}$ dBA at three reference leks, PAPA101, PAPA103, and PAPA104.

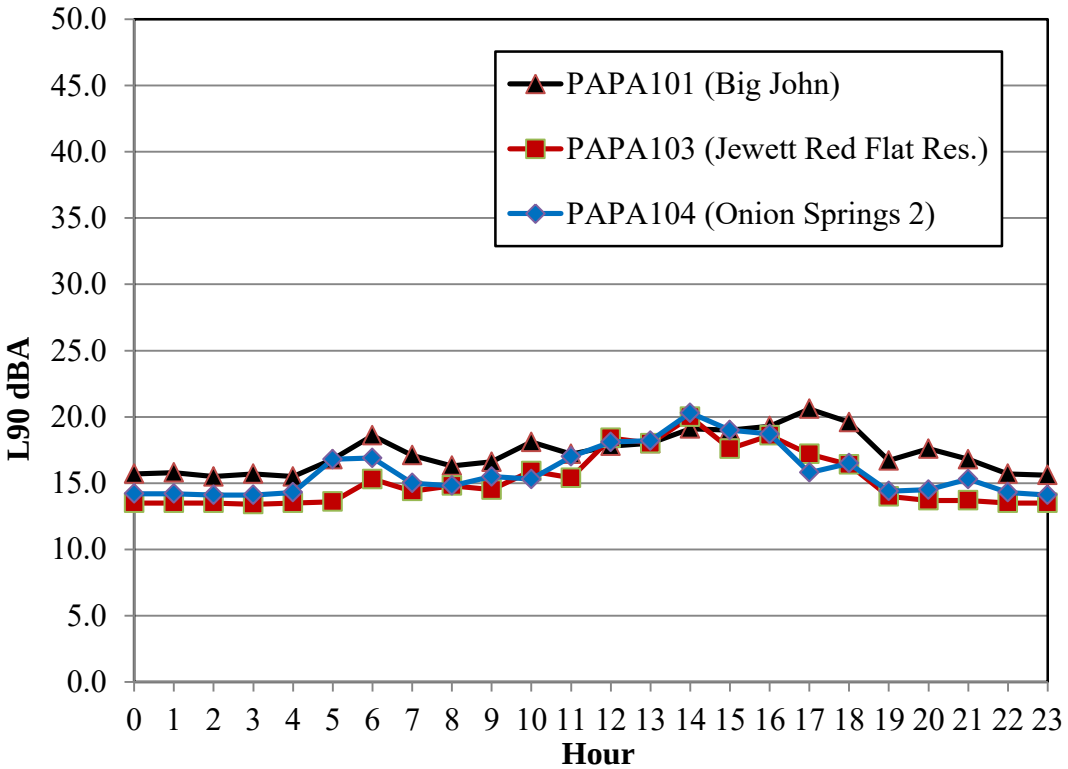



Figure 5. $L_{90}$ dBA at three reference leks, PAPA101, PAPA103, and PAPA104.

*Treatment Leks*

Sound levels at treatment leks varied a great deal. The lek with the highest median sound level ($L_{50}$) was the Big Fred lek at 36.9 dBA. This lek was 1050 m from an operating drill rig at pad 9-24 (this drill rig had the highest $L_{50}$ sound level in the gas field, estimated 62 dBA @ 100 m). The treatment lek with the lowest median sound level ($L_{50}$) was the Cat lek at 17.5 dBA, and the closest gas field activity was 2.6 km. Differences in sound levels at treatment leks were due primarily to distance from and type of gas field activity.

*Hours Exceeding Baseline Ambient + 10 dBA*

The Record of Decision (ROD) (BLM 2008) specified noise thresholds above baseline levels that should not be exceeded by industry. Specific changes requiring mitigation are described as follows: "Decibel levels at the lek more than 10 dBA above baseline measured from the edge of the lek" (BLM 2008)." The ROD also specifies concurrent declines in grouse numbers, but that aspect was not part of this project. The ROD used 39 dBA as a baseline ambient based on an EPA 1973 study that measured sound levels in a farming area in Ohio. Of the 999 hours measured at the treatment leks, no hours exceeded 49 dBA (39 + 10 = 49 dBA), and 565 (57%) exceeded 26 dBA (10 dBA over baseline ambient, 16+10 = 26 dBA). This study did not attempt to evaluate the appropriateness of either 10 dBA above an ambient of 39 dBA or 10 dBA above an ambient of 16 dBA as a trigger for mitigation. Results of this study show that 16 dBA is a more accurate baseline ambient sound level in the PAPA area, and we concur with the KC Harvey (2009) conclusion that "development of the 39 dBA background level did not include collection or analysis of any noise data from the project area. Therefore, the relevance of the 39 dBA value should be evaluated with respect to noise data from the project area"

*Sound Levels in 2013 and 2013 Counts of Greater Sage-grouse at Leks*

One should use caution in comparing 2013 sound levels at treatment leks and 2013 counts of greater sage-grouse at these leks. The 2013 count numbers may have been influenced by sound levels in 2013; however, the 2013 counts were also probably influenced by activities and sounds of gas field operations in previous years, among other factors. Sound levels in the gas field change often, depending on the activity and the duration of that activity. For example, an operational drill rig near a lek in some years before 2013 might have produced sound levels sufficient to influence grouse numbers at that lek, but in 2013, that drill rig might have been replaced by well heads only, a much quieter type of activity. The potential influence of gas field sounds on counts of greater sage-grouse, and how long those influences last, are not well understood, and any single year of data should be used with caution.

*Gas Field Sound Sources*

We measured gas field sound sources at 100 m whenever possible; however, this could not be done for all sources. When we could not measure at 100 m, we estimated sound levels at 100 m by re-computing sound levels measured at known distances (assuming a loss of 6 dBA per doubling of distance). We then used 100 m as the common distance to compared sound levels of different sources in the gas field. The drill rig (pad 9-24) in the Duke's Triangle complex was the loudest sound source (est. 62 dBA @ 100 m) followed by the injection well complex (est. 56 dBA @ 100 m) in the northern part of the

Yellowpoint complex. Other gas field sound sources with $L_{50}$ >50 dBA (est.) @ 100 m were a drill rig (pad 3-21) (54 dBA); Jonah compressor station (54 dBA); central gathering facility in the Mesa Complex, with generator (52 dBA); and a well pad with 21 well heads and generator (50 dBA). Other gas field sound sources measured had $L_{50}$ levels <50 dBA @100 m. Sound levels of gas field activities are shown in Table 8 with the estimated dBA level at 100 m. As discussed earlier, wind speed did not significantly influence sound levels in this study due to the microphones being 0.3 m high and lower than surrounding vegetation. However, sound levels measured long distances from sources can be influenced by wind speed and direction (downwind levels are higher and upwind levels are lower). We did not measure wind direction when collecting data at gas field sound sources, but the levels reported could have some directional wind influence.

At both road measurement sites (Highway 191 and North Anticline Road), median ($L_{50}$) sound levels for all hours were relatively low, 31 dBA and 21 dBA respectively. Vehicle sounds levels were highest during normal work hours, between about 0500-1900, and some maximum levels were higher than 70 dBA. At both locations, the $L_{50}$ and $L_{90}$ sound levels for all hours were generally close, while the $L_{10}$ and $L_{eq}$ levels were much higher, suggesting the vehicle events, while often at high sound levels, occurred <50% of the time at these locations.

Table 8. Estimated dBA @ 100 m of common gas field activities, PAPA, April 2013.

| Site Number | Complex | Gas Field Sound Source | Measured Dist. (m) | L50 @ Meas. Dist. | L50 (est.) @ 100 m |
|---|---|---|---|---|---|
| PAPA208 | Duke's Triangle | Drill rig, pad 9-24 | 300 | 52.5 | 62.0 |
| PAPA207 | Duke's Triangle | Drill rig, pad 9-24 | 2300 | 30.4 | 57.6 |
| PAPA001 | Duke's Triangle | Drill rig, pad 9-24 | 1055 | 36.9 | 57.4 |
| PAPA201 | Yellowpoint | Injection well | 100 | 55.8 | 55.8 |
| PAPA202 | Yellowpoint | Injection well | 200 | 48.5 | 54.5 |
| PAPA216 | Duke's Triangle | Drill rig, pad 5-19 | 435 | 41.2 | 54.0 |
| PAPA217 | Jonah | Jonah Compressor Station | 140 | 50.9 | 53.8 |
| PAPA206 | Mesa | CGF (with generator) | 255 | 37.4 | 52.3 |
| PAPA215 | Mesa | Pad 3-27 (21 wells) | 200 | 44.4 | 50.4 |
| PAPA213 | Mesa | Gobbler's Knob, North | 150 | 43.8 | 47.3 |
| PAPA211 | Mesa | Well pad ICI-30 | 100 | 45.5 | 45.5 |
| PAPA212 | Mesa | Well pad ICI-30 | 200 | 38.6 | 44.6 |
| PAPA205 | Mesa | CGF (with generator) | 555 | 35.7 | 43.8 |
| PAPA203 | Yellowpoint | Well (3) pad | 50 | 37.5 | 31.5 |
| PAPA204 | Yellowpoint | Well (3) pad | 100 | 31.3 | 31.3 |
| PAPA210 | Speedway | Hwy 191 | 200 | 24.9 | 30.9 |
| PAPA209 | Speedway | Hwy 191 | 100 | 25.8 | 25.8 |
| PAPA214 | Mesa | North Anticline Road | 50 | 26.9 | 20.9 |

Human-caused mechanical sounds tend to have more energy in the lower frequencies (<1,000 Hz), and common sound sources in the gas field followed this trend. Some gas field sound sources had levels higher than ambient at higher frequencies, up to 8,000 Hz. Figure 6 shows the $L_{eq}$ levels for frequency data, 12.5-20,000 Hz, for three measurement locations: PAPA103 (Jewett Red Flat Reservoir reference lek); PAPA208 (drill rig, pad 9-24 in Duke's Triangle complex); and PAPA201 (Yellowpoint injection well complex). Note that Figure 3 is a plot of $L_{50}$ values, whereas this figure is a plot of $L_{eq}$ values

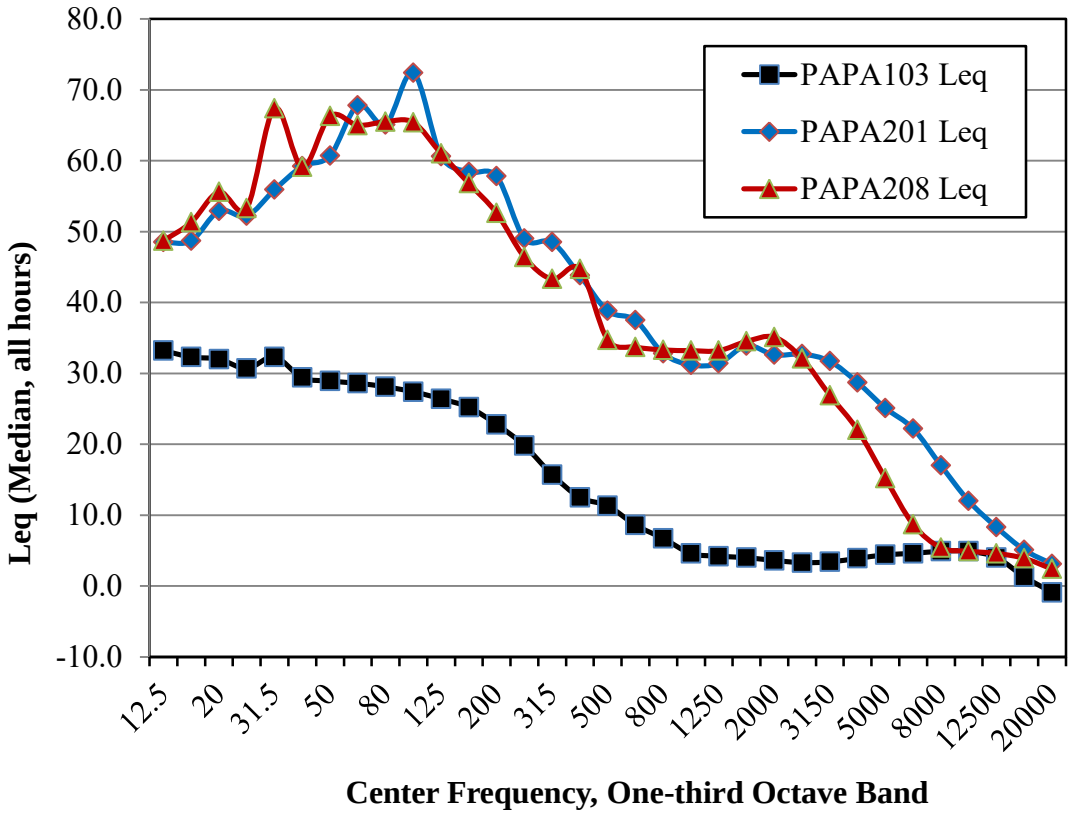



Figure 6. $L_{eq}$ (median, all hours) one-third octave band frequency levels for three measurement sites: PAPA103 (Jewett Red Flat Reservoir reference lek); PAPA201 (Yellowpoint injection wells); and PAPA208 (Drill rig at pad 9-24).

*Sound Levels at Treatment Leks Relative to Gas Field Activities*

Acoustic measurements at the treatment leks were generally made 100-200 m from the lek (in an effort to minimize lekking sounds influence on dB data). Most of these treatment leks were relatively close to some type of gas field activity (average distance 1690 m, range 375-5800 m). In Table 9, the distance to the nearest gas field activity and the 24-hour $L_{50}$ dBA are presented. As one would expect, the farther the lek was from the sound source, the lower the $L_{50}$ value. However, some gas field activities were much louder than others, especially the active drill rigs, and had a greater influence on sound levels at leks.

Table 9. Sound levels ($L_{50}$ dBA, 0000-2400) of gas field activities as measured at treatment leks, distance from lek to activity, and type of closest activity.

| Treatment Lek Name | Treatment Lek | Distance to Activity (m) | $L_{50}$ dBA (24-hr) | Type of Activity |
|---|---|---|---|---|
| Big Fred | PAPA001 | 1050 | 36.9 | Drill rig, active |
| Little Fred | PAPA002 | 1250 | 29.3 | Pump pad, small, no generator |
| Lower Sand Springs Draw | PAPA003 | 1723 | 29.0 | Drill rig, active |
| Two Buttes | PAPA004 | 1931 | 26.4 | Pump pad, large (out of view) |
| Mesa Spring | PAPA005 | 913 | 29.9 | Pump pad, large (out of view) |
| Lovatt Draw Res. | PAPA006 | 710 | 32.1 | Drill rig, maintenance |
| Shelter Cabin Res. | PAPA007 | 780 | 26.6 | Pump pad, small, no generator |
| The Rocks | PAPA008 | 1590 | 26.3 | Road, inactive compressor |
| South Rocks | PAPA009 | 1670 | 26.2 | Pump pad, small |
| Stud Horse Butte | PAPA010 | 580 | 27.4 | Pump pad, small, no generator |
| Little Saddle | PAPA011 | 5800 | 22.4 | Injection facility, large (out of view) |
| Alkali Draw | PAPA012 | 520 | 22.6 | Pump pad, small |
| Sand Draw | PAPA013 | 810 | 27.3 | Drill rig |
| Lovatt West | PAPA014 | 375 | 29.6 | Pump pad with injection well, generator |
| Cat | PAPA015 | 2600 | 19.0 | Pump pad, small (out of view) |
| Tyler Draw North | PAPA016 | 810 | 21.5 | Pump pad, small (out of view) |
| Oil Fork Road | PAPA017 | 2060 | 24.8 | Central Gathering Fac., generator. |
| Mesa Road 3 | PAPA018 | 2300 | 24.1 | Pump pad, small |
| Bloom Res. Sat. | PAPA019 | 4700 | 22.0 | Pump pad, small |

*Sound Levels near the Instrument Self Noise (Noise Floor)*

When sound levels are very low (near the lower measurement limit of the sound level meter, or "noise floor"), self noise of the instrument can influence decibel readings. When this occurs, actual environmental sound levels are lower than the value reported by the meter. It is important to acknowledge that very low readings reflect some influence by instrument self-noise and actual levels are lower than reported.

All sound level meters have some inherent electrical noise (self noise) in the system components, such as that introduced by the microphone, preamplifier, and power supply. All system components contribute some degree to the inherent noise of the sound level meter system. Highly sensitive, low-noise components have less inherent noise and thus can measure lower sound levels.

The sound pressure level displayed by the sound level meter is actually the addition of instrument self noise and the actual ambient sound level. Two sound levels of equal value, when added together, produce a level 3 dB greater than the sound level from one of these sources because of logarithmic addition [$10*\log_{10}(2)=3$]. For example, if the self noise of the sound level meter was 15.0 dBA, and the actual ambient sound level was 15.0

dBA, the reading on the meter would read 18.0 dBA (15 dBA + 15 dBA = 18 dBA). When two SPLs that are 10 dB different from each other are added together, there is little added influence from the lower value. For example, 15.0 dB + 25.0 dB = 25.5 dB. Thus, the influence of instrument self noise is greatest when actual sound levels are near instrument self-noise, and this influence decreases as environmental sound levels increase. When environmental sound levels are greater than10 dB above instrument self-noise, there is very little influence.

The most important aspect of this issue is that when reported sound levels are near the self noise of the instrument, actual sound levels are lower. The actual sound levels can be estimated using the log additive function. For example, at PAPA103 (reference lek near Jewett Red Flat Reservoir), the reported $L_{90}$ was 14.5 dBA (0000-2400), and the minimum reported level was 13.1 dBA. Assuming a noise floor of approximately this level, the reported $L_{90}$ of 14.5 dBA would represent an estimated $L_{90}$ of 8.9 dBA (13.1 dBA + 8.9 dBA = 14.5 dBA). Similarly, the reported $L_{50}$ of 16.8 dBA would represent an estimated $L_{50}$ of 14.4 dBA. Because these estimated $L_{90}$ and $L_{50}$ values are just estimates, they are generally not reported. Regardless, in such situations, one can be sure that actual values are lower than reported.

*Wind Speed*

For the five locations where wind speed data were collected, winds rarely exceeded 5 m/s (<0.022% on average). This was due to the sage vegetation being higher than the anemometer and thus providing a "natural" windscreen. The same benefit likely shields greater sage-grouse from experiencing high winds when they are in sage vegetation. Based on these wind speed data collected in 2013, it may not be necessary to collect wind speed relative to decibel data; however, wind speed and wind direction data may be important for other needs, such as modeling sound levels at specific locations upwind or downwind from a sound source.

*Audibility and Common Sound Sources*

At one location, reference lek PAPA103, Jewett Red Flat Reservoir, we used the digital recordings to determine the percent time that common sound sources were audible for one day, April 19, 2013. We sampled the continuous recording by listening to a 10-second recording every 4 minutes of that day, and logging all sounds heard on those samples. The most common natural sounds were wind (43.9%) and birds (28.9%). The most common non-natural sounds were jet aircraft (16.1%) and vehicles/motors (6.7%). In Table 10, percent time audible of common sound sources, natural and non-natural, are presented for three time periods of the day, all day (0000-2400), day time (0700-1900), and night time (1900-0700).

Table 10. Percent time common sound sources were audible at PAPA103, Jewett Flat Red Reservoir, April 19, 2013, for three time periods of the day.

| Sound Source | 0000-2400 | 0700-1900 | 1900-0700 |
|---|---|---|---|
| No Sound Audible | 22.2 | 2.8 | 41.7 |
| Wind | 43.9 | 80.0 | 7.8 |
| Bird | 28.9 | 18.9 | 38.9 |
| Jet | 16.1 | 20.0 | 12.2 |
| Prop | 2.5 | 2.8 | 2.2 |
| Helicopter | 0.0 | 0.0 | 0.0 |
| Road Vehicles | 2.8 | 5.0 | 0.6 |
| Motor Sounds | 3.9 | 2.8 | 5.0 |
| | | | |
| Total Non-natural | 25.0 | 30.0 | 20.0 |
| Total Natural | 69.7 | 92.8 | 46.7 |

**Recommendations**

*Establish Protocol for Measuring Sound Levels Relative to Greater Sage-grouse*

In previous acoustic studies regarding greater sage-grouse and gas exploration and production activities, several different measurement approaches and instrument types have been used. Noise floors of instruments used in those studies have ranged from less than15 dBA (this study) to 25 dBA (McGregor 2008). Microphone height has ranged from 0.3 m (this study) to 2.4 m (BLM 2012). Measure periods have ranged from less than 1 hour to more than 14 days. A standard protocol for measuring sound levels is necessary to ensure all data are useful for greater sage-grouse management. The measurement protocol below is proposed for acoustic studies regarding greater sage-grouse and anthropogenic noise. This proposed protocol follows recommendations by Blickley and Patricelli (2013) as well as those by the FAA and NPS (NPS 2005 and 2013, Lee et al. 2006, Lynch et al. 2011, Hari 2005, Rapoza et al. 2008), and based on our experience in and near the PAPA in 2013. We recommend that this draft protocol be reviewed by all parties involved in acoustic studies relative to greater sage-grouse, including federal, state, and industry officials, and a common protocol be developed and agreed upon for future acoustic studies.

Sound level measurements must be representative of the sound levels experienced by the target species (Grubb et al. 1998, Delaney et al. 1999, Pater et al. 2009, Blickley and Patricelli 2013). This includes both microphone height as well as equipment sensitivity. For greater sage-grouse, average ear height is about 0.3 m and this species is a ground nester, hence microphones should be 0.3 m high. Although ANSI standards recommend placing microphones at 1.5 m, these standards were written specifically for assessing impacts to human, and use the typical height of a human ear, 1.5 m.

Sound levels vary greater due to seasonal and meteorological conditions, and the appropriate measurement duration for the breeding season of greater sage-grouse is not well understood. This period lasts from approximately mid-March to July. Long-term NPS studies demonstrated that summer and winter seasons vary considerable, and a 25-day measurement period would generally ensure measurement accuracy to ±3 dBA for either season (Hari 2005). Given that the breeding season of greater sage-grouse is typically four to five months, and wind speeds are considerably less at 0.3 m, we recommend a minimum 14-day measurement period until more is known about sound level variability during the March-July period.

*Recommended Protocol for Measuring Sound Levels relative to Greater Sage-grouse.*

- Sound level meters should meet ANSI Type 1 standards.
- Sound level meters should be capable of measuring <15 dBA.
- Data collected should include dBA, dBC, and dBF, and unweighted one-third octave band frequency data, 12.5-20,000 Hz.
- Decibel data should be collected continuously, at 1-second intervals.
- Data analysis: At a minimum, report hourly dBA, dBC, and dBF, and unweighted one-third octave band metrics, including $L_{eq}$, $L_{10}$, $L_{50}$, $L_{90}$, $L_{min}$, and $L_{max}$.
- Microphone height should be 0.3 m, approximate ear height of greater sage-grouse.
- Measurement duration should be a minimum of 14 days at each location.
- Continuous digital recordings should be collected at all measurement locations. This will ensure all unusual sound sources and sound levels can be reviewed, and will allow the opportunity to determine the percent time that different sound sources are audible. Recording quality should be at a minimum MP3, 16-bit, 128 kbps; uncompressed .wav, 16-bit, 44,100 kHz preferred.
- In most acoustic studies, wind speed data are needed to assess influence of wind pressure on dB data. However, when microphones are placed at 0.3 m and good windscreens are used, and measurements are made in sage habitat that is higher than 0.3 meters, it is unlikely that wind pressure over microphone will influence dB data. Therefore, wind speed data are not required if the microphone height of 0.3 meters is used. If meteorological data are needed for modeling efforts, such should be collected during the measurement period.
- Instruments should be placed >500 m from any lek to ensure grouse display sounds do not significantly influence dB data.
- For determining baseline ambient sound levels, the $L_{90}$ metric should be used if human-caused sounds are audible >25% of the time. If human-caused sounds are audible <25% of the time, the $L_{50}$ metric should be used. Audibility of human-caused sounds should be determined by logging sound sources from a sample of continuous digital recordings (7 days minimum and a sampling rate of 10 seconds every 4 minutes minimum). It is important that all hours of the day be considered when determining baseline ambient sound levels. While lekking hours are important to grouse, females with nestlings rely on relatively low-level calls to maintain contact with each other and to warn of potential predators. Therefore, all hours should be measured and reported.

**Acknowledgements**
Several individuals assisted us during this study, including Therese Hartman (WGFD), Dean Clause (WGFD), Theresa Gulbrandson (BLM), and Josh Hemenway (BLM). We especially appreciate Therese Hartman's assistance during the duration of the study. Dr. John MacDonald, PE, reviewed the report and offered numerous improvements.

**Literature Cited**

American National Standard (ANSI). 1994. Procedures for Outdoor Measurement of Sound Pressure Level. American National Standards, Inc. New York, NY.

Bruel & Kjaer. 2000. Environmental Sound. Sound and Vibration Measurement A/S. Denmark.

Blickley, J. L., and G. L. Patricelli. 2012. Potential acoustic masking of greater sage-grouse (*Centrocercus urophasianus*) display components by chronic industrial noise. Ornithological Monographs Volume (2012), No. 74, 23–35.

Blickley, J. L, and G. L. Patricelli. 2013. Noise monitoring recommendations for Greater Sage Grouse habitat in Wyoming. Prepared for the PAPA, Pinedale, WY.

Bureau of Land Management (BLM). 2008. Record of Decision, Final Supplemental Environmental Impact Statement for the Pinedale Anticline Oil and Gas Exploration and Development Project, Sublette County, Wyoming. US Department of the Interior, Bureau of Land Management, Cheyenne, Wyoming.

Bureau of Land Management (BLM). 2012. Normally pressured Lance Natural Gas Development Project, Noise Technical Report. BLM Pinedale Field Office, Pinedale, WY.

Crocker, M. J. 1997. Encyclopedia of Acoustics. John Wiley and Sons, New York.

Delaney, D. K., T. G. Grubb, P. Beier, L. L. Pater, and M. H. Reiser. 1999. Effects of helicopter noise on Mexican spotted owls. Journal of Wildlife Management 63:60–76.

Dantzker, M. S., G. B. Deane, and J. W. Bradbury. Directional acoustic radiation in the strut display of male sage grouse Centrocercus urophasianus. Journal of Experimental Biology 202, 2893–2909 (1999).

Environmental Protection Agency (EPA). 1971. Community Noise. U.S. Environmental Protection Agency, Office of Noise Abatement and Control, Washington, D.C. 20460.

Fay, R. R. 1988. Hearing in Vertebrates: a Psychophysics Databook. Hill-Fay Associates, Winnetka, IL.

Fristrup, K. M., and D. Mennitt. 2012. Bioacoustical Monitoring in Terrestrial Environments. Acoustics Today, July 2012.

Grubb, T. G., L. L. Pater, and D. K. Delaney. 1998. Logging truck noise near nesting northern goshawks. U.S. Forest Service Research Note RM-RMRSRN-3, Rocky Mountain Research Station, Ft. Collins, Colorado, USA.

Hari, I. 2005. Determination of Adequate Measurement Periods (temporal sampling). Draft Report to Natural Park Serv. Dept. of Statistics, Colorado State University. 12pp.

Jakobsen, J. and B. Andersen. 1983. Measurements of Wind-generated Noise from Vegetation and Microphone System. Danish National Agency of Environmental Protection.

Lee, C. S. Y., G. G. Fleming, C. J. Roof, J. M. MacDonald, C. J. Scarpone, A. R. Malwitz, and G. Baker. 2006. Background Ambient Sound Levels in Hawai`i Volcanoes National Park, Report No. DOT-VNTSC-FAA-06-07. John A. Volpe National Transportation Systems Center, Cambridge, MA.

Lynch, E., D. Joyce, and K. Fristrup. 2011. An assessment of noise audibility and sound levels in U.S. National Parks. Landscape Ecology, DOI 10.1007/s10980-011-9643.

McGregor, H. 2008. Ambient noise level measurements, sage grouse lek, Sand Draw Reservoir, Sublette County, Wyoming. Engineering Dynamics Incorporated, Englewood, CO.

Miller, N. P., R. H. Thompson, G. B. Holey, and J. A. True. 1997. LOWNOMS User's Manual. Harris Miller Miller & Hanson Inc., Burlington, MA.

Mueller, T. J. 2002. Aeroacoustic measurements. Springer Verlag.

National Park Service (NPS). 2005. Acoustics and Soundscape Studies in National Parks. Draft. Natural Sounds Program, National Park Service, Fort Collins, CO.

National Park Service (NPS). 2013. Acoustics Monitoring Training Manual. Natural Sounds Program, National Park Service, Fort Collins, CO.

National Weather Service (NWS). 2013. National Climate Data, National Oceanic and Atmospheric Administration. Silver Springs, MD.

Patricelli, G. L., J. L. Blickley, and S. L. Hooper. 2013. Recommended management strategies to limit anthropogenic noise impacts on greater sage-grouse in Wyoming. Human-Wildlife Interactions 7(2):, Fall 2013.

Pater, L. L., T. G. Grubb, and D. K. Delaney. 2009. Recommendations for Improved Assessment of Noise Impacts on Wildlife. J. Wildlife Management 73(5):788-795.

Plotkin, K. J. 2002. Review of Technical Acoustical Issues Regarding Noise Measurements in National Parks. Wyle Report WR-01-20. Wyle Laboratories, Arlington, VA.

Rapoza, A. S., J. M. MacDonald, A. L. Hastings, C. J. Scarpone, C. S. Y. Lee, and G. G. Fleming. 2008. Development of Improved Ambient Computation Methods in Support of the National Parks Air Tour Management Act. John A. Volpe National Transportation Systems Center, Cambridge, MA

## Appendix A. dBA and One-third Octave Metrics for PAPA Reference Leks.

Table 11. PAPA101 (Big John lek) hourly dBA metrics, April 6-21, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/6/2013 | 4/21/2013 | 0 | 14 | 13.7 | 49.7 | 23.4 | 19.3 | 16.6 | 15.7 |
| 4/6/2013 | 4/21/2013 | 1 | 14 | 13.8 | 49.0 | 22.4 | 20.0 | 17.6 | 15.8 |
| 4/6/2013 | 4/21/2013 | 2 | 14 | 13.7 | 47.1 | 21.1 | 18.4 | 16.4 | 15.5 |
| 4/6/2013 | 4/21/2013 | 3 | 14 | 13.7 | 46.3 | 21.6 | 17.8 | 16.6 | 15.7 |
| 4/6/2013 | 4/21/2013 | 4 | 14 | 13.7 | 48.1 | 22.3 | 20.2 | 16.3 | 15.5 |
| 4/6/2013 | 4/21/2013 | 5 | 14 | 13.8 | 50.2 | 24.4 | 27.0 | 21.5 | 16.8 |
| 4/6/2013 | 4/21/2013 | 6 | 14 | 13.8 | 49.3 | 25.5 | 28.0 | 23.3 | 18.6 |
| 4/6/2013 | 4/21/2013 | 7 | 14 | 13.8 | 68.9 | 33.0 | 24.3 | 19.4 | 17.1 |
| 4/6/2013 | 4/21/2013 | 8 | 13 | 13.9 | 54.7 | 26.4 | 25.6 | 18.0 | 16.3 |
| 4/6/2013 | 4/21/2013 | 9 | 13 | 14.0 | 51.7 | 26.3 | 24.8 | 19.4 | 16.6 |
| 4/6/2013 | 4/21/2013 | 10 | 14 | 14.2 | 53.2 | 30.3 | 24.7 | 20.6 | 18.1 |
| 4/6/2013 | 4/21/2013 | 11 | 14 | 14.4 | 55.0 | 31.9 | 24.4 | 18.5 | 17.2 |
| 4/6/2013 | 4/21/2013 | 12 | 15 | 14.4 | 67.6 | 34.1 | 28.5 | 21.3 | 17.8 |
| 4/6/2013 | 4/21/2013 | 13 | 15 | 14.9 | 56.4 | 33.1 | 32.3 | 23.2 | 18.0 |
| 4/6/2013 | 4/21/2013 | 14 | 15 | 14.5 | 56.9 | 33.8 | 31.1 | 24.2 | 19.1 |
| 4/6/2013 | 4/21/2013 | 15 | 15 | 14.4 | 57.0 | 34.0 | 31.4 | 24.2 | 19.0 |
| 4/6/2013 | 4/21/2013 | 16 | 15 | 14.2 | 53.8 | 32.3 | 33.6 | 25.7 | 19.3 |
| 4/6/2013 | 4/21/2013 | 17 | 15 | 14.3 | 54.8 | 31.8 | 34.5 | 26.6 | 20.6 |
| 4/6/2013 | 4/21/2013 | 18 | 15 | 14.0 | 56.6 | 32.8 | 31.2 | 25.0 | 19.6 |
| 4/6/2013 | 4/21/2013 | 19 | 15 | 14.1 | 57.4 | 32.7 | 30.2 | 23.5 | 16.7 |
| 4/6/2013 | 4/21/2013 | 20 | 15 | 14.0 | 60.2 | 30.7 | 25.4 | 21.4 | 17.6 |
| 4/6/2013 | 4/21/2013 | 21 | 15 | 13.8 | 60.4 | 31.2 | 23.8 | 20.2 | 16.8 |
| 4/6/2013 | 4/21/2013 | 22 | 15 | 13.8 | 60.7 | 32.8 | 22.2 | 16.7 | 15.7 |
| 4/6/2013 | 4/21/2013 | 23 | 15 | 13.7 | 54.7 | 24.0 | 20.9 | 16.8 | 15.6 |

## Appendix A. dBA and One-third Octave Metrics for PAPA Reference Leks (cont.).

Table 12. PAPA101 (Big John lek) dBA and one-third octave band metrics, April 6-12, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/6/13 | 4/21/13 | dBA | 346 | 13.7 | 68.9 | 30.8 | 25.8 | 20.1 | 17.1 |
| 4/6/13 | 4/21/13 | 12.5 | 346 | 14.2 | 78.7 | 54.2 | 46.0 | 39.2 | 34.0 |
| 4/6/13 | 4/21/13 | 16 | 346 | 16.2 | 76.3 | 51.7 | 45.7 | 39.3 | 34.7 |
| 4/6/13 | 4/21/13 | 20 | 346 | 17.2 | 75.3 | 50.1 | 48.0 | 42.6 | 37.6 |
| 4/6/13 | 4/21/13 | 25 | 346 | 17.2 | 74.5 | 46.5 | 41.5 | 36.1 | 32.1 |
| 4/6/13 | 4/21/13 | 31.5 | 346 | 15.5 | 71.4 | 44.3 | 41.7 | 36.3 | 31.7 |
| 4/6/13 | 4/21/13 | 40 | 346 | 13.2 | 70.7 | 41.4 | 36.8 | 32.5 | 29.1 |
| 4/6/13 | 4/21/13 | 50 | 346 | 11.1 | 74.7 | 38.9 | 35.5 | 30.7 | 27.3 |
| 4/6/13 | 4/21/13 | 63 | 346 | 8.8 | 81.6 | 37.3 | 34.7 | 29.6 | 26.1 |
| 4/6/13 | 4/21/13 | 80 | 346 | 4.7 | 82.2 | 36.3 | 33.5 | 28.0 | 24.4 |
| 4/6/13 | 4/21/13 | 100 | 346 | 2.7 | 86.2 | 35.4 | 32.0 | 26.4 | 22.6 |
| 4/6/13 | 4/21/13 | 125 | 346 | 0.5 | 74.4 | 33.0 | 30.7 | 24.9 | 20.8 |
| 4/6/13 | 4/21/13 | 160 | 346 | -2.5 | 69.3 | 30.3 | 29.7 | 23.0 | 18.1 |
| 4/6/13 | 4/21/13 | 200 | 346 | -3.1 | 71.6 | 28.5 | 27.2 | 20.3 | 14.9 |
| 4/6/13 | 4/21/13 | 250 | 346 | -3.9 | 64.7 | 26.6 | 24.7 | 17.0 | 11.2 |
| 4/6/13 | 4/21/13 | 315 | 346 | -5.0 | 62.6 | 24.2 | 21.9 | 13.8 | 7.0 |
| 4/6/13 | 4/21/13 | 400 | 346 | -4.8 | 57.7 | 21.5 | 17.2 | 9.2 | 2.4 |
| 4/6/13 | 4/21/13 | 500 | 346 | -4.7 | 53.7 | 19.7 | 14.9 | 5.9 | -0.1 |
| 4/6/13 | 4/21/13 | 630 | 346 | -4.5 | 50.0 | 17.3 | 7.2 | 0.9 | -1.9 |
| 4/6/13 | 4/21/13 | 800 | 346 | -4.0 | 47.6 | 15.8 | 5.6 | -0.4 | -2.0 |
| 4/6/13 | 4/21/13 | 1000 | 346 | -3.3 | 45.5 | 15.5 | 5.5 | -0.4 | -1.7 |
| 4/6/13 | 4/21/13 | 1250 | 346 | -2.6 | 44.8 | 15.1 | 5.0 | -0.1 | -1.1 |
| 4/6/13 | 4/21/13 | 1600 | 346 | -1.8 | 42.5 | 14.8 | 4.9 | 0.4 | -0.5 |
| 4/6/13 | 4/21/13 | 2000 | 346 | -0.8 | 45.7 | 14.7 | 4.7 | 1.0 | 0.4 |
| 4/6/13 | 4/21/13 | 2500 | 346 | 0.1 | 56.8 | 14.4 | 4.3 | 1.7 | 1.2 |
| 4/6/13 | 4/21/13 | 3150 | 346 | 0.3 | 65.1 | 16.2 | 3.8 | 2.5 | 2.1 |
| 4/6/13 | 4/21/13 | 4000 | 346 | -0.2 | 64.3 | 14.4 | 4.2 | 3.4 | 3.1 |
| 4/6/13 | 4/21/13 | 5000 | 346 | -0.4 | 51.0 | 8.9 | 4.8 | 4.2 | 3.9 |
| 4/6/13 | 4/21/13 | 6300 | 346 | -0.7 | 45.7 | 8.3 | 5.4 | 4.9 | 4.7 |
| 4/6/13 | 4/21/13 | 8000 | 346 | -0.9 | 46.0 | 8.5 | 5.8 | 5.5 | 5.3 |
| 4/6/13 | 4/21/13 | 10000 | 346 | -0.7 | 45.6 | 8.4 | 5.9 | 5.6 | 5.4 |
| 4/6/13 | 4/21/13 | 12500 | 346 | -0.9 | 44.7 | 7.4 | 5.3 | 4.8 | 4.6 |
| 4/6/13 | 4/21/13 | 16000 | 346 | -1.2 | 44.8 | 5.6 | 3.5 | 2.9 | 2.6 |
| 4/6/13 | 4/21/13 | 20000 | 346 | -1.0 | 41.3 | 2.8 | 1.4 | 0.4 | 0.0 |

## Appendix A. dBA and One-third Octave Metrics for PAPA Reference Leks (cont.).

Table 13. PAPA102 (Big John lek) hourly dBA metrics, April 6-10, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/6/2013 | 4/10/2013 | 0 | 4 | 14.8 | 48.1 | 25.4 | 24.6 | 21.0 | 18.8 |
| 4/6/2013 | 4/10/2013 | 1 | 4 | 15.0 | 48.1 | 23.7 | 23.0 | 19.2 | 17.0 |
| 4/6/2013 | 4/10/2013 | 2 | 4 | 15.4 | 42.5 | 22.7 | 22.5 | 19.8 | 16.9 |
| 4/6/2013 | 4/10/2013 | 3 | 4 | 15.4 | 39.4 | 23.9 | 24.4 | 20.9 | 18.1 |
| 4/6/2013 | 4/10/2013 | 4 | 4 | 15.6 | 48.4 | 24.9 | 21.8 | 19.2 | 17.5 |
| 4/6/2013 | 4/10/2013 | 5 | 4 | 15.8 | 41.8 | 21.9 | 24.4 | 20.5 | 17.3 |
| 4/6/2013 | 4/10/2013 | 6 | 4 | 15.4 | 44.8 | 25.3 | 28.2 | 24.7 | 19.6 |
| 4/6/2013 | 4/10/2013 | 7 | 4 | 14.6 | 46.8 | 22.5 | 24.2 | 19.9 | 17.9 |
| 4/6/2013 | 4/10/2013 | 8 | 4 | 14.6 | 49.4 | 24.6 | 23.9 | 18.0 | 16.4 |
| 4/6/2013 | 4/10/2013 | 9 | 4 | 14.9 | 49.2 | 24.1 | 23.9 | 18.6 | 17.1 |
| 4/6/2013 | 4/10/2013 | 10 | 4 | 15.4 | 49.5 | 23.1 | 23.2 | 18.4 | 17.3 |
| 4/6/2013 | 4/10/2013 | 11 | 4 | 15.9 | 45.6 | 22.8 | 22.7 | 18.2 | 16.7 |
| 4/6/2013 | 4/10/2013 | 12 | 5 | 15.6 | 68.5 | 33.5 | 24.9 | 20.3 | 17.8 |
| 4/6/2013 | 4/10/2013 | 13 | 5 | 15.5 | 48.1 | 27.9 | 29.8 | 22.6 | 18.5 |
| 4/6/2013 | 4/10/2013 | 14 | 5 | 15.3 | 51.1 | 28.8 | 28.4 | 21.2 | 19.3 |
| 4/6/2013 | 4/10/2013 | 15 | 5 | 15.2 | 47.5 | 29.5 | 28.3 | 23.5 | 19.9 |
| 4/6/2013 | 4/10/2013 | 16 | 5 | 15.1 | 48.9 | 28.0 | 27.8 | 24.1 | 18.4 |
| 4/6/2013 | 4/10/2013 | 17 | 5 | 15.2 | 52.3 | 30.2 | 27.3 | 23.0 | 17.7 |
| 4/6/2013 | 4/10/2013 | 18 | 5 | 14.7 | 52.5 | 31.1 | 30.6 | 21.6 | 19.8 |
| 4/6/2013 | 4/10/2013 | 19 | 5 | 14.9 | 51.1 | 33.7 | 29.2 | 23.2 | 20.6 |
| 4/6/2013 | 4/10/2013 | 20 | 5 | 15.0 | 60.3 | 32.2 | 27.2 | 22.4 | 20.7 |
| 4/6/2013 | 4/10/2013 | 21 | 4 | 14.8 | 52.4 | 32.1 | 26.5 | 22.5 | 19.9 |
| 4/6/2013 | 4/10/2013 | 22 | 4 | 14.7 | 53.8 | 34.7 | 26.3 | 21.5 | 17.9 |
| 4/6/2013 | 4/10/2013 | 23 | 4 | 15.0 | 47.2 | 24.8 | 25.6 | 22.0 | 18.9 |

## Appendix A. dBA and One-third Octave Metrics for PAPA Reference Leks (cont.).

Table 14. PAPA102 (Big John lek) dBA and one-third octave band metrics, April 6-10, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/6/13 | 4/10/13 | dBA | 105 | 14.6 | 68.5 | 29.3 | 25.5 | 20.9 | 17.8 |
| 4/6/13 | 4/10/13 | 12.5 | 105 | 15.8 | 79.2 | 54.1 | 45.0 | 39.2 | 34.5 |
| 4/6/13 | 4/10/13 | 16 | 105 | 18.2 | 76.2 | 51.7 | 46.1 | 40.5 | 35.5 |
| 4/6/13 | 4/10/13 | 20 | 105 | 16.9 | 74.7 | 49.2 | 48.8 | 43.1 | 38.9 |
| 4/6/13 | 4/10/13 | 25 | 105 | 17.5 | 70.5 | 44.3 | 41.5 | 37.2 | 33.3 |
| 4/6/13 | 4/10/13 | 31.5 | 105 | 16.4 | 67.5 | 42.7 | 41.8 | 37.3 | 33.2 |
| 4/6/13 | 4/10/13 | 40 | 105 | 14.1 | 65.9 | 39.4 | 37.2 | 33.4 | 30.1 |
| 4/6/13 | 4/10/13 | 50 | 105 | 11.3 | 75.1 | 37.3 | 35.2 | 31.5 | 28.6 |
| 4/6/13 | 4/10/13 | 63 | 105 | 9.3 | 80.8 | 37.3 | 34.7 | 30.5 | 27.4 |
| 4/6/13 | 4/10/13 | 80 | 105 | 8.7 | 84.1 | 37.3 | 34.0 | 28.9 | 25.2 |
| 4/6/13 | 4/10/13 | 100 | 105 | 5.4 | 84.5 | 37.7 | 32.5 | 27.7 | 24.4 |
| 4/6/13 | 4/10/13 | 125 | 105 | 3.3 | 72.7 | 33.2 | 31.0 | 26.4 | 22.3 |
| 4/6/13 | 4/10/13 | 160 | 105 | 1.1 | 69.5 | 30.5 | 30.4 | 24.0 | 19.8 |
| 4/6/13 | 4/10/13 | 200 | 105 | -0.8 | 69.4 | 28.0 | 27.3 | 21.2 | 16.5 |
| 4/6/13 | 4/10/13 | 250 | 105 | -2.8 | 66.8 | 25.2 | 23.3 | 17.6 | 12.5 |
| 4/6/13 | 4/10/13 | 315 | 105 | -3.4 | 58.2 | 23.0 | 21.2 | 14.5 | 9.0 |
| 4/6/13 | 4/10/13 | 400 | 105 | -4.2 | 58.5 | 20.9 | 16.7 | 10.1 | 4.6 |
| 4/6/13 | 4/10/13 | 500 | 105 | -4.1 | 51.2 | 18.9 | 14.6 | 6.3 | 0.3 |
| 4/6/13 | 4/10/13 | 630 | 105 | -3.7 | 48.4 | 16.3 | 8.5 | 1.3 | -1.3 |
| 4/6/13 | 4/10/13 | 800 | 105 | -3.0 | 47.2 | 14.2 | 6.2 | 0.3 | -1.1 |
| 4/6/13 | 4/10/13 | 1000 | 105 | -2.3 | 43.3 | 14.0 | 5.9 | 0.5 | -0.6 |
| 4/6/13 | 4/10/13 | 1250 | 105 | -1.3 | 40.3 | 14.1 | 5.7 | 1.0 | 0.1 |
| 4/6/13 | 4/10/13 | 1600 | 105 | -0.4 | 37.8 | 14.7 | 5.6 | 1.7 | 0.9 |
| 4/6/13 | 4/10/13 | 2000 | 105 | 0.6 | 38.5 | 13.7 | 4.8 | 2.4 | 1.8 |
| 4/6/13 | 4/10/13 | 2500 | 105 | 1.5 | 39.6 | 12.4 | 4.7 | 3.1 | 2.6 |
| 4/6/13 | 4/10/13 | 3150 | 105 | 2.6 | 40.4 | 10.4 | 4.9 | 3.8 | 3.4 |
| 4/6/13 | 4/10/13 | 4000 | 105 | 0.6 | 42.4 | 9.0 | 5.2 | 4.5 | 4.2 |
| 4/6/13 | 4/10/13 | 5000 | 105 | 0.0 | 48.7 | 8.7 | 5.6 | 5.0 | 4.8 |
| 4/6/13 | 4/10/13 | 6300 | 105 | 0.0 | 42.6 | 8.2 | 5.7 | 5.3 | 5.1 |
| 4/6/13 | 4/10/13 | 8000 | 105 | -0.3 | 39.2 | 7.8 | 5.7 | 5.4 | 5.1 |
| 4/6/13 | 4/10/13 | 10000 | 105 | -0.5 | 38.4 | 7.2 | 5.5 | 5.2 | 4.9 |
| 4/6/13 | 4/10/13 | 12500 | 105 | -0.7 | 36.9 | 6.4 | 5.1 | 4.7 | 4.4 |
| 4/6/13 | 4/10/13 | 16000 | 105 | -0.5 | 34.1 | 5.5 | 4.5 | 3.9 | 3.6 |
| 4/6/13 | 4/10/13 | 20000 | 105 | -0.2 | 30.9 | 4.2 | 3.7 | 2.8 | 2.6 |

## Appendix A. dBA and One-third Octave Metrics for PAPA Reference Leks (cont.).

Table 15. PAPA103 (Jewett Red Flat Reservoir lek) hourly dBA metrics, April 11-25, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/11/2013 | 4/25/2013 | 0 | 14 | 13.2 | 55.1 | 23.6 | 15.1 | 13.7 | 13.5 |
| 4/11/2013 | 4/25/2013 | 1 | 14 | 13.2 | 49.4 | 20.8 | 15.5 | 13.7 | 13.5 |
| 4/11/2013 | 4/25/2013 | 2 | 14 | 13.1 | 42.7 | 16.7 | 14.4 | 13.7 | 13.5 |
| 4/11/2013 | 4/25/2013 | 3 | 14 | 13.1 | 45.4 | 16.4 | 14.0 | 13.6 | 13.4 |
| 4/11/2013 | 4/25/2013 | 4 | 14 | 13.1 | 50.8 | 21.8 | 15.5 | 13.6 | 13.5 |
| 4/11/2013 | 4/25/2013 | 5 | 14 | 13.1 | 46.5 | 20.0 | 19.9 | 16.6 | 13.6 |
| 4/11/2013 | 4/25/2013 | 6 | 14 | 13.1 | 47.2 | 19.7 | 20.9 | 17.0 | 15.3 |
| 4/11/2013 | 4/25/2013 | 7 | 13 | 13.1 | 47.5 | 19.6 | 18.7 | 16.2 | 14.4 |
| 4/11/2013 | 4/25/2013 | 8 | 13 | 13.3 | 49.8 | 25.3 | 21.9 | 15.6 | 14.8 |
| 4/11/2013 | 4/25/2013 | 9 | 13 | 13.6 | 57.4 | 28.9 | 26.5 | 19.6 | 14.5 |
| 4/11/2013 | 4/25/2013 | 10 | 13 | 13.7 | 50.5 | 28.3 | 29.7 | 20.4 | 15.9 |
| 4/11/2013 | 4/25/2013 | 11 | 13 | 13.7 | 56.2 | 28.4 | 29.9 | 22.5 | 15.4 |
| 4/11/2013 | 4/25/2013 | 12 | 13 | 13.9 | 55.0 | 33.0 | 32.2 | 24.0 | 18.4 |
| 4/11/2013 | 4/25/2013 | 13 | 13 | 13.9 | 84.3 | 42.2 | 33.8 | 24.3 | 18.0 |
| 4/11/2013 | 4/25/2013 | 14 | 14 | 13.9 | 53.9 | 31.9 | 33.4 | 26.6 | 20.0 |
| 4/11/2013 | 4/25/2013 | 15 | 14 | 13.8 | 55.0 | 31.5 | 33.0 | 25.1 | 17.6 |
| 4/11/2013 | 4/25/2013 | 16 | 14 | 13.6 | 53.4 | 32.6 | 33.2 | 26.1 | 18.6 |
| 4/11/2013 | 4/25/2013 | 17 | 14 | 13.5 | 56.5 | 31.7 | 31.7 | 24.3 | 17.2 |
| 4/11/2013 | 4/25/2013 | 18 | 14 | 13.4 | 59.2 | 33.5 | 29.8 | 21.4 | 16.4 |
| 4/11/2013 | 4/25/2013 | 19 | 14 | 13.4 | 60.1 | 35.4 | 26.7 | 17.2 | 14.0 |
| 4/11/2013 | 4/25/2013 | 20 | 14 | 13.3 | 53.6 | 29.6 | 23.3 | 15.1 | 13.7 |
| 4/11/2013 | 4/25/2013 | 21 | 14 | 13.2 | 64.3 | 32.4 | 24.4 | 15.4 | 13.7 |
| 4/11/2013 | 4/25/2013 | 22 | 14 | 13.2 | 57.5 | 32.5 | 24.0 | 14.3 | 13.5 |
| 4/11/2013 | 4/25/2013 | 23 | 14 | 13.2 | 51.7 | 23.9 | 20.1 | 13.7 | 13.5 |

## Appendix A. dBA and One-third Octave Metrics for PAPA Reference Leks (cont.).

Table 16. PAPA103 (Jewett Red Flat Reservoir lek) dBA and one-third octave band metrics, April 11-25, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/11/13 | 4/25/13 | dBA | 329 | 13.1 | 84.3 | 32.0 | 24.1 | 16.4 | 14.2 |
| 4/11/13 | 4/25/13 | 12.5 | 329 | 8.8 | 77.0 | 46.2 | 34.9 | 30.1 | 26.1 |
| 4/11/13 | 4/25/13 | 16 | 329 | 9.9 | 74.2 | 43.6 | 34.0 | 29.5 | 25.9 |
| 4/11/13 | 4/25/13 | 20 | 329 | 10.8 | 73.2 | 41.6 | 34.0 | 29.3 | 25.6 |
| 4/11/13 | 4/25/13 | 25 | 329 | 9.7 | 69.6 | 37.9 | 32.8 | 27.3 | 23.7 |
| 4/11/13 | 4/25/13 | 31.5 | 329 | 9.3 | 68.1 | 36.9 | 34.8 | 28.9 | 24.6 |
| 4/11/13 | 4/25/13 | 40 | 329 | 4.2 | 64.1 | 34.0 | 31.8 | 23.5 | 20.2 |
| 4/11/13 | 4/25/13 | 50 | 329 | 1.8 | 66.3 | 32.5 | 31.4 | 21.6 | 18.3 |
| 4/11/13 | 4/25/13 | 63 | 329 | -0.4 | 77.8 | 32.1 | 30.8 | 20.3 | 16.3 |
| 4/11/13 | 4/25/13 | 80 | 329 | -1.1 | 77.5 | 31.8 | 30.0 | 18.8 | 14.1 |
| 4/11/13 | 4/25/13 | 100 | 329 | -2.2 | 77.6 | 33.5 | 29.3 | 18.0 | 12.9 |
| 4/11/13 | 4/25/13 | 125 | 329 | -4.2 | 86.8 | 36.2 | 27.9 | 18.2 | 11.2 |
| 4/11/13 | 4/25/13 | 160 | 329 | -4.6 | 77.2 | 29.5 | 26.4 | 16.8 | 8.3 |
| 4/11/13 | 4/25/13 | 200 | 329 | -4.8 | 68.5 | 27.2 | 24.5 | 14.9 | 6.1 |
| 4/11/13 | 4/25/13 | 250 | 329 | -5.2 | 75.4 | 26.5 | 20.4 | 10.0 | 2.7 |
| 4/11/13 | 4/25/13 | 315 | 329 | -5.2 | 69.6 | 22.8 | 16.7 | 7.2 | 0.1 |
| 4/11/13 | 4/25/13 | 400 | 329 | -5.3 | 72.7 | 21.0 | 12.9 | 4.4 | -1.6 |
| 4/11/13 | 4/25/13 | 500 | 329 | -5.0 | 68.8 | 19.0 | 11.4 | 2.5 | -2.4 |
| 4/11/13 | 4/25/13 | 630 | 329 | -4.7 | 65.3 | 16.8 | 7.8 | -0.9 | -2.5 |
| 4/11/13 | 4/25/13 | 800 | 329 | -4.3 | 67.7 | 16.8 | 6.7 | -1.3 | -2.3 |
| 4/11/13 | 4/25/13 | 1000 | 329 | -3.5 | 70.4 | 18.4 | 5.4 | -0.9 | -1.8 |
| 4/11/13 | 4/25/13 | 1250 | 329 | -2.8 | 71.8 | 19.5 | 4.6 | -0.4 | -1.2 |
| 4/11/13 | 4/25/13 | 1600 | 329 | -1.9 | 69.8 | 19.3 | 4.7 | 0.3 | -0.5 |
| 4/11/13 | 4/25/13 | 2000 | 329 | -1.0 | 65.6 | 18.2 | 4.4 | 1.0 | 0.3 |
| 4/11/13 | 4/25/13 | 2500 | 329 | -0.1 | 67.0 | 15.8 | 3.7 | 1.7 | 1.1 |
| 4/11/13 | 4/25/13 | 3150 | 329 | 1.0 | 65.6 | 13.9 | 3.7 | 2.4 | 2.0 |
| 4/11/13 | 4/25/13 | 4000 | 329 | 2.0 | 63.4 | 11.3 | 3.9 | 3.1 | 2.8 |
| 4/11/13 | 4/25/13 | 5000 | 329 | 1.5 | 61.3 | 10.2 | 4.2 | 3.8 | 3.6 |
| 4/11/13 | 4/25/13 | 6300 | 329 | 1.4 | 60.1 | 9.4 | 4.6 | 4.3 | 4.2 |
| 4/11/13 | 4/25/13 | 8000 | 329 | 1.6 | 56.5 | 8.7 | 5.0 | 4.7 | 4.6 |
| 4/11/13 | 4/25/13 | 10000 | 329 | 1.3 | 55.4 | 8.6 | 5.1 | 4.8 | 4.6 |
| 4/11/13 | 4/25/13 | 12500 | 329 | 0.8 | 54.6 | 7.6 | 4.2 | 3.8 | 3.6 |
| 4/11/13 | 4/25/13 | 16000 | 329 | -0.4 | 49.4 | 4.8 | 1.7 | 1.1 | 0.9 |
| 4/11/13 | 4/25/13 | 20000 | 329 | -1.9 | 43.8 | 1.1 | -0.6 | -1.1 | -1.3 |

## Appendix A. dBA and One-third Octave Metrics for PAPA Reference Leks (cont.).

Table 17. PAPA104 (Onion Springs 2 lek) hourly dBA metrics, April 11-25, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/11/2013 | 4/25/2013 | 0 | 14 | 13.8 | 52.2 | 25.3 | 21.9 | 15.5 | 14.2 |
| 4/11/2013 | 4/25/2013 | 1 | 14 | 13.8 | 53.4 | 27.2 | 28.5 | 14.8 | 14.2 |
| 4/11/2013 | 4/25/2013 | 2 | 14 | 13.8 | 42.2 | 27.2 | 22.8 | 14.4 | 14.1 |
| 4/11/2013 | 4/25/2013 | 3 | 14 | 13.8 | 58.6 | 26.2 | 20.4 | 14.5 | 14.1 |
| 4/11/2013 | 4/25/2013 | 4 | 14 | 13.7 | 55.7 | 28.6 | 24.1 | 14.6 | 14.3 |
| 4/11/2013 | 4/25/2013 | 5 | 14 | 13.7 | 52.6 | 34.3 | 38.2 | 34.2 | 16.8 |
| 4/11/2013 | 4/25/2013 | 6 | 13 | 13.7 | 51.9 | 34.1 | 36.2 | 28.8 | 16.9 |
| 4/11/2013 | 4/25/2013 | 7 | 13 | 13.7 | 51.4 | 28.9 | 28.0 | 18.0 | 15.0 |
| 4/11/2013 | 4/25/2013 | 8 | 13 | 14.0 | 61.4 | 28.8 | 26.5 | 16.5 | 14.8 |
| 4/11/2013 | 4/25/2013 | 9 | 13 | 14.3 | 62.8 | 28.6 | 28.0 | 19.1 | 15.5 |
| 4/11/2013 | 4/25/2013 | 10 | 13 | 14.3 | 65.5 | 29.6 | 30.9 | 19.0 | 15.3 |
| 4/11/2013 | 4/25/2013 | 11 | 13 | 14.3 | 56.6 | 30.3 | 28.2 | 20.8 | 17.0 |
| 4/11/2013 | 4/25/2013 | 12 | 13 | 14.5 | 78.1 | 39.6 | 31.7 | 23.8 | 18.1 |
| 4/11/2013 | 4/25/2013 | 13 | 13 | 14.5 | 64.3 | 33.4 | 34.5 | 25.7 | 18.2 |
| 4/11/2013 | 4/25/2013 | 14 | 13 | 14.5 | 49.3 | 30.1 | 33.3 | 26.5 | 20.3 |
| 4/11/2013 | 4/25/2013 | 15 | 13 | 14.5 | 55.8 | 31.4 | 32.6 | 24.3 | 19.0 |
| 4/11/2013 | 4/25/2013 | 16 | 14 | 14.4 | 52.2 | 30.5 | 31.9 | 24.6 | 18.7 |
| 4/11/2013 | 4/25/2013 | 17 | 14 | 14.1 | 54.2 | 30.4 | 31.2 | 22.5 | 15.8 |
| 4/11/2013 | 4/25/2013 | 18 | 14 | 14.1 | 55.1 | 31.8 | 30.0 | 21.3 | 16.5 |
| 4/11/2013 | 4/25/2013 | 19 | 14 | 14.0 | 57.1 | 33.5 | 28.0 | 17.2 | 14.4 |
| 4/11/2013 | 4/25/2013 | 20 | 14 | 14.0 | 60.7 | 30.9 | 33.1 | 19.6 | 14.5 |
| 4/11/2013 | 4/25/2013 | 21 | 14 | 13.9 | 64.7 | 33.0 | 32.3 | 23.5 | 15.3 |
| 4/11/2013 | 4/25/2013 | 22 | 14 | 13.9 | 53.4 | 29.5 | 28.8 | 16.1 | 14.3 |
| 4/11/2013 | 4/25/2013 | 23 | 14 | 13.9 | 49.8 | 25.2 | 27.4 | 15.6 | 14.1 |

## Appendix A. dBA and One-third Octave Metrics for PAPA Reference Leks (cont.).

Table 18. PAPA104 (Onion Springs 2 lek) dBA and one-third octave band metrics, April 11-25, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/11/13 | 4/25/13 | dBA | 326 | 13.7 | 78.1 | 31.7 | 30.0 | 19.7 | 15.2 |
| 4/11/13 | 4/25/13 | 12.5 | 326 | 9.6 | 78.4 | 41.8 | 33.9 | 29.7 | 25.9 |
| 4/11/13 | 4/25/13 | 16 | 326 | 11.4 | 69.7 | 38.6 | 34.0 | 29.4 | 26.0 |
| 4/11/13 | 4/25/13 | 20 | 326 | 11.9 | 67.2 | 37.2 | 33.8 | 29.1 | 25.7 |
| 4/11/13 | 4/25/13 | 25 | 326 | 10.6 | 67.7 | 34.6 | 33.0 | 27.1 | 23.9 |
| 4/11/13 | 4/25/13 | 31.5 | 326 | 9.3 | 67.8 | 33.8 | 33.0 | 25.5 | 22.3 |
| 4/11/13 | 4/25/13 | 40 | 326 | 6.0 | 66.6 | 32.4 | 32.2 | 23.1 | 20.1 |
| 4/11/13 | 4/25/13 | 50 | 326 | 2.8 | 69.1 | 31.9 | 31.5 | 21.2 | 17.8 |
| 4/11/13 | 4/25/13 | 63 | 326 | -0.1 | 76.7 | 32.0 | 30.5 | 19.4 | 15.6 |
| 4/11/13 | 4/25/13 | 80 | 326 | -2.1 | 76.4 | 32.4 | 30.1 | 18.9 | 14.6 |
| 4/11/13 | 4/25/13 | 100 | 326 | -2.4 | 83.5 | 34.3 | 29.6 | 19.9 | 13.9 |
| 4/11/13 | 4/25/13 | 125 | 326 | -3.9 | 83.7 | 36.2 | 30.6 | 20.4 | 12.5 |
| 4/11/13 | 4/25/13 | 160 | 326 | -4.1 | 77.4 | 30.9 | 30.2 | 19.4 | 10.6 |
| 4/11/13 | 4/25/13 | 200 | 326 | -4.2 | 69.6 | 29.3 | 29.2 | 18.4 | 8.7 |
| 4/11/13 | 4/25/13 | 250 | 326 | -4.7 | 74.1 | 28.9 | 27.2 | 16.7 | 6.3 |
| 4/11/13 | 4/25/13 | 315 | 326 | -4.6 | 61.9 | 29.7 | 24.9 | 14.2 | 3.6 |
| 4/11/13 | 4/25/13 | 400 | 326 | -4.4 | 69.2 | 25.6 | 21.6 | 11.0 | 1.0 |
| 4/11/13 | 4/25/13 | 500 | 326 | -4.1 | 72.7 | 23.8 | 19.0 | 7.1 | -1.0 |
| 4/11/13 | 4/25/13 | 630 | 326 | -3.9 | 74.2 | 21.1 | 10.7 | 2.1 | -1.5 |
| 4/11/13 | 4/25/13 | 800 | 326 | -3.5 | 69.3 | 19.0 | 9.8 | 1.2 | -1.2 |
| 4/11/13 | 4/25/13 | 1000 | 326 | -2.9 | 63.1 | 17.8 | 9.6 | 1.4 | -0.7 |
| 4/11/13 | 4/25/13 | 1250 | 326 | -2.2 | 67.5 | 19.0 | 9.2 | 1.3 | -0.2 |
| 4/11/13 | 4/25/13 | 1600 | 326 | -1.2 | 63.2 | 18.0 | 7.8 | 1.4 | 0.4 |
| 4/11/13 | 4/25/13 | 2000 | 326 | -0.3 | 62.5 | 16.8 | 7.4 | 1.9 | 1.1 |
| 4/11/13 | 4/25/13 | 2500 | 326 | 0.6 | 59.7 | 14.3 | 5.9 | 2.5 | 1.9 |
| 4/11/13 | 4/25/13 | 3150 | 326 | 1.6 | 55.3 | 11.6 | 5.2 | 3.2 | 2.7 |
| 4/11/13 | 4/25/13 | 4000 | 326 | 2.6 | 56.6 | 10.1 | 5.4 | 4.0 | 3.6 |
| 4/11/13 | 4/25/13 | 5000 | 326 | 2.3 | 59.7 | 11.0 | 5.5 | 4.6 | 4.2 |
| 4/11/13 | 4/25/13 | 6300 | 326 | 1.4 | 62.5 | 10.6 | 5.6 | 5.0 | 4.7 |
| 4/11/13 | 4/25/13 | 8000 | 326 | 0.8 | 64.4 | 9.9 | 5.7 | 5.4 | 5.2 |
| 4/11/13 | 4/25/13 | 10000 | 326 | 0.9 | 40.4 | 8.1 | 5.8 | 5.5 | 5.3 |
| 4/11/13 | 4/25/13 | 12500 | 326 | -0.7 | 39.9 | 7.1 | 4.8 | 4.4 | 4.2 |
| 4/11/13 | 4/25/13 | 16000 | 326 | -0.8 | 45.3 | 5.7 | 3.3 | 2.9 | 2.7 |
| 4/11/13 | 4/25/13 | 20000 | 326 | -1.5 | 35.2 | 2.6 | 0.9 | 0.4 | 0.3 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks.

Table 19. PAPA001 (Big Fred lek) hourly dBA metrics, April 5-7, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/5/2013 | 4/7/2013 | 0 | 2 | 33.0 | 67.1 | 43.6 | 44.0 | 41.2 | 36.6 |
| 4/5/2013 | 4/7/2013 | 1 | 2 | 31.6 | 60.6 | 42.4 | 44.0 | 39.7 | 37.2 |
| 4/5/2013 | 4/7/2013 | 2 | 2 | 31.7 | 60.7 | 41.1 | 43.6 | 38.2 | 35.8 |
| 4/5/2013 | 4/7/2013 | 3 | 2 | 30.8 | 63.2 | 38.9 | 39.3 | 37.1 | 34.8 |
| 4/5/2013 | 4/7/2013 | 4 | 2 | 34.6 | 60.4 | 41.8 | 44.4 | 40.2 | 37.1 |
| 4/5/2013 | 4/7/2013 | 5 | 2 | 32.6 | 60.4 | 41.3 | 44.3 | 39.2 | 37.3 |
| 4/5/2013 | 4/7/2013 | 6 | 2 | 32.7 | 56.0 | 40.4 | 42.0 | 39.1 | 36.2 |
| 4/5/2013 | 4/7/2013 | 7 | 2 | 27.1 | 45.1 | 33.9 | 36.5 | 32.6 | 29.4 |
| 4/5/2013 | 4/7/2013 | 8 | 2 | 28.5 | 48.6 | 33.4 | 34.9 | 32.5 | 31.0 |
| 4/5/2013 | 4/7/2013 | 9 | 2 | 26.2 | 45.4 | 33.2 | 34.6 | 32.6 | 30.8 |
| 4/5/2013 | 4/7/2013 | 10 | 2 | 22.1 | 45.9 | 33.1 | 34.2 | 31.2 | 28.6 |
| 4/5/2013 | 4/7/2013 | 11 | 2 | 23.1 | 53.7 | 34.1 | 35.4 | 30.9 | 27.9 |
| 4/5/2013 | 4/7/2013 | 12 | 2 | 26.1 | 45.9 | 33.4 | 35.5 | 32.3 | 29.3 |
| 4/5/2013 | 4/7/2013 | 13 | 2 | 28.4 | 49.2 | 35.6 | 37.6 | 34.2 | 31.7 |
| 4/5/2013 | 4/7/2013 | 14 | 2 | 25.8 | 55.2 | 36.1 | 37.8 | 33.3 | 29.3 |
| 4/6/2013 | 4/6/2013 | 15 | 1 | 29.4 | 48.6 | 34.8 | 36.1 | 33.9 | 32.0 |
| 4/5/2013 | 4/7/2013 | 16 | 2 | 26.2 | 53.0 | 39.8 | 40.9 | 36.7 | 33.8 |
| 4/5/2013 | 4/7/2013 | 17 | 2 | 28.6 | 51.4 | 37.6 | 38.8 | 36.0 | 33.7 |
| 4/5/2013 | 4/7/2013 | 18 | 2 | 30.6 | 62.1 | 38.8 | 39.2 | 36.4 | 34.4 |
| 4/5/2013 | 4/7/2013 | 19 | 2 | 30.4 | 61.8 | 39.5 | 40.9 | 37.4 | 34.7 |
| 4/5/2013 | 4/7/2013 | 20 | 2 | 34.7 | 65.7 | 41.3 | 41.9 | 38.9 | 37.1 |
| 4/5/2013 | 4/7/2013 | 21 | 2 | 33.0 | 60.7 | 41.2 | 41.8 | 39.4 | 37.3 |
| 4/5/2013 | 4/7/2013 | 22 | 2 | 34.8 | 59.6 | 42.3 | 43.6 | 41.0 | 39.3 |
| 4/5/2013 | 4/7/2013 | 23 | 2 | 33.8 | 58.2 | 44.1 | 45.3 | 41.8 | 38.7 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 20. PAPA001 (Big Fred lek) dBA and one-third octave band metrics, April 5-7, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/5/13 | 4/7/13 | dBA | 47 | 22.1 | 67.1 | 39.8 | 40.3 | 36.9 | 34.8 |
| 4/5/13 | 4/7/13 | 12.5 | 47 | 22.0 | 73.0 | 47.5 | 48.2 | 43.3 | 38.7 |
| 4/5/13 | 4/7/13 | 16 | 47 | 27.0 | 70.5 | 48.3 | 49.6 | 46.0 | 42.2 |
| 4/5/13 | 4/7/13 | 20 | 47 | 34.6 | 74.0 | 53.9 | 56.0 | 52.2 | 48.1 |
| 4/5/13 | 4/7/13 | 25 | 47 | 34.9 | 67.2 | 51.6 | 53.2 | 49.0 | 45.7 |
| 4/5/13 | 4/7/13 | 31.5 | 47 | 40.2 | 75.0 | 63.8 | 66.4 | 61.5 | 56.1 |
| 4/5/13 | 4/7/13 | 40 | 47 | 32.8 | 66.1 | 51.7 | 52.5 | 49.8 | 47.3 |
| 4/5/13 | 4/7/13 | 50 | 47 | 35.5 | 68.7 | 53.5 | 55.5 | 52.9 | 50.1 |
| 4/5/13 | 4/7/13 | 63 | 47 | 34.9 | 69.5 | 52.9 | 54.8 | 52.0 | 49.6 |
| 4/5/13 | 4/7/13 | 80 | 47 | 29.0 | 71.7 | 50.2 | 51.4 | 48.3 | 45.9 |
| 4/5/13 | 4/7/13 | 100 | 47 | 28.8 | 66.5 | 49.2 | 49.4 | 45.9 | 43.0 |
| 4/5/13 | 4/7/13 | 125 | 47 | 23.7 | 67.1 | 45.8 | 44.6 | 40.4 | 37.6 |
| 4/5/13 | 4/7/13 | 160 | 47 | 19.5 | 67.1 | 42.6 | 41.3 | 36.7 | 32.2 |
| 4/5/13 | 4/7/13 | 200 | 47 | 17.7 | 66.6 | 39.7 | 39.8 | 35.4 | 30.1 |
| 4/5/13 | 4/7/13 | 250 | 47 | 13.7 | 61.5 | 37.7 | 38.3 | 33.2 | 28.5 |
| 4/5/13 | 4/7/13 | 315 | 47 | 10.8 | 57.2 | 35.2 | 36.3 | 31.6 | 26.1 |
| 4/5/13 | 4/7/13 | 400 | 47 | 8.0 | 55.6 | 32.9 | 35.0 | 30.4 | 24.8 |
| 4/5/13 | 4/7/13 | 500 | 47 | 3.5 | 53.2 | 26.5 | 27.6 | 22.7 | 16.5 |
| 4/5/13 | 4/7/13 | 630 | 47 | 1.8 | 50.8 | 22.9 | 23.0 | 18.5 | 13.5 |
| 4/5/13 | 4/7/13 | 800 | 47 | 2.1 | 49.8 | 23.7 | 24.5 | 19.8 | 14.7 |
| 4/5/13 | 4/7/13 | 1000 | 47 | 2.4 | 48.3 | 24.9 | 26.0 | 21.0 | 15.8 |
| 4/5/13 | 4/7/13 | 1250 | 47 | 2.2 | 46.8 | 25.3 | 26.3 | 20.7 | 14.9 |
| 4/5/13 | 4/7/13 | 1600 | 47 | 1.6 | 44.8 | 23.8 | 24.5 | 19.4 | 13.1 |
| 4/5/13 | 4/7/13 | 2000 | 47 | 1.8 | 58.6 | 22.4 | 21.8 | 17.3 | 12.6 |
| 4/5/13 | 4/7/13 | 2500 | 47 | 2.3 | 63.1 | 19.8 | 15.2 | 10.2 | 6.3 |
| 4/5/13 | 4/7/13 | 3150 | 47 | 3.0 | 57.3 | 14.5 | 9.7 | 5.2 | 4.1 |
| 4/5/13 | 4/7/13 | 4000 | 47 | 3.7 | 47.8 | 12.4 | 5.2 | 4.5 | 4.2 |
| 4/5/13 | 4/7/13 | 5000 | 47 | 4.3 | 47.3 | 11.9 | 5.3 | 5.0 | 4.8 |
| 4/5/13 | 4/7/13 | 6300 | 47 | 4.2 | 44.6 | 11.9 | 5.5 | 5.3 | 5.2 |
| 4/5/13 | 4/7/13 | 8000 | 47 | 3.4 | 43.8 | 11.9 | 5.5 | 5.3 | 5.2 |
| 4/5/13 | 4/7/13 | 10000 | 47 | 2.3 | 41.6 | 10.4 | 5.1 | 5.0 | 4.8 |
| 4/5/13 | 4/7/13 | 12500 | 47 | 1.6 | 39.8 | 9.2 | 4.3 | 4.2 | 4.1 |
| 4/5/13 | 4/7/13 | 16000 | 47 | 0.6 | 37.4 | 7.6 | 3.3 | 3.2 | 3.1 |
| 4/5/13 | 4/7/13 | 20000 | 47 | 1.3 | 33.4 | 4.8 | 1.9 | 1.8 | 1.7 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 21. PAPA002 (Little Fred lek) hourly dBA metrics, April 5-7, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/5/2013 | 4/7/2013 | 0 | 2 | 20.6 | 47.7 | 31.3 | 31.4 | 27.6 | 25.1 |
| 4/5/2013 | 4/7/2013 | 1 | 2 | 22.4 | 49.3 | 29.4 | 31.0 | 26.9 | 24.9 |
| 4/5/2013 | 4/7/2013 | 2 | 2 | 23.9 | 52.1 | 32.1 | 34.5 | 30.5 | 26.0 |
| 4/5/2013 | 4/7/2013 | 3 | 2 | 24.3 | 55.9 | 31.3 | 31.0 | 28.8 | 27.2 |
| 4/5/2013 | 4/7/2013 | 4 | 2 | 25.6 | 48.4 | 31.5 | 33.2 | 29.8 | 27.4 |
| 4/5/2013 | 4/7/2013 | 5 | 2 | 25.9 | 50.3 | 34.7 | 35.6 | 32.6 | 29.6 |
| 4/5/2013 | 4/7/2013 | 6 | 2 | 26.0 | 46.3 | 32.5 | 34.1 | 31.1 | 29.1 |
| 4/5/2013 | 4/7/2013 | 7 | 2 | 24.8 | 49.4 | 33.8 | 36.0 | 32.3 | 28.9 |
| 4/5/2013 | 4/7/2013 | 8 | 2 | 24.6 | 55.7 | 34.7 | 36.8 | 32.4 | 29.2 |
| 4/5/2013 | 4/7/2013 | 9 | 2 | 24.3 | 57.0 | 34.4 | 35.1 | 31.5 | 28.7 |
| 4/5/2013 | 4/7/2013 | 10 | 2 | 21.2 | 46.6 | 30.5 | 32.9 | 27.8 | 25.0 |
| 4/5/2013 | 4/7/2013 | 11 | 2 | 19.5 | 52.9 | 29.2 | 28.4 | 25.1 | 23.4 |
| 4/6/2013 | 4/6/2013 | 12 | 1 | 20.1 | 39.6 | 25.7 | 27.4 | 23.5 | 21.7 |
| 4/5/2013 | 4/7/2013 | 13 | 2 | 20.1 | 48.6 | 32.7 | 35.9 | 27.0 | 23.2 |
| 4/5/2013 | 4/7/2013 | 14 | 2 | 21.9 | 49.2 | 32.0 | 34.6 | 29.7 | 25.8 |
| 4/5/2013 | 4/7/2013 | 15 | 2 | 20.6 | 56.8 | 38.6 | 39.5 | 31.1 | 23.9 |
| 4/5/2013 | 4/7/2013 | 16 | 2 | 19.5 | 60.2 | 42.1 | 39.1 | 33.8 | 29.1 |
| 4/5/2013 | 4/7/2013 | 17 | 2 | 19.6 | 56.9 | 38.5 | 38.1 | 31.5 | 26.9 |
| 4/5/2013 | 4/7/2013 | 18 | 2 | 19.1 | 55.6 | 39.2 | 37.8 | 32.5 | 26.4 |
| 4/5/2013 | 4/7/2013 | 19 | 2 | 18.8 | 51.3 | 33.6 | 36.8 | 28.5 | 22.2 |
| 4/5/2013 | 4/7/2013 | 20 | 2 | 20.9 | 51.4 | 28.6 | 29.7 | 25.8 | 23.6 |
| 4/5/2013 | 4/7/2013 | 21 | 2 | 19.0 | 46.4 | 25.6 | 26.9 | 24.0 | 21.4 |
| 4/5/2013 | 4/7/2013 | 22 | 2 | 19.2 | 41.7 | 26.1 | 28.1 | 24.1 | 21.9 |
| 4/5/2013 | 4/7/2013 | 23 | 2 | 20.5 | 47.4 | 30.4 | 32.2 | 26.8 | 23.8 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 22. PAPA002 (Little Fred lek) dBA and one-third octave band metrics, April 5-7, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/5/13 | 4/7/13 | dBA | 47 | 18.8 | 60.2 | 34.7 | 33.1 | 28.4 | 25.2 |
| 4/5/13 | 4/7/13 | 12.5 | 47 | 23.9 | 78.7 | 55.6 | 54.5 | 47.3 | 41.0 |
| 4/5/13 | 4/7/13 | 16 | 47 | 29.8 | 75.3 | 53.3 | 51.9 | 48.1 | 44.3 |
| 4/5/13 | 4/7/13 | 20 | 47 | 36.9 | 77.4 | 57.5 | 58.2 | 54.8 | 50.6 |
| 4/5/13 | 4/7/13 | 25 | 47 | 30.4 | 74.0 | 53.4 | 55.7 | 46.5 | 42.7 |
| 4/5/13 | 4/7/13 | 31.5 | 47 | 31.2 | 72.5 | 50.8 | 52.2 | 47.1 | 43.0 |
| 4/5/13 | 4/7/13 | 40 | 47 | 29.4 | 70.4 | 46.4 | 46.5 | 43.5 | 40.8 |
| 4/5/13 | 4/7/13 | 50 | 47 | 30.6 | 67.4 | 45.2 | 46.2 | 43.3 | 40.8 |
| 4/5/13 | 4/7/13 | 63 | 47 | 27.7 | 65.6 | 42.8 | 44.2 | 40.2 | 37.0 |
| 4/5/13 | 4/7/13 | 80 | 47 | 23.3 | 71.6 | 41.0 | 42.5 | 37.2 | 34.0 |
| 4/5/13 | 4/7/13 | 100 | 47 | 21.6 | 70.5 | 39.4 | 39.9 | 35.6 | 32.2 |
| 4/5/13 | 4/7/13 | 125 | 47 | 18.9 | 62.4 | 36.7 | 37.2 | 32.9 | 30.0 |
| 4/5/13 | 4/7/13 | 160 | 47 | 16.7 | 62.1 | 36.7 | 36.5 | 31.5 | 27.4 |
| 4/5/13 | 4/7/13 | 200 | 47 | 13.6 | 59.3 | 32.9 | 32.5 | 28.8 | 25.4 |
| 4/5/13 | 4/7/13 | 250 | 47 | 12.2 | 55.4 | 30.4 | 31.4 | 25.9 | 22.2 |
| 4/5/13 | 4/7/13 | 315 | 47 | 10.3 | 55.0 | 29.2 | 29.0 | 24.5 | 20.8 |
| 4/5/13 | 4/7/13 | 400 | 47 | 5.0 | 54.0 | 25.8 | 25.8 | 20.9 | 16.4 |
| 4/5/13 | 4/7/13 | 500 | 47 | 1.0 | 51.5 | 23.8 | 21.5 | 16.7 | 12.2 |
| 4/5/13 | 4/7/13 | 630 | 47 | -0.7 | 46.9 | 22.4 | 19.9 | 13.4 | 9.0 |
| 4/5/13 | 4/7/13 | 800 | 47 | -1.5 | 42.0 | 21.4 | 18.0 | 9.9 | 5.5 |
| 4/5/13 | 4/7/13 | 1000 | 47 | -1.3 | 42.5 | 21.2 | 15.2 | 7.1 | 2.8 |
| 4/5/13 | 4/7/13 | 1250 | 47 | -0.9 | 40.5 | 21.1 | 10.6 | 4.0 | 1.5 |
| 4/5/13 | 4/7/13 | 1600 | 47 | -0.2 | 41.8 | 21.1 | 8.1 | 2.5 | 1.5 |
| 4/5/13 | 4/7/13 | 2000 | 47 | 0.6 | 42.4 | 19.5 | 4.5 | 2.5 | 1.8 |
| 4/5/13 | 4/7/13 | 2500 | 47 | 1.5 | 44.2 | 17.7 | 4.4 | 2.9 | 2.5 |
| 4/5/13 | 4/7/13 | 3150 | 47 | 2.3 | 41.9 | 14.9 | 4.1 | 3.4 | 3.1 |
| 4/5/13 | 4/7/13 | 4000 | 47 | 3.1 | 43.5 | 12.3 | 4.8 | 4.0 | 3.7 |
| 4/5/13 | 4/7/13 | 5000 | 47 | 3.7 | 53.6 | 12.9 | 5.1 | 4.4 | 4.2 |
| 4/5/13 | 4/7/13 | 6300 | 47 | 2.7 | 53.7 | 10.9 | 4.9 | 4.6 | 4.4 |
| 4/5/13 | 4/7/13 | 8000 | 47 | 2.1 | 38.2 | 8.3 | 4.7 | 4.5 | 4.4 |
| 4/5/13 | 4/7/13 | 10000 | 47 | 1.8 | 36.1 | 7.3 | 4.4 | 4.3 | 4.1 |
| 4/5/13 | 4/7/13 | 12500 | 47 | 0.4 | 35.8 | 6.7 | 3.9 | 3.8 | 3.6 |
| 4/5/13 | 4/7/13 | 16000 | 47 | 0.3 | 34.9 | 6.1 | 3.1 | 3.0 | 2.9 |
| 4/5/13 | 4/7/13 | 20000 | 47 | 1.1 | 34.8 | 4.6 | 1.8 | 1.8 | 1.7 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 23. PAPA003 (Lower Sand Springs Draw) hourly dBA metrics, April 5-7, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/5/2013 | 4/7/2013 | 0 | 2 | 21.5 | 49.0 | 34.5 | 35.0 | 29.6 | 26.5 |
| 4/5/2013 | 4/7/2013 | 1 | 2 | 21.9 | 51.3 | 30.5 | 31.5 | 29.0 | 25.7 |
| 4/5/2013 | 4/7/2013 | 2 | 2 | 22.5 | 47.8 | 32.7 | 35.1 | 30.8 | 26.8 |
| 4/5/2013 | 4/7/2013 | 3 | 2 | 23.8 | 52.2 | 30.4 | 31.0 | 28.1 | 26.1 |
| 4/5/2013 | 4/7/2013 | 4 | 2 | 25.0 | 49.6 | 33.4 | 34.4 | 31.6 | 27.5 |
| 4/5/2013 | 4/7/2013 | 5 | 2 | 24.9 | 51.7 | 37.3 | 36.3 | 33.3 | 30.8 |
| 4/5/2013 | 4/7/2013 | 6 | 2 | 26.9 | 50.5 | 33.8 | 34.7 | 32.3 | 30.9 |
| 4/5/2013 | 4/7/2013 | 7 | 2 | 26.5 | 54.3 | 35.7 | 37.8 | 34.1 | 30.3 |
| 4/5/2013 | 4/7/2013 | 8 | 2 | 28.1 | 59.1 | 37.0 | 38.3 | 34.5 | 31.9 |
| 4/5/2013 | 4/7/2013 | 9 | 2 | 22.2 | 53.0 | 35.2 | 37.8 | 33.6 | 27.4 |
| 4/5/2013 | 4/7/2013 | 10 | 2 | 18.6 | 50.5 | 28.3 | 29.3 | 26.2 | 22.7 |
| 4/5/2013 | 4/7/2013 | 11 | 2 | 19.4 | 47.8 | 29.6 | 29.7 | 25.6 | 23.4 |
| 4/5/2013 | 4/7/2013 | 12 | 2 | 19.9 | 48.7 | 29.2 | 31.5 | 24.8 | 22.1 |
| 4/5/2013 | 4/7/2013 | 13 | 2 | 19.2 | 49.4 | 29.0 | 30.5 | 25.1 | 22.1 |
| 4/5/2013 | 4/7/2013 | 14 | 3 | 19.2 | 48.6 | 30.5 | 32.9 | 28.9 | 24.9 |
| 4/5/2013 | 4/7/2013 | 15 | 3 | 20.3 | 52.2 | 33.9 | 36.6 | 26.8 | 23.9 |
| 4/5/2013 | 4/7/2013 | 16 | 2 | 19.4 | 52.7 | 35.5 | 35.6 | 30.5 | 26.2 |
| 4/5/2013 | 4/7/2013 | 17 | 2 | 18.8 | 51.9 | 34.9 | 35.5 | 29.6 | 25.7 |
| 4/5/2013 | 4/7/2013 | 18 | 2 | 19.4 | 53.5 | 35.2 | 35.9 | 30.5 | 25.6 |
| 4/5/2013 | 4/7/2013 | 19 | 2 | 18.5 | 54.5 | 32.5 | 34.6 | 28.3 | 22.8 |
| 4/5/2013 | 4/7/2013 | 20 | 2 | 22.7 | 51.4 | 30.5 | 31.6 | 28.1 | 25.7 |
| 4/5/2013 | 4/7/2013 | 21 | 2 | 20.0 | 46.9 | 27.2 | 28.0 | 25.1 | 23.1 |
| 4/5/2013 | 4/7/2013 | 22 | 2 | 17.4 | 43.3 | 27.2 | 28.7 | 25.5 | 22.1 |
| 4/5/2013 | 4/7/2013 | 23 | 2 | 20.3 | 52.3 | 32.3 | 32.7 | 28.3 | 25.1 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 24. PAPA003 (Lower Sand Springs Draw) dBA and one-third octave band metrics, April 5-7, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/5/13 | 4/7/13 | dBA | 50 | 17.4 | 59.1 | 33.3 | 32.9 | 28.4 | 24.9 |
| 4/5/13 | 4/7/13 | 12.5 | 50 | 21.8 | 81.6 | 59.0 | 51.4 | 44.9 | 39.1 |
| 4/5/13 | 4/7/13 | 16 | 50 | 29.0 | 77.8 | 55.7 | 51.3 | 46.5 | 42.0 |
| 4/5/13 | 4/7/13 | 20 | 50 | 34.9 | 74.4 | 55.8 | 56.2 | 51.3 | 47.0 |
| 4/5/13 | 4/7/13 | 25 | 50 | 31.3 | 73.2 | 51.8 | 51.9 | 46.2 | 42.3 |
| 4/5/13 | 4/7/13 | 31.5 | 50 | 33.3 | 68.2 | 53.5 | 56.1 | 51.5 | 46.3 |
| 4/5/13 | 4/7/13 | 40 | 50 | 27.5 | 66.4 | 46.8 | 47.8 | 44.1 | 40.0 |
| 4/5/13 | 4/7/13 | 50 | 50 | 26.9 | 64.8 | 44.8 | 45.8 | 42.1 | 37.7 |
| 4/5/13 | 4/7/13 | 63 | 50 | 24.8 | 67.1 | 44.3 | 45.4 | 41.1 | 37.2 |
| 4/5/13 | 4/7/13 | 80 | 50 | 14.5 | 69.1 | 42.5 | 43.4 | 39.0 | 34.1 |
| 4/5/13 | 4/7/13 | 100 | 50 | 16.9 | 70.5 | 40.6 | 40.8 | 36.4 | 32.3 |
| 4/5/13 | 4/7/13 | 125 | 50 | 16.4 | 63.0 | 38.5 | 38.0 | 33.9 | 30.5 |
| 4/5/13 | 4/7/13 | 160 | 50 | 16.0 | 65.3 | 36.8 | 36.0 | 31.5 | 27.8 |
| 4/5/13 | 4/7/13 | 200 | 50 | 13.7 | 60.1 | 34.3 | 33.1 | 29.1 | 25.3 |
| 4/5/13 | 4/7/13 | 250 | 50 | 8.7 | 56.4 | 31.3 | 31.2 | 25.9 | 22.7 |
| 4/5/13 | 4/7/13 | 315 | 50 | 7.3 | 53.8 | 30.4 | 29.1 | 24.5 | 20.3 |
| 4/5/13 | 4/7/13 | 400 | 50 | 2.9 | 50.7 | 26.2 | 26.4 | 21.0 | 17.0 |
| 4/5/13 | 4/7/13 | 500 | 50 | -0.1 | 50.8 | 23.8 | 22.8 | 16.8 | 12.4 |
| 4/5/13 | 4/7/13 | 630 | 50 | -1.4 | 47.6 | 21.5 | 20.2 | 13.9 | 8.6 |
| 4/5/13 | 4/7/13 | 800 | 50 | -2.0 | 41.6 | 18.4 | 17.7 | 10.7 | 5.3 |
| 4/5/13 | 4/7/13 | 1000 | 50 | -1.5 | 39.4 | 17.0 | 15.2 | 8.5 | 3.5 |
| 4/5/13 | 4/7/13 | 1250 | 50 | -1.0 | 39.4 | 15.2 | 12.2 | 5.1 | 1.8 |
| 4/5/13 | 4/7/13 | 1600 | 50 | -0.2 | 36.4 | 13.7 | 9.3 | 2.8 | 1.5 |
| 4/5/13 | 4/7/13 | 2000 | 50 | 0.5 | 39.4 | 12.6 | 7.1 | 2.4 | 1.8 |
| 4/5/13 | 4/7/13 | 2500 | 50 | 1.5 | 39.6 | 11.5 | 4.8 | 3.0 | 2.5 |
| 4/5/13 | 4/7/13 | 3150 | 50 | 2.3 | 38.6 | 10.5 | 4.4 | 3.5 | 3.2 |
| 4/5/13 | 4/7/13 | 4000 | 50 | 3.3 | 50.8 | 11.3 | 5.0 | 4.2 | 4.0 |
| 4/5/13 | 4/7/13 | 5000 | 50 | 3.6 | 57.9 | 14.4 | 5.4 | 4.8 | 4.6 |
| 4/5/13 | 4/7/13 | 6300 | 50 | 3.5 | 48.8 | 11.0 | 5.4 | 5.1 | 4.9 |
| 4/5/13 | 4/7/13 | 8000 | 50 | 1.7 | 41.3 | 10.7 | 5.3 | 5.1 | 5.0 |
| 4/5/13 | 4/7/13 | 10000 | 50 | 1.4 | 38.4 | 9.2 | 5.0 | 4.8 | 4.7 |
| 4/5/13 | 4/7/13 | 12500 | 50 | 1.1 | 37.8 | 8.1 | 4.3 | 4.2 | 4.1 |
| 4/5/13 | 4/7/13 | 16000 | 50 | 0.4 | 35.7 | 6.7 | 3.4 | 3.3 | 3.2 |
| 4/5/13 | 4/7/13 | 20000 | 50 | 0.9 | 31.8 | 4.7 | 2.1 | 1.9 | 1.8 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 25. PAPA004 (Two Buttes lek) hourly dBA metrics, April 18-21, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/18/2013 | 4/21/2013 | 0 | 3 | 18.0 | 41.1 | 28.2 | 30.6 | 24.9 | 23.7 |
| 4/18/2013 | 4/21/2013 | 1 | 3 | 16.5 | 48.5 | 29.3 | 26.2 | 23.8 | 21.2 |
| 4/18/2013 | 4/21/2013 | 2 | 3 | 16.1 | 39.8 | 27.1 | 30.3 | 26.8 | 24.5 |
| 4/18/2013 | 4/21/2013 | 3 | 3 | 14.8 | 49.6 | 29.3 | 29.3 | 26.7 | 23.1 |
| 4/18/2013 | 4/21/2013 | 4 | 3 | 15.0 | 43.6 | 27.3 | 29.4 | 25.5 | 22.2 |
| 4/18/2013 | 4/21/2013 | 5 | 3 | 18.3 | 57.1 | 29.9 | 30.0 | 26.0 | 23.0 |
| 4/18/2013 | 4/21/2013 | 6 | 3 | 17.0 | 43.1 | 30.2 | 29.7 | 27.2 | 23.5 |
| 4/18/2013 | 4/21/2013 | 7 | 3 | 20.0 | 44.0 | 28.1 | 29.9 | 26.1 | 23.0 |
| 4/18/2013 | 4/21/2013 | 8 | 3 | 16.8 | 52.4 | 29.1 | 28.5 | 22.6 | 19.8 |
| 4/18/2013 | 4/21/2013 | 9 | 3 | 17.3 | 43.6 | 25.4 | 26.8 | 22.7 | 19.6 |
| 4/18/2013 | 4/21/2013 | 10 | 4 | 17.2 | 52.1 | 26.8 | 24.5 | 21.2 | 19.6 |
| 4/18/2013 | 4/21/2013 | 11 | 4 | 16.3 | 51.2 | 30.0 | 29.7 | 23.5 | 20.4 |
| 4/18/2013 | 4/21/2013 | 12 | 4 | 19.8 | 49.2 | 31.5 | 33.8 | 27.2 | 23.0 |
| 4/18/2013 | 4/21/2013 | 13 | 3 | 19.2 | 51.3 | 32.6 | 35.9 | 29.0 | 23.1 |
| 4/18/2013 | 4/21/2013 | 14 | 3 | 19.7 | 54.9 | 33.8 | 38.0 | 31.4 | 25.4 |
| 4/18/2013 | 4/21/2013 | 15 | 3 | 19.0 | 52.7 | 36.1 | 40.6 | 33.5 | 27.7 |
| 4/18/2013 | 4/21/2013 | 16 | 3 | 19.1 | 52.8 | 36.5 | 39.5 | 32.7 | 26.3 |
| 4/18/2013 | 4/21/2013 | 17 | 3 | 18.5 | 58.7 | 38.6 | 41.2 | 34.5 | 28.4 |
| 4/18/2013 | 4/21/2013 | 18 | 3 | 16.6 | 52.8 | 36.5 | 41.0 | 33.5 | 27.7 |
| 4/18/2013 | 4/21/2013 | 19 | 3 | 16.4 | 55.4 | 36.7 | 35.1 | 28.8 | 25.2 |
| 4/18/2013 | 4/21/2013 | 20 | 3 | 16.4 | 61.5 | 35.9 | 30.5 | 28.1 | 26.1 |
| 4/18/2013 | 4/21/2013 | 21 | 3 | 15.3 | 43.7 | 27.0 | 31.3 | 24.7 | 22.3 |
| 4/18/2013 | 4/21/2013 | 22 | 3 | 14.6 | 50.7 | 27.2 | 29.6 | 24.2 | 21.1 |
| 4/18/2013 | 4/21/2013 | 23 | 3 | 15.1 | 44.4 | 28.7 | 28.7 | 24.7 | 21.9 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 26. PAPA004 (Two Buttes lek) dBA and one-third octave band metrics, April 18-21, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/18/13 | 4/21/13 | dBA | 75 | 14.6 | 61.5 | 32.6 | 30.6 | 26.4 | 22.7 |
| 4/18/13 | 4/21/13 | 12.5 | 75 | 15.8 | 81.6 | 61.7 | 47.7 | 41.6 | 37.4 |
| 4/18/13 | 4/21/13 | 16 | 75 | 24.7 | 78.0 | 57.3 | 47.0 | 42.3 | 38.9 |
| 4/18/13 | 4/21/13 | 20 | 75 | 31.2 | 75.9 | 56.4 | 58.6 | 52.9 | 46.8 |
| 4/18/13 | 4/21/13 | 25 | 75 | 24.2 | 72.8 | 50.8 | 44.9 | 40.4 | 36.4 |
| 4/18/13 | 4/21/13 | 31.5 | 75 | 22.3 | 70.6 | 49.9 | 50.5 | 42.5 | 36.4 |
| 4/18/13 | 4/21/13 | 40 | 75 | 21.9 | 69.3 | 46.5 | 43.8 | 38.6 | 34.2 |
| 4/18/13 | 4/21/13 | 50 | 75 | 18.8 | 67.9 | 44.0 | 42.4 | 36.8 | 32.8 |
| 4/18/13 | 4/21/13 | 63 | 75 | 15.4 | 66.3 | 41.5 | 40.8 | 35.4 | 31.7 |
| 4/18/13 | 4/21/13 | 80 | 75 | 11.8 | 69.1 | 39.1 | 38.5 | 33.6 | 30.2 |
| 4/18/13 | 4/21/13 | 100 | 75 | 10.8 | 69.4 | 37.7 | 38.7 | 33.2 | 29.0 |
| 4/18/13 | 4/21/13 | 125 | 75 | 9.0 | 65.8 | 35.6 | 37.0 | 31.4 | 27.6 |
| 4/18/13 | 4/21/13 | 160 | 75 | 5.0 | 61.9 | 32.6 | 33.3 | 28.5 | 24.7 |
| 4/18/13 | 4/21/13 | 200 | 75 | 4.5 | 62.8 | 31.2 | 32.5 | 27.1 | 23.2 |
| 4/18/13 | 4/21/13 | 250 | 75 | 2.0 | 58.9 | 28.5 | 29.1 | 24.4 | 20.6 |
| 4/18/13 | 4/21/13 | 315 | 75 | 0.7 | 53.3 | 26.8 | 27.1 | 22.3 | 18.0 |
| 4/18/13 | 4/21/13 | 400 | 75 | -1.0 | 50.3 | 24.9 | 24.7 | 19.8 | 15.5 |
| 4/18/13 | 4/21/13 | 500 | 75 | -3.0 | 47.4 | 22.5 | 21.5 | 15.9 | 12.2 |
| 4/18/13 | 4/21/13 | 630 | 75 | -3.5 | 44.3 | 20.4 | 18.3 | 11.2 | 7.6 |
| 4/18/13 | 4/21/13 | 800 | 75 | -3.2 | 47.1 | 18.6 | 14.8 | 8.5 | 5.1 |
| 4/18/13 | 4/21/13 | 1000 | 75 | -2.6 | 51.1 | 18.7 | 12.8 | 5.7 | 2.4 |
| 4/18/13 | 4/21/13 | 1250 | 75 | -1.5 | 50.7 | 19.7 | 10.5 | 4.7 | 1.2 |
| 4/18/13 | 4/21/13 | 1600 | 75 | -0.6 | 52.2 | 19.4 | 7.2 | 2.2 | 1.1 |
| 4/18/13 | 4/21/13 | 2000 | 75 | 0.3 | 53.5 | 17.8 | 5.8 | 2.2 | 1.7 |
| 4/18/13 | 4/21/13 | 2500 | 75 | 1.2 | 43.2 | 16.1 | 5.8 | 2.9 | 2.5 |
| 4/18/13 | 4/21/13 | 3150 | 75 | 2.1 | 39.7 | 13.1 | 5.1 | 3.5 | 3.2 |
| 4/18/13 | 4/21/13 | 4000 | 75 | 1.2 | 37.2 | 10.0 | 4.8 | 4.1 | 3.8 |
| 4/18/13 | 4/21/13 | 5000 | 75 | 0.3 | 35.5 | 7.5 | 4.8 | 4.5 | 4.3 |
| 4/18/13 | 4/21/13 | 6300 | 75 | -0.1 | 33.7 | 6.1 | 4.9 | 4.7 | 4.5 |
| 4/18/13 | 4/21/13 | 8000 | 75 | -0.6 | 36.3 | 5.4 | 4.7 | 4.6 | 4.4 |
| 4/18/13 | 4/21/13 | 10000 | 75 | -0.4 | 29.5 | 4.6 | 4.3 | 4.2 | 4.0 |
| 4/18/13 | 4/21/13 | 12500 | 75 | -0.5 | 27.8 | 3.8 | 3.7 | 3.5 | 3.4 |
| 4/18/13 | 4/21/13 | 16000 | 75 | -1.1 | 25.9 | 2.9 | 2.7 | 2.5 | 2.4 |
| 4/18/13 | 4/21/13 | 20000 | 75 | -0.8 | 20.2 | 1.5 | 1.1 | 0.8 | 0.7 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 27. PAPA005 (Mesa Spring lek) hourly dBA metrics, April 18-21, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/18/2013 | 4/21/2013 | 0 | 3 | 22.2 | 53.6 | 37.5 | 34.4 | 31.8 | 30.0 |
| 4/18/2013 | 4/21/2013 | 1 | 3 | 21.7 | 50.5 | 34.2 | 30.9 | 27.6 | 24.1 |
| 4/18/2013 | 4/21/2013 | 2 | 3 | 21.4 | 45.3 | 33.2 | 34.4 | 29.3 | 26.7 |
| 4/18/2013 | 4/21/2013 | 3 | 3 | 19.7 | 47.1 | 34.2 | 32.5 | 29.2 | 26.8 |
| 4/18/2013 | 4/21/2013 | 4 | 3 | 18.3 | 46.4 | 32.0 | 33.2 | 29.8 | 27.5 |
| 4/18/2013 | 4/21/2013 | 5 | 3 | 22.9 | 45.7 | 31.1 | 32.4 | 29.3 | 27.2 |
| 4/18/2013 | 4/21/2013 | 6 | 3 | 21.8 | 45.5 | 33.6 | 32.8 | 29.3 | 25.0 |
| 4/18/2013 | 4/21/2013 | 7 | 3 | 21.1 | 44.0 | 32.7 | 32.8 | 28.3 | 24.3 |
| 4/18/2013 | 4/21/2013 | 8 | 3 | 20.4 | 50.9 | 31.9 | 33.9 | 29.2 | 26.5 |
| 4/18/2013 | 4/21/2013 | 9 | 3 | 20.1 | 45.7 | 29.4 | 33.6 | 27.7 | 23.7 |
| 4/18/2013 | 4/21/2013 | 10 | 3 | 20.5 | 51.9 | 29.9 | 30.8 | 27.5 | 24.7 |
| 4/18/2013 | 4/21/2013 | 11 | 4 | 17.2 | 51.6 | 31.6 | 30.1 | 26.2 | 23.8 |
| 4/18/2013 | 4/21/2013 | 12 | 4 | 20.1 | 62.2 | 34.8 | 35.7 | 29.9 | 26.7 |
| 4/18/2013 | 4/21/2013 | 13 | 4 | 21.4 | 56.8 | 35.4 | 38.6 | 31.4 | 27.0 |
| 4/18/2013 | 4/21/2013 | 14 | 3 | 22.8 | 63.6 | 37.9 | 41.0 | 34.5 | 28.4 |
| 4/18/2013 | 4/21/2013 | 15 | 3 | 22.3 | 66.6 | 40.9 | 42.5 | 35.6 | 28.9 |
| 4/18/2013 | 4/21/2013 | 16 | 3 | 23.6 | 57.1 | 39.7 | 42.8 | 36.9 | 31.6 |
| 4/18/2013 | 4/21/2013 | 17 | 3 | 21.6 | 60.2 | 42.0 | 45.4 | 39.4 | 33.7 |
| 4/18/2013 | 4/21/2013 | 18 | 3 | 21.2 | 54.5 | 40.0 | 44.5 | 37.9 | 32.9 |
| 4/18/2013 | 4/21/2013 | 19 | 3 | 22.5 | 52.5 | 37.5 | 38.9 | 32.8 | 29.4 |
| 4/18/2013 | 4/21/2013 | 20 | 3 | 22.9 | 51.0 | 35.8 | 39.7 | 34.7 | 28.6 |
| 4/18/2013 | 4/21/2013 | 21 | 3 | 18.3 | 43.8 | 31.8 | 33.0 | 30.3 | 28.6 |
| 4/18/2013 | 4/21/2013 | 22 | 3 | 18.1 | 50.3 | 31.7 | 32.1 | 29.9 | 28.4 |
| 4/18/2013 | 4/21/2013 | 23 | 3 | 17.4 | 53.7 | 36.0 | 32.4 | 30.6 | 28.8 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 28. PAPA005 (Mesa Spring lek) dBA and one-third octave band metrics, April 18-21, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/18/13 | 4/21/13 | dBA | 75 | 17.2 | 66.6 | 36.2 | 34.6 | 30.0 | 26.7 |
| 4/18/13 | 4/21/13 | 12.5 | 75 | 23.5 | 78.5 | 58.0 | 45.8 | 41.8 | 37.8 |
| 4/18/13 | 4/21/13 | 16 | 75 | 29.2 | 78.0 | 55.8 | 50.2 | 46.3 | 42.5 |
| 4/18/13 | 4/21/13 | 20 | 75 | 36.4 | 73.6 | 59.2 | 62.9 | 57.0 | 51.6 |
| 4/18/13 | 4/21/13 | 25 | 75 | 29.7 | 71.2 | 49.1 | 48.0 | 44.0 | 40.5 |
| 4/18/13 | 4/21/13 | 31.5 | 75 | 29.3 | 67.9 | 49.4 | 51.2 | 45.3 | 41.1 |
| 4/18/13 | 4/21/13 | 40 | 75 | 29.1 | 66.7 | 45.9 | 47.1 | 43.1 | 40.3 |
| 4/18/13 | 4/21/13 | 50 | 75 | 24.8 | 63.8 | 46.5 | 48.4 | 45.2 | 41.3 |
| 4/18/13 | 4/21/13 | 63 | 75 | 22.5 | 68.5 | 43.5 | 45.2 | 41.0 | 37.2 |
| 4/18/13 | 4/21/13 | 80 | 75 | 18.6 | 77.5 | 41.9 | 42.8 | 37.9 | 33.3 |
| 4/18/13 | 4/21/13 | 100 | 75 | 16.2 | 73.8 | 41.1 | 42.0 | 36.7 | 33.1 |
| 4/18/13 | 4/21/13 | 125 | 75 | 15.7 | 72.4 | 38.1 | 38.4 | 34.6 | 31.0 |
| 4/18/13 | 4/21/13 | 160 | 75 | 9.6 | 64.1 | 35.5 | 36.2 | 31.3 | 27.6 |
| 4/18/13 | 4/21/13 | 200 | 75 | 7.1 | 60.0 | 34.2 | 35.2 | 30.7 | 26.8 |
| 4/18/13 | 4/21/13 | 250 | 75 | 4.3 | 62.9 | 32.9 | 31.8 | 27.7 | 24.3 |
| 4/18/13 | 4/21/13 | 315 | 75 | 1.4 | 56.3 | 31.0 | 30.1 | 25.6 | 21.6 |
| 4/18/13 | 4/21/13 | 400 | 75 | -0.4 | 53.0 | 28.0 | 28.0 | 22.5 | 18.3 |
| 4/18/13 | 4/21/13 | 500 | 75 | -1.9 | 56.4 | 25.1 | 25.5 | 19.5 | 13.2 |
| 4/18/13 | 4/21/13 | 630 | 75 | -2.4 | 53.7 | 23.4 | 23.5 | 16.5 | 10.2 |
| 4/18/13 | 4/21/13 | 800 | 75 | -2.4 | 45.3 | 23.9 | 23.5 | 15.6 | 8.5 |
| 4/18/13 | 4/21/13 | 1000 | 75 | -1.4 | 44.7 | 24.0 | 22.9 | 14.1 | 7.5 |
| 4/18/13 | 4/21/13 | 1250 | 75 | -0.9 | 43.0 | 23.0 | 20.4 | 12.0 | 5.6 |
| 4/18/13 | 4/21/13 | 1600 | 75 | -0.2 | 44.7 | 22.3 | 16.8 | 8.6 | 3.2 |
| 4/18/13 | 4/21/13 | 2000 | 75 | 0.9 | 44.1 | 20.5 | 9.3 | 4.1 | 2.7 |
| 4/18/13 | 4/21/13 | 2500 | 75 | 1.9 | 43.0 | 18.6 | 6.3 | 3.4 | 3.0 |
| 4/18/13 | 4/21/13 | 3150 | 75 | 2.8 | 42.2 | 15.8 | 5.7 | 4.1 | 3.7 |
| 4/18/13 | 4/21/13 | 4000 | 75 | 3.7 | 40.7 | 12.8 | 5.5 | 4.7 | 4.4 |
| 4/18/13 | 4/21/13 | 5000 | 75 | 4.4 | 62.1 | 16.4 | 5.8 | 5.2 | 5.0 |
| 4/18/13 | 4/21/13 | 6300 | 75 | 3.3 | 66.6 | 23.7 | 5.8 | 5.5 | 5.4 |
| 4/18/13 | 4/21/13 | 8000 | 75 | 3.1 | 45.7 | 7.7 | 5.8 | 5.6 | 5.4 |
| 4/18/13 | 4/21/13 | 10000 | 75 | 2.5 | 41.9 | 6.6 | 5.5 | 5.3 | 5.2 |
| 4/18/13 | 4/21/13 | 12500 | 75 | 2.0 | 50.9 | 10.7 | 4.9 | 4.8 | 4.7 |
| 4/18/13 | 4/21/13 | 16000 | 75 | 1.6 | 31.7 | 4.9 | 4.1 | 4.0 | 3.9 |
| 4/18/13 | 4/21/13 | 20000 | 75 | 1.9 | 31.8 | 3.7 | 3.0 | 2.8 | 2.7 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 29. PAPA006 (Lovatt Draw Reservoir lek) hourly dBA metrics, April 18-21, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/18/2013 | 4/20/2013 | 0 | 2 | 22.0 | 49.8 | 31.8 | 33.2 | 30.3 | 27.6 |
| 4/18/2013 | 4/20/2013 | 1 | 2 | 25.7 | 45.1 | 32.0 | 33.8 | 31.2 | 29.0 |
| 4/18/2013 | 4/20/2013 | 2 | 2 | 27.9 | 47.1 | 33.8 | 35.7 | 32.9 | 31.2 |
| 4/18/2013 | 4/20/2013 | 3 | 2 | 27.0 | 41.4 | 33.9 | 35.6 | 32.9 | 30.6 |
| 4/18/2013 | 4/20/2013 | 4 | 2 | 29.5 | 42.0 | 34.1 | 35.8 | 33.4 | 31.7 |
| 4/18/2013 | 4/20/2013 | 5 | 2 | 28.7 | 52.6 | 33.5 | 34.8 | 32.7 | 30.9 |
| 4/18/2013 | 4/20/2013 | 6 | 2 | 31.4 | 60.4 | 47.5 | 52.9 | 37.3 | 33.4 |
| 4/18/2013 | 4/20/2013 | 7 | 2 | 28.4 | 54.4 | 35.7 | 37.0 | 34.4 | 32.5 |
| 4/18/2013 | 4/20/2013 | 8 | 2 | 26.8 | 53.0 | 33.7 | 35.2 | 31.1 | 28.8 |
| 4/18/2013 | 4/20/2013 | 9 | 2 | 25.4 | 47.7 | 30.7 | 32.6 | 29.4 | 27.7 |
| 4/18/2013 | 4/20/2013 | 10 | 2 | 24.8 | 46.6 | 31.2 | 32.6 | 29.8 | 28.0 |
| 4/18/2013 | 4/20/2013 | 11 | 3 | 23.2 | 50.9 | 32.6 | 34.0 | 30.2 | 28.2 |
| 4/18/2013 | 4/20/2013 | 12 | 3 | 23.8 | 60.6 | 33.8 | 35.2 | 31.0 | 28.1 |
| 4/18/2013 | 4/20/2013 | 13 | 3 | 25.1 | 58.0 | 34.6 | 36.1 | 31.2 | 28.6 |
| 4/18/2013 | 4/20/2013 | 14 | 3 | 25.1 | 50.7 | 34.4 | 37.3 | 33.0 | 29.8 |
| 4/18/2013 | 4/20/2013 | 15 | 3 | 24.8 | 55.5 | 36.7 | 41.1 | 33.9 | 29.9 |
| 4/18/2013 | 4/20/2013 | 16 | 3 | 23.7 | 55.4 | 36.6 | 38.7 | 34.1 | 31.4 |
| 4/18/2013 | 4/20/2013 | 17 | 3 | 23.2 | 54.9 | 38.0 | 39.5 | 34.8 | 30.7 |
| 4/18/2013 | 4/20/2013 | 18 | 3 | 22.6 | 52.9 | 35.7 | 39.4 | 35.0 | 31.5 |
| 4/18/2013 | 4/20/2013 | 19 | 3 | 22.4 | 54.2 | 36.8 | 33.7 | 29.8 | 27.1 |
| 4/18/2013 | 4/20/2013 | 20 | 3 | 25.0 | 51.3 | 34.1 | 33.8 | 31.5 | 26.9 |
| 4/18/2013 | 4/20/2013 | 21 | 3 | 24.6 | 47.0 | 33.7 | 35.6 | 33.2 | 31.4 |
| 4/18/2013 | 4/20/2013 | 22 | 2 | 23.7 | 45.9 | 32.4 | 33.6 | 30.1 | 28.1 |
| 4/18/2013 | 4/20/2013 | 23 | 2 | 21.4 | 51.6 | 31.2 | 32.9 | 28.7 | 26.1 |

**Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).**

Table 30. PAPA006 (Lovatt Draw Reservoir lek) dBA and one-third octave band metrics, April 18-21, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/18/13 | 4/20/13 | dBA | 59 | 21.4 | 60.6 | 36.7 | 35.2 | 32.0 | 29.7 |
| 4/18/13 | 4/20/13 | 12.5 | 59 | 27.7 | 74.8 | 51.1 | 48.5 | 44.5 | 40.3 |
| 4/18/13 | 4/20/13 | 16 | 59 | 33.9 | 74.2 | 51.4 | 52.3 | 48.4 | 45.1 |
| 4/18/13 | 4/20/13 | 20 | 59 | 42.2 | 75.8 | 60.6 | 63.4 | 58.5 | 54.6 |
| 4/18/13 | 4/20/13 | 25 | 59 | 35.8 | 70.1 | 50.6 | 52.5 | 49.0 | 46.1 |
| 4/18/13 | 4/20/13 | 31.5 | 59 | 36.2 | 71.1 | 56.5 | 59.0 | 55.1 | 48.4 |
| 4/18/13 | 4/20/13 | 40 | 59 | 33.2 | 75.1 | 51.3 | 52.7 | 49.0 | 46.0 |
| 4/18/13 | 4/20/13 | 50 | 59 | 29.5 | 73.6 | 49.7 | 50.4 | 46.1 | 43.0 |
| 4/18/13 | 4/20/13 | 63 | 59 | 28.5 | 69.4 | 48.0 | 49.4 | 45.7 | 42.3 |
| 4/18/13 | 4/20/13 | 80 | 59 | 22.9 | 75.3 | 43.1 | 43.7 | 39.7 | 36.7 |
| 4/18/13 | 4/20/13 | 100 | 59 | 23.6 | 72.5 | 40.8 | 41.9 | 38.1 | 35.3 |
| 4/18/13 | 4/20/13 | 125 | 59 | 22.4 | 72.2 | 38.6 | 39.4 | 35.9 | 32.0 |
| 4/18/13 | 4/20/13 | 160 | 59 | 14.2 | 66.4 | 35.8 | 36.7 | 33.7 | 30.8 |
| 4/18/13 | 4/20/13 | 200 | 59 | 11.1 | 66.5 | 35.9 | 35.8 | 32.2 | 28.7 |
| 4/18/13 | 4/20/13 | 250 | 59 | 8.0 | 60.7 | 31.7 | 32.5 | 29.2 | 26.4 |
| 4/18/13 | 4/20/13 | 315 | 59 | 6.3 | 56.6 | 29.4 | 29.3 | 26.1 | 23.4 |
| 4/18/13 | 4/20/13 | 400 | 59 | 3.8 | 52.1 | 27.2 | 27.3 | 23.5 | 20.4 |
| 4/18/13 | 4/20/13 | 500 | 59 | 0.4 | 52.9 | 24.8 | 23.6 | 19.5 | 16.1 |
| 4/18/13 | 4/20/13 | 630 | 59 | -0.9 | 50.3 | 23.2 | 21.4 | 16.4 | 12.6 |
| 4/18/13 | 4/20/13 | 800 | 59 | -0.6 | 53.4 | 25.4 | 21.1 | 15.8 | 11.8 |
| 4/18/13 | 4/20/13 | 1000 | 59 | -0.4 | 52.0 | 26.5 | 22.3 | 15.3 | 11.1 |
| 4/18/13 | 4/20/13 | 1250 | 59 | 0.1 | 54.8 | 27.6 | 20.4 | 12.9 | 8.3 |
| 4/18/13 | 4/20/13 | 1600 | 59 | 0.5 | 53.9 | 25.1 | 17.5 | 10.7 | 6.0 |
| 4/18/13 | 4/20/13 | 2000 | 59 | 0.9 | 54.6 | 23.4 | 14.9 | 7.5 | 4.3 |
| 4/18/13 | 4/20/13 | 2500 | 59 | 1.6 | 51.3 | 20.1 | 11.1 | 5.5 | 3.7 |
| 4/18/13 | 4/20/13 | 3150 | 59 | 2.4 | 51.2 | 15.1 | 7.3 | 4.4 | 3.8 |
| 4/18/13 | 4/20/13 | 4000 | 59 | 3.4 | 47.0 | 10.2 | 6.0 | 4.6 | 4.3 |
| 4/18/13 | 4/20/13 | 5000 | 59 | 3.5 | 41.7 | 7.5 | 5.3 | 5.0 | 4.9 |
| 4/18/13 | 4/20/13 | 6300 | 59 | 3.5 | 38.3 | 6.8 | 5.6 | 5.4 | 5.2 |
| 4/18/13 | 4/20/13 | 8000 | 59 | 2.9 | 40.8 | 6.4 | 5.6 | 5.4 | 5.3 |
| 4/18/13 | 4/20/13 | 10000 | 59 | 1.5 | 39.6 | 5.9 | 5.3 | 5.2 | 5.0 |
| 4/18/13 | 4/20/13 | 12500 | 59 | 1.2 | 40.0 | 5.2 | 4.7 | 4.6 | 4.4 |
| 4/18/13 | 4/20/13 | 16000 | 59 | 0.5 | 37.1 | 4.3 | 3.9 | 3.7 | 3.5 |
| 4/18/13 | 4/20/13 | 20000 | 59 | 1.0 | 34.8 | 3.1 | 2.6 | 2.4 | 2.2 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 31. PAPA007 (Shelter Cabin Reservoir lek) hourly dBA metrics, April 10-12, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/10/2013 | 4/12/2013 | 0 | 2 | 18.1 | 38.6 | 23.1 | 24.4 | 21.8 | 20.1 |
| 4/10/2013 | 4/12/2013 | 1 | 2 | 18.0 | 32.8 | 23.0 | 24.9 | 22.6 | 20.3 |
| 4/10/2013 | 4/12/2013 | 2 | 2 | 17.1 | 40.5 | 24.1 | 25.2 | 22.0 | 20.6 |
| 4/10/2013 | 4/12/2013 | 3 | 2 | 18.3 | 39.2 | 23.2 | 24.9 | 22.7 | 20.7 |
| 4/10/2013 | 4/12/2013 | 4 | 2 | 17.9 | 39.1 | 23.5 | 25.4 | 22.6 | 20.9 |
| 4/10/2013 | 4/12/2013 | 5 | 2 | 19.4 | 44.0 | 25.8 | 27.6 | 24.3 | 22.1 |
| 4/10/2013 | 4/12/2013 | 6 | 2 | 21.8 | 38.5 | 27.7 | 29.6 | 26.9 | 24.7 |
| 4/10/2013 | 4/12/2013 | 7 | 2 | 22.3 | 46.2 | 27.3 | 28.8 | 26.1 | 24.3 |
| 4/10/2013 | 4/12/2013 | 8 | 2 | 19.5 | 49.3 | 28.2 | 30.2 | 26.3 | 23.4 |
| 4/10/2013 | 4/12/2013 | 9 | 2 | 18.6 | 48.9 | 30.6 | 33.1 | 25.5 | 22.4 |
| 4/10/2013 | 4/12/2013 | 10 | 3 | 19.7 | 52.0 | 33.3 | 35.8 | 29.7 | 24.5 |
| 4/10/2013 | 4/12/2013 | 11 | 2 | 22.1 | 52.8 | 34.3 | 34.8 | 29.9 | 26.0 |
| 4/10/2013 | 4/12/2013 | 12 | 2 | 21.7 | 73.2 | 40.8 | 34.0 | 29.4 | 25.8 |
| 4/10/2013 | 4/12/2013 | 13 | 2 | 21.4 | 50.8 | 32.7 | 33.6 | 28.5 | 24.6 |
| 4/10/2013 | 4/12/2013 | 14 | 2 | 20.9 | 47.7 | 31.8 | 33.8 | 28.5 | 24.7 |
| 4/10/2013 | 4/12/2013 | 15 | 2 | 21.4 | 50.8 | 33.0 | 34.6 | 29.0 | 25.5 |
| 4/10/2013 | 4/12/2013 | 16 | 2 | 19.6 | 50.0 | 34.8 | 38.4 | 30.7 | 25.3 |
| 4/10/2013 | 4/12/2013 | 17 | 2 | 20.4 | 49.1 | 34.8 | 38.3 | 31.6 | 26.3 |
| 4/10/2013 | 4/12/2013 | 18 | 2 | 23.1 | 54.3 | 37.8 | 41.1 | 34.8 | 29.8 |
| 4/10/2013 | 4/12/2013 | 19 | 2 | 19.5 | 50.0 | 34.9 | 37.6 | 31.5 | 26.7 |
| 4/10/2013 | 4/12/2013 | 20 | 2 | 20.8 | 49.6 | 32.8 | 34.0 | 28.8 | 25.6 |
| 4/10/2013 | 4/12/2013 | 21 | 2 | 20.0 | 44.1 | 27.7 | 29.6 | 25.8 | 23.6 |
| 4/10/2013 | 4/12/2013 | 22 | 2 | 20.2 | 45.0 | 26.6 | 28.7 | 24.0 | 22.1 |
| 4/10/2013 | 4/12/2013 | 23 | 2 | 20.4 | 36.7 | 24.0 | 25.9 | 23.2 | 21.9 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 32. PAPA007 (Shelter Cabin Reservoir lek) dBA and one-third octave band metrics, April 10-12, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/10/13 | 4/12/13 | dBA | 49 | 17.1 | 73.2 | 32.7 | 29.6 | 26.0 | 24.1 |
| 4/10/13 | 4/12/13 | 12.5 | 49 | 24.4 | 78.3 | 58.4 | 53.8 | 47.2 | 41.8 |
| 4/10/13 | 4/12/13 | 16 | 49 | 29.0 | 76.0 | 56.3 | 50.9 | 45.4 | 41.2 |
| 4/10/13 | 4/12/13 | 20 | 49 | 36.8 | 73.9 | 56.3 | 58.3 | 54.8 | 50.5 |
| 4/10/13 | 4/12/13 | 25 | 49 | 33.9 | 70.6 | 50.3 | 50.6 | 46.6 | 43.1 |
| 4/10/13 | 4/12/13 | 31.5 | 49 | 30.4 | 69.3 | 47.3 | 49.3 | 43.2 | 39.2 |
| 4/10/13 | 4/12/13 | 40 | 49 | 27.8 | 68.6 | 44.5 | 44.5 | 40.6 | 37.3 |
| 4/10/13 | 4/12/13 | 50 | 49 | 26.5 | 75.7 | 42.3 | 42.5 | 38.1 | 35.2 |
| 4/10/13 | 4/12/13 | 63 | 49 | 23.9 | 80.7 | 42.4 | 41.8 | 36.9 | 34.2 |
| 4/10/13 | 4/12/13 | 80 | 49 | 22.1 | 85.3 | 42.4 | 39.6 | 34.6 | 31.5 |
| 4/10/13 | 4/12/13 | 100 | 49 | 20.7 | 83.3 | 39.8 | 37.5 | 33.3 | 30.2 |
| 4/10/13 | 4/12/13 | 125 | 49 | 20.8 | 73.3 | 36.0 | 36.7 | 32.6 | 29.4 |
| 4/10/13 | 4/12/13 | 160 | 49 | 14.5 | 73.6 | 33.4 | 33.0 | 29.3 | 26.3 |
| 4/10/13 | 4/12/13 | 200 | 49 | 11.9 | 78.8 | 32.5 | 30.4 | 26.6 | 24.1 |
| 4/10/13 | 4/12/13 | 250 | 49 | 10.3 | 63.6 | 27.5 | 27.3 | 23.5 | 21.0 |
| 4/10/13 | 4/12/13 | 315 | 49 | 7.1 | 65.9 | 25.4 | 25.1 | 20.5 | 17.6 |
| 4/10/13 | 4/12/13 | 400 | 49 | 1.2 | 68.6 | 24.1 | 20.6 | 15.8 | 12.7 |
| 4/10/13 | 4/12/13 | 500 | 49 | -1.5 | 65.3 | 21.5 | 19.2 | 12.7 | 8.8 |
| 4/10/13 | 4/12/13 | 630 | 49 | -2.4 | 56.9 | 19.2 | 17.7 | 10.0 | 5.4 |
| 4/10/13 | 4/12/13 | 800 | 49 | -2.4 | 53.8 | 18.7 | 17.3 | 9.0 | 3.9 |
| 4/10/13 | 4/12/13 | 1000 | 49 | -1.9 | 49.6 | 18.9 | 14.9 | 7.0 | 2.2 |
| 4/10/13 | 4/12/13 | 1250 | 49 | -1.2 | 48.6 | 18.8 | 11.6 | 4.6 | 1.1 |
| 4/10/13 | 4/12/13 | 1600 | 49 | -0.2 | 43.8 | 18.8 | 10.4 | 4.3 | 1.8 |
| 4/10/13 | 4/12/13 | 2000 | 49 | 0.5 | 41.5 | 17.3 | 9.7 | 3.5 | 2.1 |
| 4/10/13 | 4/12/13 | 2500 | 49 | 1.3 | 38.4 | 15.0 | 8.2 | 3.7 | 2.8 |
| 4/10/13 | 4/12/13 | 3150 | 49 | 2.3 | 46.6 | 12.9 | 7.7 | 3.8 | 3.4 |
| 4/10/13 | 4/12/13 | 4000 | 49 | 2.0 | 46.8 | 10.3 | 6.3 | 4.3 | 4.0 |
| 4/10/13 | 4/12/13 | 5000 | 49 | 1.3 | 41.7 | 7.3 | 5.2 | 4.6 | 4.4 |
| 4/10/13 | 4/12/13 | 6300 | 49 | 0.2 | 34.4 | 5.7 | 5.0 | 4.7 | 4.5 |
| 4/10/13 | 4/12/13 | 8000 | 49 | 0.1 | 25.5 | 5.0 | 4.9 | 4.6 | 4.4 |
| 4/10/13 | 4/12/13 | 10000 | 49 | -0.6 | 23.5 | 4.5 | 4.5 | 4.3 | 4.0 |
| 4/10/13 | 4/12/13 | 12500 | 49 | -1.3 | 21.9 | 3.8 | 4.0 | 3.7 | 3.4 |
| 4/10/13 | 4/12/13 | 16000 | 49 | -1.3 | 21.1 | 3.0 | 3.2 | 2.8 | 2.5 |
| 4/10/13 | 4/12/13 | 20000 | 49 | -1.2 | 25.8 | 1.8 | 2.0 | 1.2 | 0.9 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 33. PAPA008 (The Rocks lek) hourly dBA metrics, April 10-12, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/10/2013 | 4/12/2013 | 0 | 2 | 19.7 | 36.5 | 23.7 | 25.0 | 22.5 | 21.1 |
| 4/10/2013 | 4/12/2013 | 1 | 2 | 20.4 | 34.5 | 24.3 | 25.9 | 23.6 | 21.9 |
| 4/10/2013 | 4/12/2013 | 2 | 2 | 19.5 | 46.0 | 26.0 | 26.6 | 23.9 | 22.4 |
| 4/10/2013 | 4/12/2013 | 3 | 2 | 19.5 | 36.2 | 24.8 | 25.8 | 24.0 | 22.4 |
| 4/10/2013 | 4/12/2013 | 4 | 2 | 18.8 | 34.7 | 23.7 | 25.7 | 22.8 | 21.1 |
| 4/10/2013 | 4/12/2013 | 5 | 2 | 20.2 | 36.7 | 24.5 | 26.2 | 23.8 | 22.0 |
| 4/10/2013 | 4/12/2013 | 6 | 2 | 21.3 | 51.5 | 26.9 | 28.4 | 25.2 | 23.3 |
| 4/10/2013 | 4/12/2013 | 7 | 2 | 21.2 | 43.8 | 27.3 | 29.3 | 26.1 | 24.1 |
| 4/10/2013 | 4/12/2013 | 8 | 2 | 19.2 | 53.6 | 29.2 | 30.2 | 25.6 | 23.5 |
| 4/10/2013 | 4/12/2013 | 9 | 2 | 18.9 | 50.9 | 30.5 | 31.7 | 26.5 | 23.5 |
| 4/10/2013 | 4/12/2013 | 10 | 2 | 20.9 | 47.1 | 33.6 | 36.0 | 30.8 | 26.2 |
| 4/10/2013 | 4/12/2013 | 11 | 3 | 19.2 | 49.5 | 33.1 | 32.3 | 26.5 | 25.1 |
| 4/10/2013 | 4/12/2013 | 12 | 3 | 18.0 | 64.5 | 35.8 | 31.3 | 26.5 | 25.0 |
| 4/10/2013 | 4/12/2013 | 13 | 2 | 22.4 | 49.8 | 33.6 | 34.4 | 29.9 | 25.8 |
| 4/10/2013 | 4/12/2013 | 14 | 2 | 20.5 | 52.6 | 32.7 | 34.2 | 30.0 | 26.4 |
| 4/10/2013 | 4/12/2013 | 15 | 2 | 21.5 | 47.6 | 32.2 | 34.2 | 29.1 | 25.5 |
| 4/10/2013 | 4/12/2013 | 16 | 2 | 22.3 | 49.0 | 34.1 | 36.9 | 30.7 | 26.4 |
| 4/10/2013 | 4/12/2013 | 17 | 2 | 22.9 | 47.6 | 35.2 | 38.2 | 32.7 | 27.8 |
| 4/10/2013 | 4/12/2013 | 18 | 2 | 21.2 | 49.6 | 36.6 | 39.5 | 33.8 | 27.9 |
| 4/10/2013 | 4/12/2013 | 19 | 2 | 22.4 | 51.7 | 35.9 | 38.5 | 33.1 | 28.1 |
| 4/10/2013 | 4/12/2013 | 20 | 2 | 21.5 | 49.9 | 34.3 | 35.8 | 30.3 | 26.3 |
| 4/10/2013 | 4/12/2013 | 21 | 2 | 20.9 | 42.9 | 25.9 | 28.2 | 24.8 | 22.8 |
| 4/10/2013 | 4/12/2013 | 22 | 2 | 21.2 | 38.6 | 26.2 | 28.6 | 24.7 | 23.1 |
| 4/10/2013 | 4/12/2013 | 23 | 2 | 20.3 | 35.2 | 24.2 | 25.8 | 23.5 | 22.3 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 34. PAPA008 (The Rocks lek) dBA and one-third octave band metrics, April 10-12, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/10/13 | 4/12/13 | dBA | 50 | 18.0 | 64.5 | 32.0 | 29.5 | 26.2 | 24.0 |
| 4/10/13 | 4/12/13 | 12.5 | 50 | 26.7 | 78.6 | 54.6 | 53.5 | 47.5 | 41.7 |
| 4/10/13 | 4/12/13 | 16 | 50 | 24.1 | 75.8 | 52.7 | 52.2 | 46.2 | 41.0 |
| 4/10/13 | 4/12/13 | 20 | 50 | 32.2 | 73.6 | 53.5 | 55.5 | 51.2 | 47.3 |
| 4/10/13 | 4/12/13 | 25 | 50 | 28.7 | 71.0 | 48.3 | 50.7 | 45.0 | 41.4 |
| 4/10/13 | 4/12/13 | 31.5 | 50 | 28.9 | 69.1 | 46.3 | 48.1 | 44.1 | 41.0 |
| 4/10/13 | 4/12/13 | 40 | 50 | 29.7 | 66.8 | 43.8 | 45.7 | 42.0 | 38.8 |
| 4/10/13 | 4/12/13 | 50 | 50 | 26.1 | 66.7 | 40.4 | 41.2 | 37.5 | 34.9 |
| 4/10/13 | 4/12/13 | 63 | 50 | 24.3 | 85.0 | 42.0 | 41.9 | 37.6 | 34.6 |
| 4/10/13 | 4/12/13 | 80 | 50 | 22.7 | 84.1 | 41.3 | 38.4 | 34.1 | 31.0 |
| 4/10/13 | 4/12/13 | 100 | 50 | 21.1 | 79.3 | 38.1 | 37.1 | 33.2 | 30.2 |
| 4/10/13 | 4/12/13 | 125 | 50 | 20.0 | 66.9 | 34.3 | 35.5 | 31.7 | 29.0 |
| 4/10/13 | 4/12/13 | 160 | 50 | 16.9 | 70.4 | 31.7 | 32.4 | 28.4 | 25.6 |
| 4/10/13 | 4/12/13 | 200 | 50 | 14.9 | 65.3 | 30.1 | 31.2 | 27.1 | 24.0 |
| 4/10/13 | 4/12/13 | 250 | 50 | 13.0 | 53.3 | 27.6 | 28.3 | 24.0 | 21.3 |
| 4/10/13 | 4/12/13 | 315 | 50 | 9.8 | 46.0 | 25.7 | 25.0 | 21.2 | 18.2 |
| 4/10/13 | 4/12/13 | 400 | 50 | 4.9 | 47.5 | 23.2 | 21.3 | 16.5 | 12.9 |
| 4/10/13 | 4/12/13 | 500 | 50 | 1.6 | 52.4 | 21.4 | 19.1 | 14.3 | 10.4 |
| 4/10/13 | 4/12/13 | 630 | 50 | -1.9 | 48.6 | 19.2 | 17.4 | 11.2 | 6.5 |
| 4/10/13 | 4/12/13 | 800 | 50 | -1.7 | 43.5 | 18.0 | 16.7 | 9.5 | 4.4 |
| 4/10/13 | 4/12/13 | 1000 | 50 | -1.0 | 46.5 | 18.0 | 16.0 | 7.9 | 3.3 |
| 4/10/13 | 4/12/13 | 1250 | 50 | -0.9 | 48.7 | 18.5 | 14.8 | 5.5 | 1.5 |
| 4/10/13 | 4/12/13 | 1600 | 50 | -0.2 | 36.1 | 19.4 | 12.6 | 4.1 | 1.6 |
| 4/10/13 | 4/12/13 | 2000 | 50 | 0.5 | 36.7 | 18.7 | 9.7 | 3.3 | 2.2 |
| 4/10/13 | 4/12/13 | 2500 | 50 | 1.5 | 35.9 | 16.4 | 8.1 | 3.4 | 3.0 |
| 4/10/13 | 4/12/13 | 3150 | 50 | 2.4 | 34.8 | 13.0 | 7.2 | 4.1 | 3.7 |
| 4/10/13 | 4/12/13 | 4000 | 50 | 2.2 | 49.3 | 10.0 | 5.9 | 4.7 | 4.4 |
| 4/10/13 | 4/12/13 | 5000 | 50 | 2.3 | 52.5 | 10.7 | 6.4 | 5.2 | 4.8 |
| 4/10/13 | 4/12/13 | 6300 | 50 | 2.6 | 38.1 | 6.7 | 5.9 | 5.4 | 5.1 |
| 4/10/13 | 4/12/13 | 8000 | 50 | 2.2 | 26.1 | 6.2 | 5.9 | 5.4 | 5.2 |
| 4/10/13 | 4/12/13 | 10000 | 50 | 0.7 | 28.8 | 5.8 | 5.6 | 5.2 | 4.9 |
| 4/10/13 | 4/12/13 | 12500 | 50 | 0.4 | 23.9 | 5.1 | 5.1 | 4.7 | 4.4 |
| 4/10/13 | 4/12/13 | 16000 | 50 | -0.3 | 22.7 | 4.3 | 4.4 | 3.9 | 3.5 |
| 4/10/13 | 4/12/13 | 20000 | 50 | 0.5 | 22.3 | 3.2 | 3.4 | 2.7 | 2.3 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 35. PAPA009 (South Rocks lek) hourly dBA metrics, April 10-12, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/10/2013 | 4/12/2013 | 0 | 2 | 18.6 | 34.8 | 24.2 | 26.6 | 23.1 | 21.0 |
| 4/10/2013 | 4/12/2013 | 1 | 2 | 17.2 | 40.1 | 27.2 | 27.6 | 23.8 | 22.1 |
| 4/10/2013 | 4/12/2013 | 2 | 2 | 17.6 | 49.2 | 29.9 | 27.8 | 25.2 | 23.4 |
| 4/10/2013 | 4/12/2013 | 3 | 2 | 18.1 | 38.8 | 27.6 | 29.0 | 24.9 | 22.2 |
| 4/10/2013 | 4/12/2013 | 4 | 2 | 19.4 | 33.6 | 25.0 | 27.1 | 24.3 | 22.1 |
| 4/10/2013 | 4/12/2013 | 5 | 2 | 21.6 | 32.9 | 25.9 | 28.0 | 25.3 | 23.3 |
| 4/10/2013 | 4/12/2013 | 6 | 2 | 21.5 | 39.8 | 25.4 | 26.9 | 25.1 | 23.5 |
| 4/10/2013 | 4/12/2013 | 7 | 2 | 21.8 | 44.6 | 27.1 | 28.6 | 26.3 | 24.4 |
| 4/10/2013 | 4/12/2013 | 8 | 2 | 18.7 | 46.2 | 28.9 | 30.5 | 26.2 | 23.0 |
| 4/10/2013 | 4/12/2013 | 9 | 2 | 18.8 | 47.6 | 31.3 | 32.3 | 26.6 | 23.9 |
| 4/10/2013 | 4/12/2013 | 10 | 2 | 19.9 | 47.6 | 33.3 | 35.1 | 29.8 | 25.6 |
| 4/10/2013 | 4/12/2013 | 11 | 2 | 19.6 | 50.4 | 32.9 | 34.6 | 28.7 | 24.6 |
| 4/10/2013 | 4/12/2013 | 12 | 3 | 18.2 | 59.0 | 33.4 | 30.0 | 23.5 | 22.1 |
| 4/10/2013 | 4/12/2013 | 13 | 3 | 18.4 | 54.2 | 32.0 | 32.9 | 26.2 | 23.3 |
| 4/10/2013 | 4/12/2013 | 14 | 2 | 22.1 | 47.3 | 32.0 | 33.6 | 29.5 | 26.1 |
| 4/10/2013 | 4/12/2013 | 15 | 2 | 21.5 | 47.7 | 32.4 | 33.9 | 29.4 | 25.9 |
| 4/10/2013 | 4/12/2013 | 16 | 2 | 23.5 | 49.6 | 33.9 | 35.6 | 30.0 | 26.1 |
| 4/10/2013 | 4/12/2013 | 17 | 2 | 22.9 | 48.3 | 34.1 | 37.1 | 31.5 | 27.3 |
| 4/10/2013 | 4/12/2013 | 18 | 2 | 22.3 | 48.7 | 35.5 | 38.2 | 33.1 | 28.2 |
| 4/10/2013 | 4/12/2013 | 19 | 2 | 22.1 | 52.1 | 33.6 | 36.2 | 31.1 | 27.1 |
| 4/10/2013 | 4/12/2013 | 20 | 2 | 21.6 | 45.0 | 32.8 | 34.3 | 29.8 | 27.0 |
| 4/10/2013 | 4/12/2013 | 21 | 2 | 20.8 | 38.7 | 26.1 | 28.3 | 25.0 | 23.1 |
| 4/10/2013 | 4/12/2013 | 22 | 2 | 21.6 | 37.0 | 26.3 | 28.3 | 25.5 | 23.6 |
| 4/10/2013 | 4/12/2013 | 23 | 2 | 20.0 | 39.8 | 26.7 | 28.6 | 25.7 | 23.7 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 36. PAPA009 (South Rocks lek) dBA and one-third octave band metrics, April 10-12, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/10/13 | 4/12/13 | dBA | 50 | 17.2 | 59.0 | 31.2 | 30.0 | 26.2 | 24.0 |
| 4/10/13 | 4/12/13 | 12.5 | 50 | 26.6 | 77.2 | 58.6 | 56.9 | 50.5 | 45.6 |
| 4/10/13 | 4/12/13 | 16 | 50 | 30.2 | 73.1 | 55.4 | 55.3 | 50.6 | 45.7 |
| 4/10/13 | 4/12/13 | 20 | 50 | 33.0 | 71.5 | 54.0 | 55.4 | 50.8 | 46.6 |
| 4/10/13 | 4/12/13 | 25 | 50 | 30.5 | 68.1 | 50.6 | 51.5 | 47.2 | 43.4 |
| 4/10/13 | 4/12/13 | 31.5 | 50 | 30.7 | 66.9 | 49.0 | 50.7 | 45.8 | 41.4 |
| 4/10/13 | 4/12/13 | 40 | 50 | 28.8 | 64.0 | 45.6 | 45.5 | 41.8 | 38.2 |
| 4/10/13 | 4/12/13 | 50 | 50 | 24.0 | 73.6 | 42.5 | 42.7 | 38.0 | 33.6 |
| 4/10/13 | 4/12/13 | 63 | 50 | 24.6 | 75.9 | 41.3 | 42.5 | 37.9 | 34.1 |
| 4/10/13 | 4/12/13 | 80 | 50 | 21.6 | 75.3 | 39.3 | 40.1 | 35.5 | 31.7 |
| 4/10/13 | 4/12/13 | 100 | 50 | 20.5 | 73.8 | 37.8 | 38.0 | 34.2 | 31.2 |
| 4/10/13 | 4/12/13 | 125 | 50 | 19.6 | 66.0 | 35.7 | 37.7 | 32.6 | 29.7 |
| 4/10/13 | 4/12/13 | 160 | 50 | 16.0 | 68.3 | 32.6 | 33.7 | 30.1 | 27.8 |
| 4/10/13 | 4/12/13 | 200 | 50 | 13.8 | 66.1 | 30.9 | 31.7 | 27.5 | 24.9 |
| 4/10/13 | 4/12/13 | 250 | 50 | 11.6 | 56.4 | 28.0 | 28.3 | 24.6 | 21.6 |
| 4/10/13 | 4/12/13 | 315 | 50 | 5.9 | 45.9 | 25.1 | 25.0 | 20.8 | 16.8 |
| 4/10/13 | 4/12/13 | 400 | 50 | 2.2 | 43.4 | 23.0 | 22.6 | 17.5 | 13.4 |
| 4/10/13 | 4/12/13 | 500 | 50 | -0.2 | 49.1 | 20.8 | 19.8 | 14.0 | 9.7 |
| 4/10/13 | 4/12/13 | 630 | 50 | -1.9 | 45.4 | 17.9 | 15.5 | 9.7 | 5.5 |
| 4/10/13 | 4/12/13 | 800 | 50 | -2.3 | 40.7 | 16.2 | 14.0 | 7.0 | 3.3 |
| 4/10/13 | 4/12/13 | 1000 | 50 | -1.6 | 37.3 | 16.0 | 13.1 | 5.7 | 1.9 |
| 4/10/13 | 4/12/13 | 1250 | 50 | -1.1 | 40.3 | 16.3 | 12.4 | 3.4 | 1.5 |
| 4/10/13 | 4/12/13 | 1600 | 50 | -0.2 | 40.0 | 16.0 | 11.1 | 2.4 | 1.7 |
| 4/10/13 | 4/12/13 | 2000 | 50 | 0.7 | 35.6 | 15.1 | 9.0 | 2.8 | 2.4 |
| 4/10/13 | 4/12/13 | 2500 | 50 | 1.7 | 34.6 | 13.6 | 7.7 | 3.5 | 3.1 |
| 4/10/13 | 4/12/13 | 3150 | 50 | 2.5 | 41.4 | 11.0 | 6.9 | 4.1 | 3.8 |
| 4/10/13 | 4/12/13 | 4000 | 50 | 1.7 | 35.4 | 8.3 | 5.8 | 4.6 | 4.4 |
| 4/10/13 | 4/12/13 | 5000 | 50 | 0.2 | 46.6 | 7.3 | 5.6 | 4.9 | 4.6 |
| 4/10/13 | 4/12/13 | 6300 | 50 | -0.1 | 42.6 | 5.9 | 5.3 | 5.0 | 4.6 |
| 4/10/13 | 4/12/13 | 8000 | 50 | -0.9 | 33.4 | 5.3 | 5.2 | 4.9 | 4.5 |
| 4/10/13 | 4/12/13 | 10000 | 50 | -0.7 | 23.6 | 4.9 | 5.0 | 4.7 | 4.3 |
| 4/10/13 | 4/12/13 | 12500 | 50 | -0.6 | 25.4 | 4.5 | 4.7 | 4.4 | 3.9 |
| 4/10/13 | 4/12/13 | 16000 | 50 | -0.8 | 25.1 | 4.0 | 4.4 | 3.9 | 3.4 |
| 4/10/13 | 4/12/13 | 20000 | 50 | -0.3 | 22.5 | 3.2 | 4.1 | 2.8 | 2.5 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 37. PAPA010 (Stud Horse Butte lek) hourly dBA metrics, April 10-12, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/10/2013 | 4/12/2013 | 0 | 2 | 19.5 | 36.7 | 24.6 | 26.6 | 23.4 | 21.9 |
| 4/10/2013 | 4/12/2013 | 1 | 2 | 18.9 | 40.1 | 28.6 | 29.8 | 25.8 | 23.2 |
| 4/10/2013 | 4/12/2013 | 2 | 2 | 19.7 | 50.0 | 30.9 | 31.5 | 26.5 | 24.1 |
| 4/10/2013 | 4/12/2013 | 3 | 2 | 18.1 | 42.0 | 30.4 | 29.8 | 25.8 | 22.6 |
| 4/10/2013 | 4/12/2013 | 4 | 2 | 20.4 | 36.2 | 25.9 | 27.9 | 25.0 | 23.0 |
| 4/10/2013 | 4/12/2013 | 5 | 2 | 21.5 | 37.4 | 28.4 | 29.4 | 27.1 | 25.4 |
| 4/10/2013 | 4/12/2013 | 6 | 2 | 22.6 | 40.1 | 30.0 | 31.2 | 28.1 | 26.2 |
| 4/10/2013 | 4/12/2013 | 7 | 2 | 22.9 | 43.4 | 27.5 | 29.3 | 26.7 | 25.1 |
| 4/10/2013 | 4/12/2013 | 8 | 2 | 19.0 | 46.0 | 29.9 | 31.5 | 26.6 | 23.1 |
| 4/10/2013 | 4/12/2013 | 9 | 2 | 19.4 | 48.5 | 32.7 | 33.7 | 27.6 | 24.3 |
| 4/10/2013 | 4/12/2013 | 10 | 2 | 20.1 | 60.3 | 34.5 | 36.3 | 30.3 | 25.7 |
| 4/10/2013 | 4/12/2013 | 11 | 2 | 19.8 | 51.6 | 34.1 | 35.3 | 29.2 | 24.8 |
| 4/10/2013 | 4/12/2013 | 12 | 2 | 19.1 | 49.9 | 34.9 | 35.9 | 29.4 | 25.2 |
| 4/10/2013 | 4/12/2013 | 13 | 3 | 19.9 | 52.0 | 32.6 | 33.0 | 26.6 | 23.5 |
| 4/10/2013 | 4/12/2013 | 14 | 2 | 23.1 | 50.8 | 33.5 | 34.6 | 30.3 | 26.9 |
| 4/10/2013 | 4/12/2013 | 15 | 2 | 22.6 | 50.4 | 33.3 | 34.4 | 30.1 | 26.8 |
| 4/10/2013 | 4/12/2013 | 16 | 2 | 22.4 | 50.6 | 35.4 | 36.8 | 31.0 | 27.2 |
| 4/10/2013 | 4/12/2013 | 17 | 2 | 22.8 | 51.7 | 35.2 | 37.8 | 31.9 | 27.7 |
| 4/10/2013 | 4/12/2013 | 18 | 2 | 24.5 | 50.0 | 36.3 | 39.4 | 34.1 | 29.5 |
| 4/10/2013 | 4/12/2013 | 19 | 2 | 22.5 | 53.8 | 33.3 | 35.9 | 29.9 | 26.3 |
| 4/10/2013 | 4/12/2013 | 20 | 2 | 22.7 | 48.9 | 32.5 | 34.0 | 29.2 | 26.5 |
| 4/10/2013 | 4/12/2013 | 21 | 2 | 22.1 | 42.4 | 28.3 | 31.0 | 26.7 | 24.6 |
| 4/10/2013 | 4/12/2013 | 22 | 2 | 22.7 | 36.6 | 27.6 | 29.5 | 26.9 | 25.1 |
| 4/10/2013 | 4/12/2013 | 23 | 2 | 20.8 | 39.4 | 26.9 | 28.6 | 25.8 | 24.2 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 38. PAPA010 (Stud Horse Butte lek) dBA and one-third octave band metrics, April 10-12, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/10/13 | 4/12/13 | dBA | 49 | 18.1 | 60.3 | 32.2 | 31.6 | 27.3 | 25.4 |
| 4/10/13 | 4/12/13 | 12.5 | 49 | 25.2 | 76.7 | 57.0 | 55.3 | 49.9 | 45.1 |
| 4/10/13 | 4/12/13 | 16 | 49 | 33.0 | 74.8 | 55.9 | 55.7 | 52.0 | 47.6 |
| 4/10/13 | 4/12/13 | 20 | 49 | 34.8 | 74.5 | 55.1 | 56.5 | 51.9 | 47.3 |
| 4/10/13 | 4/12/13 | 25 | 49 | 31.6 | 73.6 | 51.9 | 53.0 | 48.1 | 44.4 |
| 4/10/13 | 4/12/13 | 31.5 | 49 | 32.9 | 69.6 | 49.1 | 50.7 | 46.9 | 42.9 |
| 4/10/13 | 4/12/13 | 40 | 49 | 29.9 | 65.6 | 44.8 | 45.5 | 42.5 | 39.1 |
| 4/10/13 | 4/12/13 | 50 | 49 | 25.0 | 64.1 | 43.6 | 45.4 | 40.8 | 37.6 |
| 4/10/13 | 4/12/13 | 63 | 49 | 24.6 | 61.2 | 40.2 | 41.9 | 38.4 | 35.4 |
| 4/10/13 | 4/12/13 | 80 | 49 | 21.9 | 70.4 | 38.3 | 39.5 | 35.5 | 32.6 |
| 4/10/13 | 4/12/13 | 100 | 49 | 18.9 | 66.3 | 37.9 | 37.6 | 34.0 | 31.4 |
| 4/10/13 | 4/12/13 | 125 | 49 | 18.6 | 69.5 | 34.7 | 36.4 | 32.7 | 29.8 |
| 4/10/13 | 4/12/13 | 160 | 49 | 15.4 | 63.9 | 32.7 | 33.6 | 30.4 | 27.6 |
| 4/10/13 | 4/12/13 | 200 | 49 | 14.1 | 59.4 | 31.7 | 33.2 | 29.2 | 26.4 |
| 4/10/13 | 4/12/13 | 250 | 49 | 11.5 | 55.1 | 29.4 | 30.8 | 26.4 | 23.4 |
| 4/10/13 | 4/12/13 | 315 | 49 | 5.9 | 44.7 | 26.9 | 27.4 | 22.6 | 19.0 |
| 4/10/13 | 4/12/13 | 400 | 49 | 3.1 | 43.4 | 25.1 | 25.7 | 19.5 | 16.1 |
| 4/10/13 | 4/12/13 | 500 | 49 | 0.0 | 48.9 | 22.9 | 20.8 | 14.7 | 11.4 |
| 4/10/13 | 4/12/13 | 630 | 49 | -1.7 | 43.8 | 20.5 | 18.8 | 12.5 | 8.3 |
| 4/10/13 | 4/12/13 | 800 | 49 | -1.3 | 41.1 | 18.3 | 16.1 | 9.7 | 5.5 |
| 4/10/13 | 4/12/13 | 1000 | 49 | -1.1 | 40.8 | 17.9 | 16.5 | 8.6 | 4.8 |
| 4/10/13 | 4/12/13 | 1250 | 49 | -0.4 | 37.5 | 18.3 | 15.5 | 7.2 | 3.6 |
| 4/10/13 | 4/12/13 | 1600 | 49 | 0.2 | 36.5 | 18.0 | 13.0 | 5.1 | 2.9 |
| 4/10/13 | 4/12/13 | 2000 | 49 | 1.2 | 41.2 | 17.4 | 9.7 | 3.7 | 2.9 |
| 4/10/13 | 4/12/13 | 2500 | 49 | 2.0 | 58.5 | 16.4 | 8.6 | 3.8 | 3.4 |
| 4/10/13 | 4/12/13 | 3150 | 49 | 3.0 | 50.0 | 12.6 | 7.0 | 4.5 | 4.1 |
| 4/10/13 | 4/12/13 | 4000 | 49 | 3.3 | 42.6 | 9.1 | 6.8 | 5.1 | 4.8 |
| 4/10/13 | 4/12/13 | 5000 | 49 | 1.4 | 50.8 | 9.6 | 6.4 | 5.5 | 5.3 |
| 4/10/13 | 4/12/13 | 6300 | 49 | 1.6 | 42.0 | 6.7 | 6.1 | 5.8 | 5.5 |
| 4/10/13 | 4/12/13 | 8000 | 49 | -0.2 | 27.3 | 6.2 | 6.0 | 5.7 | 5.5 |
| 4/10/13 | 4/12/13 | 10000 | 49 | -0.3 | 23.9 | 5.7 | 5.7 | 5.4 | 5.2 |
| 4/10/13 | 4/12/13 | 12500 | 49 | -0.6 | 22.8 | 5.0 | 5.2 | 4.8 | 4.5 |
| 4/10/13 | 4/12/13 | 16000 | 49 | -0.9 | 20.7 | 4.2 | 4.5 | 3.9 | 3.6 |
| 4/10/13 | 4/12/13 | 20000 | 49 | -1.1 | 19.4 | 3.1 | 3.1 | 2.5 | 2.2 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 39. PAPA011 (Little Saddle lek) hourly dBA metrics, April 12-14, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/12/2013 | 4/14/2013 | 0 | 2 | 15.3 | 39.0 | 21.3 | 21.8 | 19.4 | 17.8 |
| 4/12/2013 | 4/14/2013 | 1 | 2 | 16.0 | 38.6 | 21.9 | 23.5 | 20.4 | 18.0 |
| 4/12/2013 | 4/14/2013 | 2 | 2 | 16.0 | 36.9 | 22.0 | 23.2 | 19.8 | 18.1 |
| 4/12/2013 | 4/14/2013 | 3 | 2 | 16.0 | 41.8 | 24.4 | 24.4 | 21.2 | 19.3 |
| 4/12/2013 | 4/14/2013 | 4 | 2 | 15.8 | 42.7 | 25.9 | 25.7 | 22.1 | 20.1 |
| 4/12/2013 | 4/14/2013 | 5 | 2 | 16.0 | 40.0 | 26.5 | 30.5 | 23.4 | 19.5 |
| 4/12/2013 | 4/14/2013 | 6 | 2 | 17.2 | 44.1 | 29.4 | 32.3 | 25.0 | 19.9 |
| 4/12/2013 | 4/14/2013 | 7 | 2 | 16.8 | 39.5 | 24.6 | 27.6 | 21.7 | 19.2 |
| 4/12/2013 | 4/14/2013 | 8 | 2 | 18 | 49 | 27 | 29 | 22 | 20 |
| 4/13/2013 | 4/13/2013 | 9 | 1 | 17 | 50 | 28 | 28 | 21 | 19 |
| 4/12/2013 | 4/14/2013 | 10 | 2 | 18 | 57 | 31 | 32 | 27 | 23 |
| 4/12/2013 | 4/14/2013 | 11 | 2 | 17 | 52 | 32 | 32 | 26 | 22 |
| 4/12/2013 | 4/14/2013 | 12 | 2 | 17 | 51 | 33 | 34 | 27 | 23 |
| 4/12/2013 | 4/14/2013 | 13 | 2 | 17 | 55 | 38 | 39 | 33 | 27 |
| 4/12/2013 | 4/14/2013 | 14 | 2 | 17 | 49 | 34 | 34 | 27 | 23 |
| 4/12/2013 | 4/14/2013 | 15 | 2 | 16.6 | 51.0 | 35.1 | 35.3 | 29.1 | 23.9 |
| 4/12/2013 | 4/14/2013 | 16 | 2 | 16.1 | 48.8 | 30.5 | 33.5 | 26.5 | 20.7 |
| 4/12/2013 | 4/14/2013 | 17 | 2 | 16.0 | 51.3 | 26.2 | 28.0 | 21.6 | 18.1 |
| 4/12/2013 | 4/14/2013 | 18 | 2 | 15.5 | 54.2 | 28.1 | 28.3 | 22.5 | 19.1 |
| 4/12/2013 | 4/14/2013 | 19 | 2 | 15.1 | 47.2 | 24.4 | 25.2 | 19.8 | 17.4 |
| 4/12/2013 | 4/14/2013 | 20 | 2 | 14.9 | 50.5 | 26.6 | 27.3 | 21.4 | 17.9 |
| 4/12/2013 | 4/14/2013 | 21 | 2 | 15.3 | 50.9 | 29.2 | 28.0 | 23.2 | 20.1 |
| 4/12/2013 | 4/14/2013 | 22 | 2 | 15.2 | 46.2 | 26.1 | 25.6 | 21.3 | 18.7 |
| 4/12/2013 | 4/14/2013 | 23 | 2 | 15.1 | 44.0 | 27.7 | 26.9 | 22.7 | 18.1 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 40. PAPA011 (Little Saddle lek) dBA and one-third octave band metrics, April 12-14, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/12/13 | 4/14/13 | dBA | 47 | 14.9 | 57.4 | 30.2 | 29.3 | 22.3 | 18.8 |
| 4/12/13 | 4/14/13 | 12.5 | 47 | 19.3 | 77.8 | 56.2 | 52.0 | 40.4 | 34.7 |
| 4/12/13 | 4/14/13 | 16 | 47 | 20.7 | 76.6 | 54.3 | 48.0 | 40.3 | 34.6 |
| 4/12/13 | 4/14/13 | 20 | 47 | 21.2 | 77.6 | 52.3 | 49.0 | 42.4 | 37.2 |
| 4/12/13 | 4/14/13 | 25 | 47 | 17.3 | 71.3 | 48.1 | 41.5 | 35.2 | 30.8 |
| 4/12/13 | 4/14/13 | 31.5 | 47 | 17.8 | 69.6 | 46.1 | 45.0 | 39.0 | 33.3 |
| 4/12/13 | 4/14/13 | 40 | 47 | 13.6 | 67.4 | 42.4 | 37.1 | 32.7 | 29.2 |
| 4/12/13 | 4/14/13 | 50 | 47 | 13.4 | 65.7 | 39.9 | 37.0 | 32.2 | 28.7 |
| 4/12/13 | 4/14/13 | 63 | 47 | 12.8 | 64.5 | 38.1 | 36.9 | 31.5 | 28.4 |
| 4/12/13 | 4/14/13 | 80 | 47 | 13.1 | 69.3 | 36.0 | 34.2 | 29.9 | 26.5 |
| 4/12/13 | 4/14/13 | 100 | 47 | 12.5 | 68.1 | 35.7 | 36.7 | 31.5 | 27.1 |
| 4/12/13 | 4/14/13 | 125 | 47 | 10.3 | 73.3 | 34.1 | 31.5 | 26.7 | 23.0 |
| 4/12/13 | 4/14/13 | 160 | 47 | 6.2 | 62.7 | 30.5 | 30.4 | 24.7 | 20.0 |
| 4/12/13 | 4/14/13 | 200 | 47 | 4.2 | 55.9 | 28.4 | 29.2 | 23.2 | 18.7 |
| 4/12/13 | 4/14/13 | 250 | 47 | 0.0 | 60.0 | 26.4 | 26.6 | 19.7 | 13.7 |
| 4/12/13 | 4/14/13 | 315 | 47 | -2.3 | 55.8 | 25.1 | 25.2 | 17.8 | 10.7 |
| 4/12/13 | 4/14/13 | 400 | 47 | -3.4 | 50.1 | 22.5 | 23.0 | 15.2 | 7.2 |
| 4/12/13 | 4/14/13 | 500 | 47 | -3.8 | 44.7 | 20.2 | 19.0 | 11.8 | 3.2 |
| 4/12/13 | 4/14/13 | 630 | 47 | -3.5 | 44.5 | 17.5 | 16.3 | 7.4 | 0.6 |
| 4/12/13 | 4/14/13 | 800 | 47 | -3.1 | 41.5 | 15.5 | 14.3 | 5.1 | -0.1 |
| 4/12/13 | 4/14/13 | 1000 | 47 | -2.1 | 34.6 | 15.1 | 14.0 | 4.0 | 0.0 |
| 4/12/13 | 4/14/13 | 1250 | 47 | -1.2 | 34.1 | 15.2 | 13.1 | 3.9 | 0.5 |
| 4/12/13 | 4/14/13 | 1600 | 47 | -0.3 | 35.1 | 15.7 | 11.8 | 3.4 | 1.3 |
| 4/12/13 | 4/14/13 | 2000 | 47 | 0.7 | 34.7 | 15.0 | 10.2 | 3.4 | 1.9 |
| 4/12/13 | 4/14/13 | 2500 | 47 | 1.6 | 34.6 | 13.4 | 8.7 | 3.8 | 2.7 |
| 4/12/13 | 4/14/13 | 3150 | 47 | 2.2 | 38.6 | 11.4 | 7.7 | 4.4 | 3.4 |
| 4/12/13 | 4/14/13 | 4000 | 47 | 1.6 | 45.5 | 9.3 | 6.3 | 4.6 | 4.2 |
| 4/12/13 | 4/14/13 | 5000 | 47 | 1.5 | 49.2 | 9.9 | 6.1 | 5.0 | 4.7 |
| 4/12/13 | 4/14/13 | 6300 | 47 | 1.5 | 41.2 | 7.1 | 5.8 | 5.3 | 5.0 |
| 4/12/13 | 4/14/13 | 8000 | 47 | 1.0 | 23.4 | 5.8 | 5.7 | 5.3 | 5.1 |
| 4/12/13 | 4/14/13 | 10000 | 47 | 0.7 | 27.3 | 5.5 | 5.4 | 5.1 | 4.9 |
| 4/12/13 | 4/14/13 | 12500 | 47 | 0.4 | 26.8 | 5.1 | 5.0 | 4.6 | 4.3 |
| 4/12/13 | 4/14/13 | 16000 | 47 | 0.2 | 28.5 | 4.4 | 4.5 | 3.8 | 3.6 |
| 4/12/13 | 4/14/13 | 20000 | 47 | 0.4 | 27.2 | 3.5 | 4.1 | 2.7 | 2.4 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 41. PAPA012 (Alkali Draw lek) hourly dBA metrics, April 12-14, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/12/2013 | 4/14/2013 | 0 | 2 | 16.0 | 36.0 | 22.1 | 23.5 | 20.7 | 19.0 |
| 4/12/2013 | 4/14/2013 | 1 | 2 | 18.4 | 44.2 | 23.8 | 24.9 | 21.6 | 19.9 |
| 4/12/2013 | 4/14/2013 | 2 | 2 | 16.7 | 39.7 | 23.6 | 24.4 | 21.2 | 19.7 |
| 4/12/2013 | 4/14/2013 | 3 | 2 | 16.7 | 40.5 | 23.7 | 24.3 | 21.2 | 19.7 |
| 4/12/2013 | 4/14/2013 | 4 | 2 | 16.1 | 42.0 | 23.8 | 25.1 | 21.3 | 19.4 |
| 4/12/2013 | 4/14/2013 | 5 | 2 | 17.3 | 44.0 | 24.2 | 27.2 | 21.8 | 20.0 |
| 4/12/2013 | 4/14/2013 | 6 | 2 | 19.2 | 41.0 | 27.5 | 30.0 | 26.1 | 22.7 |
| 4/12/2013 | 4/14/2013 | 7 | 2 | 18.0 | 59.5 | 27.9 | 28.7 | 24.3 | 21.7 |
| 4/12/2013 | 4/14/2013 | 8 | 2 | 19.0 | 48.9 | 28.6 | 31.2 | 24.5 | 21.6 |
| 4/12/2013 | 4/14/2013 | 9 | 2 | 17.4 | 50.6 | 30.8 | 31.5 | 26.0 | 21.6 |
| 4/13/2013 | 4/13/2013 | 10 | 1 | 17.6 | 65.5 | 37.3 | 33.9 | 27.1 | 21.4 |
| 4/13/2013 | 4/13/2013 | 11 | 1 | 19.8 | 47.0 | 33.1 | 36.7 | 29.8 | 23.7 |
| 4/12/2013 | 4/14/2013 | 12 | 2 | 17.1 | 49.0 | 33.5 | 35.8 | 28.6 | 22.6 |
| 4/12/2013 | 4/14/2013 | 13 | 2 | 17.0 | 53.2 | 37.7 | 39.2 | 31.7 | 25.2 |
| 4/12/2013 | 4/14/2013 | 14 | 2 | 16.9 | 54.5 | 37.1 | 36.7 | 29.8 | 24.9 |
| 4/12/2013 | 4/14/2013 | 15 | 2 | 16.7 | 57.0 | 37.5 | 37.8 | 30.1 | 24.0 |
| 4/12/2013 | 4/14/2013 | 16 | 2 | 16.6 | 51.2 | 32.6 | 35.5 | 28.1 | 22.4 |
| 4/12/2013 | 4/14/2013 | 17 | 2 | 15.6 | 47.0 | 26.3 | 29.3 | 22.1 | 18.1 |
| 4/12/2013 | 4/14/2013 | 18 | 2 | 14.7 | 49.8 | 27.8 | 28.3 | 21.9 | 18.6 |
| 4/12/2013 | 4/14/2013 | 19 | 2 | 14.6 | 41.7 | 23.7 | 25.9 | 19.6 | 17.7 |
| 4/12/2013 | 4/14/2013 | 20 | 2 | 15.4 | 38.2 | 22.9 | 25.0 | 19.7 | 17.9 |
| 4/12/2013 | 4/14/2013 | 21 | 2 | 15.2 | 46.7 | 29.4 | 28.0 | 23.0 | 19.7 |
| 4/12/2013 | 4/14/2013 | 22 | 2 | 15.2 | 43.1 | 26.6 | 25.9 | 21.9 | 19.2 |
| 4/12/2013 | 4/14/2013 | 23 | 2 | 15.1 | 38.9 | 23.5 | 24.1 | 20.6 | 18.4 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 42. PAPA012 (Alkali Draw lek) dBA and one-third octave band metrics, April 12-14, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/12/13 | 4/14/13 | dBA | 46 | 14.6 | 65.5 | 31.4 | 28.7 | 23.3 | 20.4 |
| 4/12/13 | 4/14/13 | 12.5 | 46 | 20.7 | 73.9 | 49.7 | 48.5 | 43.2 | 38.1 |
| 4/12/13 | 4/14/13 | 16 | 46 | 23.0 | 70.9 | 47.0 | 47.1 | 42.3 | 38.7 |
| 4/12/13 | 4/14/13 | 20 | 46 | 25.3 | 69.0 | 48.1 | 50.5 | 46.1 | 41.8 |
| 4/12/13 | 4/14/13 | 25 | 46 | 21.3 | 67.2 | 43.2 | 44.3 | 38.6 | 35.1 |
| 4/12/13 | 4/14/13 | 31.5 | 46 | 21.8 | 67.6 | 43.4 | 45.5 | 40.3 | 35.8 |
| 4/12/13 | 4/14/13 | 40 | 46 | 16.2 | 63.5 | 37.4 | 38.0 | 34.2 | 31.3 |
| 4/12/13 | 4/14/13 | 50 | 46 | 15.2 | 59.7 | 36.4 | 37.3 | 33.6 | 30.9 |
| 4/12/13 | 4/14/13 | 63 | 46 | 15.8 | 57.6 | 36.4 | 38.3 | 33.9 | 30.7 |
| 4/12/13 | 4/14/13 | 80 | 46 | 14.6 | 66.2 | 34.1 | 35.3 | 31.5 | 28.5 |
| 4/12/13 | 4/14/13 | 100 | 46 | 12.6 | 73.4 | 34.5 | 34.9 | 31.3 | 28.3 |
| 4/12/13 | 4/14/13 | 125 | 46 | 11.8 | 77.0 | 33.7 | 32.0 | 28.4 | 25.5 |
| 4/12/13 | 4/14/13 | 160 | 46 | 9.2 | 70.0 | 30.8 | 30.0 | 25.6 | 22.8 |
| 4/12/13 | 4/14/13 | 200 | 46 | 7.4 | 68.1 | 28.3 | 28.5 | 23.6 | 20.5 |
| 4/12/13 | 4/14/13 | 250 | 46 | 3.3 | 66.7 | 26.6 | 26.1 | 20.6 | 16.5 |
| 4/12/13 | 4/14/13 | 315 | 46 | -0.3 | 60.5 | 24.0 | 23.7 | 17.4 | 12.4 |
| 4/12/13 | 4/14/13 | 400 | 46 | -3.0 | 56.7 | 20.9 | 20.0 | 12.5 | 6.9 |
| 4/12/13 | 4/14/13 | 500 | 46 | -3.8 | 55.1 | 18.2 | 15.5 | 8.0 | 2.1 |
| 4/12/13 | 4/14/13 | 630 | 46 | -3.7 | 53.2 | 16.2 | 13.8 | 5.8 | -0.3 |
| 4/12/13 | 4/14/13 | 800 | 46 | -3.7 | 56.5 | 17.2 | 16.1 | 6.3 | -1.0 |
| 4/12/13 | 4/14/13 | 1000 | 46 | -2.9 | 54.9 | 18.6 | 17.1 | 6.4 | -0.9 |
| 4/12/13 | 4/14/13 | 1250 | 46 | -2.2 | 51.2 | 19.1 | 16.6 | 5.3 | -0.5 |
| 4/12/13 | 4/14/13 | 1600 | 46 | -1.4 | 45.2 | 19.0 | 15.0 | 3.6 | 0.3 |
| 4/12/13 | 4/14/13 | 2000 | 46 | -0.7 | 42.8 | 18.1 | 12.7 | 2.8 | 0.8 |
| 4/12/13 | 4/14/13 | 2500 | 46 | 0.4 | 41.9 | 16.3 | 10.3 | 2.3 | 1.4 |
| 4/12/13 | 4/14/13 | 3150 | 46 | 1.3 | 42.3 | 13.4 | 7.1 | 2.6 | 2.2 |
| 4/12/13 | 4/14/13 | 4000 | 46 | 1.4 | 43.5 | 10.3 | 5.7 | 3.3 | 3.0 |
| 4/12/13 | 4/14/13 | 5000 | 46 | 1.4 | 41.0 | 9.0 | 4.9 | 4.0 | 3.7 |
| 4/12/13 | 4/14/13 | 6300 | 46 | 1.0 | 43.5 | 8.1 | 5.0 | 4.6 | 4.4 |
| 4/12/13 | 4/14/13 | 8000 | 46 | 0.4 | 46.2 | 8.6 | 5.3 | 5.1 | 4.9 |
| 4/12/13 | 4/14/13 | 10000 | 46 | 0.1 | 38.4 | 7.7 | 5.5 | 5.3 | 5.1 |
| 4/12/13 | 4/14/13 | 12500 | 46 | 0.3 | 39.7 | 7.7 | 5.2 | 4.9 | 4.7 |
| 4/12/13 | 4/14/13 | 16000 | 46 | -0.4 | 36.7 | 5.7 | 3.4 | 2.8 | 2.7 |
| 4/12/13 | 4/14/13 | 20000 | 46 | -0.7 | 29.3 | 2.3 | 2.1 | 0.3 | 0.1 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 43. PAPA013 (Sand Draw lek) hourly dBA metrics, April 12-14, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/12/2013 | 4/14/2013 | 0 | 2 | 18.5 | 36.7 | 26.3 | 27.6 | 24.7 | 22.2 |
| 4/12/2013 | 4/14/2013 | 1 | 2 | 16.7 | 36.9 | 27.0 | 27.6 | 24.9 | 21.6 |
| 4/12/2013 | 4/14/2013 | 2 | 2 | 17.2 | 39.1 | 29.2 | 29.5 | 25.8 | 23.8 |
| 4/12/2013 | 4/14/2013 | 3 | 2 | 19.2 | 41.6 | 30.5 | 32.7 | 28.4 | 25.6 |
| 4/12/2013 | 4/14/2013 | 4 | 2 | 18.7 | 42.2 | 31.1 | 31.7 | 27.5 | 25.2 |
| 4/12/2013 | 4/14/2013 | 5 | 2 | 17.8 | 38.7 | 26.4 | 27.4 | 23.9 | 21.0 |
| 4/12/2013 | 4/14/2013 | 6 | 2 | 17.7 | 53.6 | 25.1 | 25.3 | 22.5 | 20.3 |
| 4/12/2013 | 4/14/2013 | 7 | 2 | 19.1 | 63.1 | 31.7 | 25.8 | 23.6 | 21.2 |
| 4/12/2013 | 4/14/2013 | 8 | 2 | 19.8 | 75.0 | 44.8 | 32.3 | 26.5 | 23.2 |
| 4/12/2013 | 4/14/2013 | 9 | 2 | 20.3 | 50.5 | 34.1 | 35.5 | 29.9 | 25.1 |
| 4/12/2013 | 4/14/2013 | 10 | 2 | 21.4 | 51.6 | 37.7 | 41.2 | 35.0 | 29.3 |
| 4/13/2013 | 4/13/2013 | 11 | 1 | 24.8 | 49.0 | 37.8 | 41.6 | 35.1 | 29.5 |
| 4/13/2013 | 4/13/2013 | 12 | 1 | 24.5 | 51.7 | 38.8 | 42.5 | 36.3 | 30.3 |
| 4/12/2013 | 4/14/2013 | 13 | 2 | 19.6 | 53.7 | 37.6 | 40.2 | 33.0 | 27.4 |
| 4/12/2013 | 4/14/2013 | 14 | 2 | 21.3 | 56.3 | 40.2 | 40.6 | 34.3 | 29.4 |
| 4/12/2013 | 4/14/2013 | 15 | 2 | 18.6 | 56.2 | 41.5 | 40.2 | 33.6 | 28.8 |
| 4/12/2013 | 4/14/2013 | 16 | 2 | 18.6 | 57.1 | 36.5 | 38.9 | 30.9 | 24.4 |
| 4/12/2013 | 4/14/2013 | 17 | 2 | 18.2 | 48.6 | 29.2 | 32.4 | 24.7 | 20.4 |
| 4/12/2013 | 4/14/2013 | 18 | 2 | 17.4 | 44.4 | 28.6 | 31.6 | 24.9 | 20.5 |
| 4/12/2013 | 4/14/2013 | 19 | 2 | 17.5 | 39.8 | 26.0 | 28.5 | 23.6 | 21.2 |
| 4/12/2013 | 4/14/2013 | 20 | 2 | 20.6 | 47.1 | 28.1 | 30.4 | 26.6 | 23.7 |
| 4/12/2013 | 4/14/2013 | 21 | 2 | 23.2 | 53.8 | 33.2 | 34.2 | 29.9 | 26.6 |
| 4/12/2013 | 4/14/2013 | 22 | 2 | 22.6 | 47.4 | 31.4 | 33.4 | 29.3 | 26.3 |
| 4/12/2013 | 4/14/2013 | 23 | 2 | 19.4 | 45.5 | 29.0 | 31.9 | 27.1 | 23.1 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 44. PAPA013 (Sand Draw lek) dBA and one-third octave band metrics, April 12-14, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/12/13 | 4/14/13 | dBA | 46 | 16.7 | 75.0 | 36.1 | 32.0 | 27.3 | 23.1 |
| 4/12/13 | 4/14/13 | 12.5 | 46 | 23.7 | 79.5 | 60.1 | 56.1 | 49.9 | 43.8 |
| 4/12/13 | 4/14/13 | 16 | 46 | 27.0 | 76.5 | 57.2 | 54.8 | 47.0 | 41.3 |
| 4/12/13 | 4/14/13 | 20 | 46 | 29.2 | 73.1 | 54.4 | 53.6 | 48.3 | 42.4 |
| 4/12/13 | 4/14/13 | 25 | 46 | 24.3 | 71.3 | 50.9 | 50.6 | 45.5 | 40.6 |
| 4/12/13 | 4/14/13 | 31.5 | 46 | 28.3 | 68.3 | 49.9 | 51.1 | 46.4 | 41.7 |
| 4/12/13 | 4/14/13 | 40 | 46 | 25.6 | 65.9 | 45.9 | 44.3 | 40.0 | 36.7 |
| 4/12/13 | 4/14/13 | 50 | 46 | 24.0 | 65.1 | 42.9 | 40.2 | 35.8 | 32.5 |
| 4/12/13 | 4/14/13 | 63 | 46 | 24.1 | 61.9 | 40.7 | 39.7 | 35.3 | 32.2 |
| 4/12/13 | 4/14/13 | 80 | 46 | 20.6 | 61.8 | 38.1 | 37.1 | 33.3 | 30.1 |
| 4/12/13 | 4/14/13 | 100 | 46 | 18.7 | 63.9 | 39.8 | 37.8 | 33.9 | 30.5 |
| 4/12/13 | 4/14/13 | 125 | 46 | 16.3 | 66.3 | 35.3 | 35.1 | 31.2 | 27.5 |
| 4/12/13 | 4/14/13 | 160 | 46 | 15.1 | 70.2 | 32.6 | 32.1 | 28.4 | 24.7 |
| 4/12/13 | 4/14/13 | 200 | 46 | 13.4 | 55.5 | 31.1 | 31.9 | 27.8 | 23.5 |
| 4/12/13 | 4/14/13 | 250 | 46 | 9.7 | 57.3 | 28.8 | 29.9 | 25.3 | 21.2 |
| 4/12/13 | 4/14/13 | 315 | 46 | 6.4 | 51.2 | 26.8 | 27.2 | 22.3 | 17.2 |
| 4/12/13 | 4/14/13 | 400 | 46 | 2.6 | 50.5 | 24.8 | 25.2 | 19.8 | 14.5 |
| 4/12/13 | 4/14/13 | 500 | 46 | -0.7 | 49.2 | 22.7 | 22.8 | 17.1 | 11.2 |
| 4/12/13 | 4/14/13 | 630 | 46 | -2.6 | 42.7 | 20.8 | 20.0 | 13.5 | 7.5 |
| 4/12/13 | 4/14/13 | 800 | 46 | -2.8 | 38.2 | 20.5 | 20.0 | 12.3 | 5.5 |
| 4/12/13 | 4/14/13 | 1000 | 46 | -1.9 | 38.1 | 21.2 | 21.1 | 12.5 | 5.4 |
| 4/12/13 | 4/14/13 | 1250 | 46 | -1.6 | 38.5 | 20.9 | 18.1 | 8.2 | 2.4 |
| 4/12/13 | 4/14/13 | 1600 | 46 | -0.7 | 39.4 | 21.0 | 15.8 | 6.2 | 2.0 |
| 4/12/13 | 4/14/13 | 2000 | 46 | 0.4 | 44.9 | 20.0 | 11.8 | 3.6 | 1.7 |
| 4/12/13 | 4/14/13 | 2500 | 46 | 1.3 | 62.8 | 21.7 | 10.1 | 3.2 | 2.4 |
| 4/12/13 | 4/14/13 | 3150 | 46 | 2.1 | 71.2 | 28.4 | 8.8 | 3.6 | 3.1 |
| 4/12/13 | 4/14/13 | 4000 | 46 | 3.1 | 69.5 | 24.8 | 7.0 | 4.1 | 3.8 |
| 4/12/13 | 4/14/13 | 5000 | 46 | 2.7 | 45.2 | 10.8 | 6.1 | 4.5 | 4.2 |
| 4/12/13 | 4/14/13 | 6300 | 46 | 1.6 | 46.7 | 8.6 | 5.3 | 4.7 | 4.5 |
| 4/12/13 | 4/14/13 | 8000 | 46 | 1.6 | 57.9 | 11.0 | 4.8 | 4.6 | 4.4 |
| 4/12/13 | 4/14/13 | 10000 | 46 | 0.3 | 38.0 | 6.1 | 4.4 | 4.2 | 4.1 |
| 4/12/13 | 4/14/13 | 12500 | 46 | 0.1 | 34.6 | 5.3 | 3.8 | 3.5 | 3.3 |
| 4/12/13 | 4/14/13 | 16000 | 46 | -0.3 | 35.7 | 4.4 | 3.0 | 2.6 | 2.4 |
| 4/12/13 | 4/14/13 | 20000 | 46 | -1.1 | 29.5 | 2.7 | 1.9 | 1.0 | 0.7 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 45. PAPA014 (Lovatt West lek) hourly dBA metrics, April 18-21, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/18/2013 | 4/21/2013 | 0 | 3 | 19.8 | 36.4 | 29.3 | 30.7 | 29.5 | 28.5 |
| 4/18/2013 | 4/21/2013 | 1 | 3 | 24.9 | 38.9 | 30.9 | 33.0 | 30.2 | 27.3 |
| 4/18/2013 | 4/21/2013 | 2 | 3 | 23.7 | 41.6 | 31.5 | 32.0 | 30.5 | 28.9 |
| 4/18/2013 | 4/21/2013 | 3 | 3 | 25.9 | 42.4 | 32.9 | 30.0 | 28.9 | 27.7 |
| 4/18/2013 | 4/21/2013 | 4 | 3 | 25.6 | 43.1 | 34.0 | 33.3 | 29.7 | 27.3 |
| 4/18/2013 | 4/21/2013 | 5 | 3 | 27.0 | 46.7 | 34.0 | 35.3 | 32.6 | 29.7 |
| 4/18/2013 | 4/21/2013 | 6 | 3 | 27.6 | 43.6 | 31.9 | 32.5 | 30.9 | 29.6 |
| 4/18/2013 | 4/21/2013 | 7 | 3 | 23.1 | 43.7 | 31.2 | 33.9 | 30.2 | 28.4 |
| 4/18/2013 | 4/21/2013 | 8 | 3 | 21.0 | 52.4 | 31.4 | 32.4 | 28.0 | 24.1 |
| 4/18/2013 | 4/21/2013 | 9 | 3 | 19.8 | 48.7 | 26.4 | 28.7 | 24.8 | 22.6 |
| 4/18/2013 | 4/21/2013 | 10 | 3 | 19.0 | 58.0 | 29.8 | 28.4 | 25.4 | 23.1 |
| 4/18/2013 | 4/21/2013 | 11 | 3 | 19.6 | 47.0 | 29.4 | 33.3 | 26.9 | 23.3 |
| 4/18/2013 | 4/21/2013 | 12 | 4 | 19.8 | 56.8 | 32.5 | 34.6 | 28.2 | 23.9 |
| 4/18/2013 | 4/21/2013 | 13 | 4 | 19.9 | 58.3 | 34.1 | 36.2 | 29.3 | 24.9 |
| 4/18/2013 | 4/21/2013 | 14 | 4 | 19.8 | 49.3 | 33.9 | 36.8 | 30.6 | 25.4 |
| 4/18/2013 | 4/21/2013 | 15 | 3 | 20.9 | 55.0 | 36.3 | 40.8 | 31.9 | 25.0 |
| 4/18/2013 | 4/21/2013 | 16 | 3 | 21.1 | 59.5 | 36.8 | 40.2 | 34.7 | 28.9 |
| 4/18/2013 | 4/21/2013 | 17 | 3 | 20.5 | 55.0 | 38.1 | 40.1 | 34.8 | 29.8 |
| 4/18/2013 | 4/21/2013 | 18 | 3 | 19.9 | 50.9 | 35.7 | 38.9 | 33.2 | 27.8 |
| 4/18/2013 | 4/21/2013 | 19 | 3 | 20.0 | 52.6 | 36.0 | 33.6 | 28.4 | 24.5 |
| 4/18/2013 | 4/21/2013 | 20 | 3 | 21.6 | 51.5 | 32.8 | 30.6 | 28.9 | 24.5 |
| 4/18/2013 | 4/21/2013 | 21 | 3 | 22.6 | 44.2 | 31.2 | 30.8 | 29.2 | 27.1 |
| 4/18/2013 | 4/21/2013 | 22 | 3 | 23.7 | 44.7 | 33.1 | 36.5 | 30.0 | 27.0 |
| 4/18/2013 | 4/21/2013 | 23 | 3 | 21.2 | 38.7 | 29.2 | 31.8 | 29.1 | 27.2 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 46. PAPA014 (Lovatt West lek) dBA and one-third octave band metrics, April 18-21, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/18/13 | 4/21/13 | dBA | 75 | 19.0 | 59.5 | 33.5 | 33.7 | 29.6 | 27.0 |
| 4/18/13 | 4/21/13 | 12.5 | 75 | 20.5 | 73.7 | 49.9 | 45.7 | 41.4 | 35.5 |
| 4/18/13 | 4/21/13 | 16 | 75 | 24.6 | 71.1 | 49.6 | 50.6 | 44.4 | 40.1 |
| 4/18/13 | 4/21/13 | 20 | 75 | 31.0 | 76.1 | 59.9 | 61.4 | 52.6 | 48.4 |
| 4/18/13 | 4/21/13 | 25 | 75 | 23.6 | 66.3 | 44.7 | 46.0 | 42.4 | 39.2 |
| 4/18/13 | 4/21/13 | 31.5 | 75 | 26.3 | 66.1 | 49.3 | 51.8 | 47.5 | 42.6 |
| 4/18/13 | 4/21/13 | 40 | 75 | 25.6 | 64.0 | 45.1 | 47.0 | 44.0 | 41.1 |
| 4/18/13 | 4/21/13 | 50 | 75 | 25.9 | 67.6 | 43.7 | 45.2 | 41.4 | 38.8 |
| 4/18/13 | 4/21/13 | 63 | 75 | 25.1 | 68.3 | 42.5 | 43.8 | 40.0 | 36.5 |
| 4/18/13 | 4/21/13 | 80 | 75 | 22.8 | 70.9 | 39.4 | 40.3 | 36.1 | 33.3 |
| 4/18/13 | 4/21/13 | 100 | 75 | 22.2 | 72.8 | 38.7 | 39.7 | 36.2 | 33.0 |
| 4/18/13 | 4/21/13 | 125 | 75 | 21.6 | 70.4 | 39.3 | 40.3 | 36.8 | 34.1 |
| 4/18/13 | 4/21/13 | 160 | 75 | 19.1 | 65.4 | 34.1 | 34.8 | 31.5 | 28.0 |
| 4/18/13 | 4/21/13 | 200 | 75 | 8.6 | 66.2 | 32.6 | 32.9 | 28.1 | 24.2 |
| 4/18/13 | 4/21/13 | 250 | 75 | 5.8 | 62.0 | 29.2 | 29.7 | 25.2 | 21.4 |
| 4/18/13 | 4/21/13 | 315 | 75 | 3.4 | 57.5 | 27.2 | 28.2 | 22.6 | 18.9 |
| 4/18/13 | 4/21/13 | 400 | 75 | 0.3 | 50.6 | 24.2 | 23.7 | 19.0 | 15.5 |
| 4/18/13 | 4/21/13 | 500 | 75 | -1.6 | 48.6 | 21.4 | 22.9 | 15.3 | 10.6 |
| 4/18/13 | 4/21/13 | 630 | 75 | -2.9 | 46.9 | 17.9 | 18.3 | 10.3 | 5.8 |
| 4/18/13 | 4/21/13 | 800 | 75 | -2.1 | 41.9 | 17.8 | 19.4 | 8.7 | 5.4 |
| 4/18/13 | 4/21/13 | 1000 | 75 | -1.8 | 38.4 | 18.8 | 20.4 | 8.7 | 4.7 |
| 4/18/13 | 4/21/13 | 1250 | 75 | -1.4 | 42.4 | 20.9 | 21.8 | 11.7 | 5.1 |
| 4/18/13 | 4/21/13 | 1600 | 75 | -0.9 | 48.6 | 20.9 | 22.1 | 11.0 | 4.2 |
| 4/18/13 | 4/21/13 | 2000 | 75 | -0.4 | 51.8 | 19.6 | 17.6 | 8.2 | 2.8 |
| 4/18/13 | 4/21/13 | 2500 | 75 | 0.3 | 53.9 | 17.9 | 12.8 | 5.2 | 2.1 |
| 4/18/13 | 4/21/13 | 3150 | 75 | 1.3 | 52.6 | 14.8 | 12.2 | 4.5 | 2.9 |
| 4/18/13 | 4/21/13 | 4000 | 75 | 2.2 | 52.8 | 11.2 | 4.6 | 3.4 | 3.0 |
| 4/18/13 | 4/21/13 | 5000 | 75 | 1.9 | 57.1 | 12.7 | 4.3 | 3.9 | 3.7 |
| 4/18/13 | 4/21/13 | 6300 | 75 | 1.1 | 43.7 | 7.2 | 4.7 | 4.5 | 4.4 |
| 4/18/13 | 4/21/13 | 8000 | 75 | 0.6 | 40.0 | 6.3 | 5.2 | 5.0 | 4.9 |
| 4/18/13 | 4/21/13 | 10000 | 75 | -0.2 | 31.8 | 5.9 | 5.5 | 5.3 | 5.2 |
| 4/18/13 | 4/21/13 | 12500 | 75 | -0.5 | 33.1 | 5.6 | 5.0 | 4.9 | 4.7 |
| 4/18/13 | 4/21/13 | 16000 | 75 | -1.1 | 29.3 | 3.6 | 2.9 | 2.8 | 2.6 |
| 4/18/13 | 4/21/13 | 20000 | 75 | -1.0 | 22.6 | 1.3 | 0.5 | 0.2 | 0.1 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 47. PAPA015 (Cat lek) hourly dBA metrics, April 21-23, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/21/2013 | 4/23/2013 | 0 | 2 | 13.9 | 44.6 | 21.3 | 17.2 | 15.3 | 14.6 |
| 4/21/2013 | 4/23/2013 | 1 | 2 | 14.4 | 44.1 | 22.7 | 22.3 | 16.4 | 15.3 |
| 4/21/2013 | 4/23/2013 | 2 | 2 | 13.9 | 48.6 | 23.7 | 23.8 | 16.7 | 14.9 |
| 4/21/2013 | 4/23/2013 | 3 | 2 | 13.8 | 35.5 | 20.9 | 21.3 | 17.9 | 15.1 |
| 4/21/2013 | 4/23/2013 | 4 | 2 | 13.8 | 50.0 | 26.6 | 22.6 | 19.1 | 17.8 |
| 4/21/2013 | 4/23/2013 | 5 | 2 | 13.9 | 36.8 | 22.0 | 22.2 | 18.9 | 17.2 |
| 4/21/2013 | 4/23/2013 | 6 | 2 | 13.8 | 34.6 | 18.0 | 19.1 | 16.3 | 15.2 |
| 4/21/2013 | 4/23/2013 | 7 | 2 | 14.0 | 46.6 | 21.8 | 20.7 | 16.4 | 14.7 |
| 4/21/2013 | 4/23/2013 | 8 | 2 | 14.9 | 47.1 | 26.8 | 25.7 | 20.2 | 17.0 |
| 4/21/2013 | 4/23/2013 | 9 | 2 | 15.1 | 40.3 | 23.3 | 24.8 | 18.8 | 16.3 |
| 4/21/2013 | 4/23/2013 | 10 | 2 | 14.9 | 45.1 | 23.6 | 26.9 | 17.4 | 15.7 |
| 4/21/2013 | 4/23/2013 | 11 | 2 | 15.3 | 50.9 | 35.4 | 32.7 | 24.3 | 19.5 |
| 4/21/2013 | 4/23/2013 | 12 | 3 | 14.9 | 49.9 | 29.2 | 24.8 | 19.0 | 17.2 |
| 4/21/2013 | 4/23/2013 | 13 | 2 | 15.9 | 51.9 | 30.0 | 32.5 | 24.6 | 20.2 |
| 4/21/2013 | 4/23/2013 | 14 | 2 | 16.1 | 53.6 | 31.0 | 33.9 | 26.1 | 20.1 |
| 4/21/2013 | 4/23/2013 | 15 | 2 | 16.2 | 51.9 | 31.4 | 34.6 | 26.9 | 20.7 |
| 4/21/2013 | 4/23/2013 | 16 | 2 | 15.6 | 49.3 | 29.9 | 32.1 | 24.5 | 19.1 |
| 4/21/2013 | 4/23/2013 | 17 | 2 | 15.0 | 52.2 | 34.0 | 33.8 | 24.3 | 18.6 |
| 4/21/2013 | 4/23/2013 | 18 | 2 | 15.0 | 55.6 | 33.3 | 30.4 | 22.7 | 17.1 |
| 4/21/2013 | 4/23/2013 | 19 | 2 | 15.3 | 44.7 | 25.1 | 26.2 | 20.2 | 16.8 |
| 4/21/2013 | 4/23/2013 | 20 | 2 | 14.7 | 42.0 | 25.3 | 26.7 | 19.5 | 16.3 |
| 4/21/2013 | 4/23/2013 | 21 | 2 | 14.1 | 38.4 | 19.2 | 20.3 | 15.2 | 14.4 |
| 4/21/2013 | 4/23/2013 | 22 | 2 | 14.1 | 41.4 | 20.5 | 19.5 | 15.9 | 14.9 |
| 4/21/2013 | 4/23/2013 | 23 | 2 | 14.2 | 41.7 | 19.9 | 17.0 | 15.5 | 14.8 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 48. PAPA015 (Cat lek) dBA and one-third octave band metrics, April 21-23, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/21/13 | 4/23/13 | dBA | 49 | 13.8 | 55.6 | 28.5 | 24.8 | 17.5 | 16.0 |
| 4/21/13 | 4/23/13 | 12.5 | 49 | 16.0 | 78.4 | 55.6 | 43.0 | 38.5 | 34.1 |
| 4/21/13 | 4/23/13 | 16 | 49 | 16.8 | 76.1 | 52.3 | 46.4 | 41.9 | 35.8 |
| 4/21/13 | 4/23/13 | 20 | 49 | 18.3 | 74.0 | 50.3 | 51.6 | 44.6 | 37.4 |
| 4/21/13 | 4/23/13 | 25 | 49 | 14.2 | 71.8 | 43.6 | 40.9 | 35.0 | 29.0 |
| 4/21/13 | 4/23/13 | 31.5 | 49 | 13.4 | 68.3 | 43.0 | 42.6 | 35.2 | 29.1 |
| 4/21/13 | 4/23/13 | 40 | 49 | 11.5 | 65.4 | 37.9 | 34.7 | 28.9 | 24.8 |
| 4/21/13 | 4/23/13 | 50 | 49 | 9.5 | 64.3 | 35.7 | 33.6 | 27.8 | 23.9 |
| 4/21/13 | 4/23/13 | 63 | 49 | 8.9 | 66.8 | 34.8 | 33.0 | 27.2 | 23.2 |
| 4/21/13 | 4/23/13 | 80 | 49 | 7.3 | 72.0 | 35.1 | 32.0 | 24.6 | 20.9 |
| 4/21/13 | 4/23/13 | 100 | 49 | 3.6 | 71.5 | 33.0 | 29.9 | 23.4 | 19.1 |
| 4/21/13 | 4/23/13 | 125 | 49 | 1.6 | 67.9 | 30.5 | 28.4 | 21.8 | 17.2 |
| 4/21/13 | 4/23/13 | 160 | 49 | -0.5 | 60.3 | 28.0 | 25.8 | 19.0 | 13.5 |
| 4/21/13 | 4/23/13 | 200 | 49 | -1.2 | 59.2 | 26.3 | 23.7 | 17.2 | 11.3 |
| 4/21/13 | 4/23/13 | 250 | 49 | -3.2 | 53.3 | 22.8 | 21.8 | 12.4 | 6.9 |
| 4/21/13 | 4/23/13 | 315 | 49 | -3.8 | 45.8 | 20.0 | 17.8 | 8.5 | 3.5 |
| 4/21/13 | 4/23/13 | 400 | 49 | -3.7 | 47.9 | 19.3 | 13.3 | 5.0 | 1.7 |
| 4/21/13 | 4/23/13 | 500 | 49 | -4.0 | 50.0 | 19.2 | 9.5 | 3.3 | 0.1 |
| 4/21/13 | 4/23/13 | 630 | 49 | -3.8 | 46.0 | 18.3 | 7.0 | 1.0 | -0.8 |
| 4/21/13 | 4/23/13 | 800 | 49 | -3.8 | 41.4 | 16.8 | 5.0 | -0.5 | -1.4 |
| 4/21/13 | 4/23/13 | 1000 | 49 | -3.3 | 37.7 | 16.6 | 1.9 | -0.6 | -1.3 |
| 4/21/13 | 4/23/13 | 1250 | 49 | -2.6 | 37.1 | 16.8 | 0.4 | -0.7 | -1.1 |
| 4/21/13 | 4/23/13 | 1600 | 49 | -1.9 | 38.1 | 16.1 | 1.0 | 0.0 | -0.5 |
| 4/21/13 | 4/23/13 | 2000 | 49 | -0.8 | 39.8 | 14.7 | 1.6 | 0.9 | 0.5 |
| 4/21/13 | 4/23/13 | 2500 | 49 | 0.0 | 39.8 | 12.4 | 2.4 | 1.8 | 1.3 |
| 4/21/13 | 4/23/13 | 3150 | 49 | 1.2 | 41.0 | 10.7 | 3.2 | 2.5 | 2.2 |
| 4/21/13 | 4/23/13 | 4000 | 49 | 2.3 | 38.3 | 10.3 | 3.9 | 3.4 | 3.2 |
| 4/21/13 | 4/23/13 | 5000 | 49 | 3.4 | 43.2 | 10.8 | 4.7 | 4.3 | 4.1 |
| 4/21/13 | 4/23/13 | 6300 | 49 | 3.8 | 39.0 | 11.4 | 5.4 | 5.0 | 4.8 |
| 4/21/13 | 4/23/13 | 8000 | 49 | 3.4 | 39.4 | 11.9 | 5.9 | 5.5 | 5.4 |
| 4/21/13 | 4/23/13 | 10000 | 49 | 3.3 | 45.7 | 12.0 | 6.1 | 5.8 | 5.5 |
| 4/21/13 | 4/23/13 | 12500 | 49 | 3.0 | 44.1 | 11.1 | 5.5 | 5.2 | 4.8 |
| 4/21/13 | 4/23/13 | 16000 | 49 | 1.8 | 38.5 | 9.5 | 3.7 | 3.3 | 2.8 |
| 4/21/13 | 4/23/13 | 20000 | 49 | -0.5 | 35.6 | 5.3 | 1.6 | 0.6 | 0.2 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 49. PAPA016 (Tyler Draw North lek) hourly dBA metrics, April 15-17, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/15/2013 | 4/17/2013 | 0 | 2 | 15.7 | 32.7 | 20.3 | 22.2 | 19.0 | 17.6 |
| 4/15/2013 | 4/17/2013 | 1 | 2 | 16.6 | 57.3 | 29.7 | 23.5 | 20.5 | 18.5 |
| 4/15/2013 | 4/17/2013 | 2 | 2 | 14.9 | 31.6 | 21.6 | 22.3 | 20.2 | 17.9 |
| 4/15/2013 | 4/17/2013 | 3 | 2 | 14.4 | 45.3 | 25.7 | 22.6 | 20.5 | 19.3 |
| 4/15/2013 | 4/17/2013 | 4 | 2 | 14.3 | 38.1 | 26.7 | 23.4 | 21.6 | 20.6 |
| 4/15/2013 | 4/17/2013 | 5 | 2 | 14.3 | 41.4 | 25.0 | 24.8 | 21.3 | 19.8 |
| 4/15/2013 | 4/17/2013 | 6 | 2 | 15.7 | 45.3 | 25.0 | 25.9 | 22.7 | 20.8 |
| 4/15/2013 | 4/17/2013 | 7 | 2 | 18.6 | 41.1 | 25.7 | 27.6 | 24.5 | 21.9 |
| 4/15/2013 | 4/17/2013 | 8 | 2 | 20.3 | 43.3 | 30.5 | 32.1 | 28.0 | 24.4 |
| 4/16/2013 | 4/16/2013 | 9 | 1 | 22.1 | 41.8 | 27.8 | 29.5 | 26.1 | 24.3 |
| 4/16/2013 | 4/16/2013 | 10 | 1 | 22.0 | 39.4 | 27.5 | 29.7 | 26.5 | 24.4 |
| 4/15/2013 | 4/17/2013 | 11 | 2 | 15.2 | 43.5 | 24.1 | 24.5 | 19.4 | 17.6 |
| 4/15/2013 | 4/17/2013 | 12 | 2 | 15.4 | 45.1 | 26.2 | 28.0 | 19.6 | 16.3 |
| 4/15/2013 | 4/17/2013 | 13 | 2 | 15.3 | 54.7 | 29.7 | 29.9 | 19.1 | 16.2 |
| 4/15/2013 | 4/17/2013 | 14 | 2 | 16.0 | 43.4 | 27.4 | 28.0 | 22.3 | 18.7 |
| 4/15/2013 | 4/17/2013 | 15 | 2 | 16.0 | 42.2 | 28.1 | 31.4 | 23.9 | 18.9 |
| 4/15/2013 | 4/17/2013 | 16 | 2 | 16.5 | 46.1 | 30.5 | 32.7 | 25.5 | 19.7 |
| 4/15/2013 | 4/17/2013 | 17 | 2 | 15.7 | 53.6 | 31.6 | 30.9 | 23.6 | 18.6 |
| 4/15/2013 | 4/17/2013 | 18 | 2 | 14.9 | 48.9 | 30.4 | 29.1 | 22.7 | 17.1 |
| 4/15/2013 | 4/17/2013 | 19 | 2 | 14.8 | 48.9 | 31.3 | 30.2 | 22.9 | 19.2 |
| 4/15/2013 | 4/17/2013 | 20 | 2 | 14.5 | 40.6 | 23.7 | 24.4 | 19.7 | 17.7 |
| 4/15/2013 | 4/17/2013 | 21 | 2 | 14.3 | 42.3 | 26.1 | 26.0 | 20.6 | 19.1 |
| 4/15/2013 | 4/17/2013 | 22 | 2 | 14.7 | 38.5 | 23.4 | 24.7 | 19.5 | 17.1 |
| 4/15/2013 | 4/17/2013 | 23 | 2 | 14.7 | 40.4 | 24.3 | 26.2 | 20.3 | 17.4 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 50. PAPA016 (Tyler Draw North lek) dBA and one-third octave band metrics, April 15-17, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/15/13 | 4/17/13 | dBA | 46 | 14.3 | 57.3 | 27.7 | 26.5 | 21.8 | 18.5 |
| 4/15/13 | 4/17/13 | 12.5 | 46 | 16.5 | 74.5 | 45.6 | 40.6 | 35.7 | 31.1 |
| 4/15/13 | 4/17/13 | 16 | 46 | 22.3 | 71.8 | 44.3 | 43.4 | 37.0 | 32.4 |
| 4/15/13 | 4/17/13 | 20 | 46 | 22.9 | 68.9 | 49.7 | 49.1 | 41.6 | 36.3 |
| 4/15/13 | 4/17/13 | 25 | 46 | 20.2 | 65.2 | 40.9 | 39.6 | 33.6 | 29.9 |
| 4/15/13 | 4/17/13 | 31.5 | 46 | 18.0 | 65.9 | 44.8 | 41.3 | 34.3 | 29.8 |
| 4/15/13 | 4/17/13 | 40 | 46 | 15.8 | 58.3 | 37.3 | 35.9 | 30.6 | 27.0 |
| 4/15/13 | 4/17/13 | 50 | 46 | 13.9 | 58.7 | 37.0 | 36.4 | 29.8 | 25.2 |
| 4/15/13 | 4/17/13 | 63 | 46 | 12.7 | 66.1 | 37.6 | 36.6 | 29.9 | 24.9 |
| 4/15/13 | 4/17/13 | 80 | 46 | 9.2 | 71.4 | 36.1 | 35.7 | 28.9 | 25.0 |
| 4/15/13 | 4/17/13 | 100 | 46 | 7.0 | 75.7 | 36.2 | 34.6 | 28.3 | 24.6 |
| 4/15/13 | 4/17/13 | 125 | 46 | 4.4 | 73.4 | 34.5 | 32.7 | 26.6 | 23.1 |
| 4/15/13 | 4/17/13 | 160 | 46 | 2.2 | 64.3 | 30.2 | 29.3 | 23.7 | 20.2 |
| 4/15/13 | 4/17/13 | 200 | 46 | 0.2 | 56.5 | 26.5 | 27.8 | 21.9 | 17.7 |
| 4/15/13 | 4/17/13 | 250 | 46 | -3.3 | 52.6 | 22.0 | 21.4 | 17.1 | 12.4 |
| 4/15/13 | 4/17/13 | 315 | 46 | -4.4 | 46.4 | 18.1 | 17.3 | 13.3 | 7.7 |
| 4/15/13 | 4/17/13 | 400 | 46 | -4.5 | 52.3 | 16.6 | 13.1 | 8.6 | 2.5 |
| 4/15/13 | 4/17/13 | 500 | 46 | -4.5 | 48.1 | 15.4 | 9.1 | 2.5 | -0.8 |
| 4/15/13 | 4/17/13 | 630 | 46 | -4.0 | 40.4 | 14.8 | 9.2 | 1.1 | -1.4 |
| 4/15/13 | 4/17/13 | 800 | 46 | -3.2 | 42.0 | 16.1 | 9.4 | 1.5 | -1.0 |
| 4/15/13 | 4/17/13 | 1000 | 46 | -2.4 | 38.5 | 16.9 | 8.3 | 1.2 | -0.5 |
| 4/15/13 | 4/17/13 | 1250 | 46 | -1.6 | 38.7 | 15.9 | 6.9 | 1.0 | -0.1 |
| 4/15/13 | 4/17/13 | 1600 | 46 | -0.6 | 48.1 | 15.1 | 6.2 | 1.5 | 0.8 |
| 4/15/13 | 4/17/13 | 2000 | 46 | 0.4 | 37.8 | 13.3 | 4.4 | 2.1 | 1.5 |
| 4/15/13 | 4/17/13 | 2500 | 46 | 1.3 | 35.5 | 10.6 | 3.8 | 2.8 | 2.3 |
| 4/15/13 | 4/17/13 | 3150 | 46 | 2.2 | 35.0 | 8.2 | 4.1 | 3.5 | 3.1 |
| 4/15/13 | 4/17/13 | 4000 | 46 | 3.2 | 33.2 | 6.5 | 4.7 | 4.1 | 3.9 |
| 4/15/13 | 4/17/13 | 5000 | 46 | 3.6 | 37.7 | 6.3 | 5.3 | 4.8 | 4.5 |
| 4/15/13 | 4/17/13 | 6300 | 46 | 3.5 | 38.0 | 6.6 | 5.6 | 5.2 | 5.0 |
| 4/15/13 | 4/17/13 | 8000 | 46 | 3.6 | 41.3 | 7.5 | 5.6 | 5.3 | 5.1 |
| 4/15/13 | 4/17/13 | 10000 | 46 | 3.1 | 35.5 | 6.0 | 5.4 | 5.0 | 4.8 |
| 4/15/13 | 4/17/13 | 12500 | 46 | 2.8 | 35.7 | 5.2 | 4.7 | 4.3 | 4.1 |
| 4/15/13 | 4/17/13 | 16000 | 46 | 2.5 | 33.5 | 4.5 | 3.8 | 3.3 | 3.1 |
| 4/15/13 | 4/17/13 | 20000 | 46 | 1.2 | 32.9 | 3.2 | 2.6 | 2.0 | 1.7 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 51. PAPA017 (Oil Fork Road lek) hourly dBA metrics, April 15-17, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/15/2013 | 4/17/2013 | 0 | 2 | 20.3 | 37.0 | 25.4 | 27.4 | 24.7 | 22.6 |
| 4/15/2013 | 4/17/2013 | 1 | 2 | 19.3 | 53.6 | 28.5 | 27.7 | 25.3 | 22.9 |
| 4/15/2013 | 4/17/2013 | 2 | 2 | 18.1 | 37.5 | 24.7 | 26.0 | 23.6 | 21.3 |
| 4/15/2013 | 4/17/2013 | 3 | 2 | 17.4 | 42.6 | 27.0 | 28.9 | 23.6 | 22.0 |
| 4/15/2013 | 4/17/2013 | 4 | 2 | 15.2 | 46.5 | 31.4 | 28.5 | 24.6 | 22.9 |
| 4/15/2013 | 4/17/2013 | 5 | 2 | 15.2 | 54.3 | 32.3 | 31.1 | 27.3 | 23.8 |
| 4/15/2013 | 4/17/2013 | 6 | 2 | 17.5 | 50.1 | 32.7 | 33.1 | 29.7 | 26.9 |
| 4/15/2013 | 4/17/2013 | 7 | 2 | 18.5 | 40.8 | 25.4 | 27.5 | 24.5 | 21.9 |
| 4/15/2013 | 4/17/2013 | 8 | 2 | 18.6 | 47.0 | 27.8 | 29.6 | 25.4 | 22.3 |
| 4/15/2013 | 4/17/2013 | 9 | 2 | 17.8 | 40.8 | 28.4 | 30.7 | 26.5 | 22.8 |
| 4/16/2013 | 4/16/2013 | 10 | 1 | 19.7 | 52.4 | 28.1 | 31.3 | 24.4 | 21.9 |
| 4/16/2013 | 4/16/2013 | 11 | 1 | 19.2 | 27.5 | 21.7 | 23.1 | 21.3 | 20.3 |
| 4/15/2013 | 4/17/2013 | 12 | 2 | 18.0 | 43.7 | 26.9 | 29.3 | 23.7 | 20.5 |
| 4/15/2013 | 4/17/2013 | 13 | 2 | 19.0 | 58.2 | 31.6 | 29.5 | 23.7 | 21.3 |
| 4/15/2013 | 4/17/2013 | 14 | 2 | 19.4 | 44.1 | 26.8 | 28.2 | 24.4 | 22.3 |
| 4/15/2013 | 4/17/2013 | 15 | 2 | 19.4 | 42.1 | 27.5 | 30.0 | 24.3 | 21.9 |
| 4/15/2013 | 4/17/2013 | 16 | 2 | 19.5 | 45.4 | 28.5 | 30.5 | 25.4 | 22.6 |
| 4/15/2013 | 4/17/2013 | 17 | 2 | 19.3 | 56.7 | 31.9 | 30.3 | 25.4 | 22.9 |
| 4/15/2013 | 4/17/2013 | 18 | 2 | 18.1 | 47.7 | 30.8 | 30.6 | 26.3 | 23.5 |
| 4/15/2013 | 4/17/2013 | 19 | 2 | 18.7 | 49.4 | 31.6 | 31.9 | 27.3 | 24.5 |
| 4/15/2013 | 4/17/2013 | 20 | 2 | 18.9 | 50.4 | 27.6 | 28.9 | 26.6 | 24.4 |
| 4/15/2013 | 4/17/2013 | 21 | 2 | 17.6 | 47.7 | 29.2 | 29.4 | 27.0 | 23.9 |
| 4/15/2013 | 4/17/2013 | 22 | 2 | 16.4 | 36.2 | 27.8 | 27.2 | 24.7 | 22.6 |
| 4/15/2013 | 4/17/2013 | 23 | 2 | 18.3 | 36.0 | 25.7 | 27.9 | 24.9 | 22.1 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 52. PAPA017 (Oil Fork Road lek) dBA and one-third octave band metrics, April 15-17, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/15/13 | 4/17/13 | dBA | 46 | 15.2 | 58.2 | 29.2 | 28.6 | 24.9 | 22.2 |
| 4/15/13 | 4/17/13 | 12.5 | 46 | 25.3 | 78.3 | 53.5 | 50.6 | 44.1 | 39.3 |
| 4/15/13 | 4/17/13 | 16 | 46 | 25.1 | 77.6 | 51.2 | 49.7 | 44.1 | 39.3 |
| 4/15/13 | 4/17/13 | 20 | 46 | 29.6 | 75.9 | 57.6 | 60.8 | 50.8 | 46.2 |
| 4/15/13 | 4/17/13 | 25 | 46 | 27.6 | 70.6 | 48.9 | 50.3 | 46.3 | 42.8 |
| 4/15/13 | 4/17/13 | 31.5 | 46 | 26.1 | 69.4 | 55.9 | 58.2 | 52.7 | 46.8 |
| 4/15/13 | 4/17/13 | 40 | 46 | 24.6 | 64.5 | 43.8 | 45.1 | 41.8 | 38.0 |
| 4/15/13 | 4/17/13 | 50 | 46 | 24.1 | 63.8 | 40.7 | 41.5 | 37.7 | 34.8 |
| 4/15/13 | 4/17/13 | 63 | 46 | 21.8 | 62.8 | 40.8 | 40.0 | 36.8 | 33.7 |
| 4/15/13 | 4/17/13 | 80 | 46 | 17.2 | 68.7 | 38.0 | 36.7 | 32.8 | 29.2 |
| 4/15/13 | 4/17/13 | 100 | 46 | 13.4 | 69.9 | 37.4 | 35.5 | 30.1 | 26.7 |
| 4/15/13 | 4/17/13 | 125 | 46 | 7.5 | 74.7 | 37.8 | 34.8 | 29.2 | 25.6 |
| 4/15/13 | 4/17/13 | 160 | 46 | 4.5 | 71.3 | 32.9 | 32.3 | 27.6 | 24.0 |
| 4/15/13 | 4/17/13 | 200 | 46 | 4.5 | 57.8 | 30.9 | 30.6 | 26.5 | 22.5 |
| 4/15/13 | 4/17/13 | 250 | 46 | 1.1 | 55.1 | 26.8 | 26.9 | 23.0 | 19.2 |
| 4/15/13 | 4/17/13 | 315 | 46 | -1.1 | 47.9 | 23.1 | 23.5 | 18.9 | 15.6 |
| 4/15/13 | 4/17/13 | 400 | 46 | -3.0 | 49.2 | 19.9 | 19.1 | 15.1 | 11.1 |
| 4/15/13 | 4/17/13 | 500 | 46 | -3.4 | 47.3 | 16.8 | 14.8 | 9.3 | 6.1 |
| 4/15/13 | 4/17/13 | 630 | 46 | -3.4 | 41.4 | 13.9 | 10.7 | 4.9 | 1.2 |
| 4/15/13 | 4/17/13 | 800 | 46 | -3.1 | 39.4 | 12.2 | 8.5 | 2.9 | -0.1 |
| 4/15/13 | 4/17/13 | 1000 | 46 | -2.1 | 50.9 | 12.2 | 9.1 | 1.7 | -0.1 |
| 4/15/13 | 4/17/13 | 1250 | 46 | -1.3 | 42.2 | 11.6 | 7.7 | 1.3 | 0.3 |
| 4/15/13 | 4/17/13 | 1600 | 46 | -0.5 | 37.5 | 11.6 | 5.6 | 1.6 | 1.0 |
| 4/15/13 | 4/17/13 | 2000 | 46 | 0.6 | 33.7 | 10.1 | 3.8 | 2.3 | 1.7 |
| 4/15/13 | 4/17/13 | 2500 | 46 | 1.6 | 35.2 | 8.5 | 3.6 | 2.9 | 2.5 |
| 4/15/13 | 4/17/13 | 3150 | 46 | 2.5 | 48.5 | 11.2 | 4.1 | 3.7 | 3.3 |
| 4/15/13 | 4/17/13 | 4000 | 46 | 3.2 | 38.5 | 6.6 | 4.8 | 4.4 | 4.1 |
| 4/15/13 | 4/17/13 | 5000 | 46 | 2.7 | 45.2 | 7.0 | 5.3 | 4.9 | 4.7 |
| 4/15/13 | 4/17/13 | 6300 | 46 | 2.7 | 41.5 | 5.9 | 5.5 | 5.2 | 5.0 |
| 4/15/13 | 4/17/13 | 8000 | 46 | 2.2 | 29.5 | 5.7 | 5.5 | 5.3 | 5.1 |
| 4/15/13 | 4/17/13 | 10000 | 46 | 2.4 | 26.2 | 5.5 | 5.2 | 5.0 | 4.9 |
| 4/15/13 | 4/17/13 | 12500 | 46 | 1.9 | 26.2 | 5.0 | 4.7 | 4.5 | 4.3 |
| 4/15/13 | 4/17/13 | 16000 | 46 | 1.8 | 23.6 | 4.3 | 3.9 | 3.6 | 3.5 |
| 4/15/13 | 4/17/13 | 20000 | 46 | 1.7 | 20.5 | 3.1 | 3.0 | 2.4 | 2.3 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 53. PAPA018 (Mesa Road 3 lek) hourly dBA metrics, April 15-17, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/15/2013 | 4/17/2013 | 0 | 2 | 16.2 | 35.7 | 26.6 | 30.1 | 24.2 | 20.2 |
| 4/15/2013 | 4/17/2013 | 1 | 2 | 21.6 | 47.6 | 28.2 | 30.2 | 27.0 | 25.0 |
| 4/15/2013 | 4/17/2013 | 2 | 2 | 22.4 | 36.7 | 28.8 | 31.0 | 28.2 | 25.5 |
| 4/15/2013 | 4/17/2013 | 3 | 2 | 19.0 | 40.6 | 29.7 | 29.4 | 27.2 | 25.3 |
| 4/15/2013 | 4/17/2013 | 4 | 2 | 14.9 | 48.5 | 33.7 | 30.5 | 25.4 | 23.3 |
| 4/15/2013 | 4/17/2013 | 5 | 2 | 14.4 | 50.7 | 33.0 | 30.5 | 24.5 | 23.0 |
| 4/15/2013 | 4/17/2013 | 6 | 2 | 19.6 | 49.2 | 33.5 | 34.7 | 29.9 | 26.3 |
| 4/15/2013 | 4/17/2013 | 7 | 2 | 19.2 | 45.3 | 31.1 | 33.3 | 28.2 | 23.2 |
| 4/15/2013 | 4/17/2013 | 8 | 2 | 16.7 | 46.5 | 26.4 | 27.6 | 22.5 | 20.1 |
| 4/15/2013 | 4/17/2013 | 9 | 2 | 17.4 | 50.1 | 27.3 | 29.7 | 24.3 | 19.7 |
| 4/15/2013 | 4/17/2013 | 10 | 2 | 17.4 | 42.2 | 26.5 | 29.7 | 23.3 | 19.8 |
| 4/16/2013 | 4/16/2013 | 11 | 1 | 18.0 | 34.6 | 21.7 | 23.4 | 20.8 | 19.6 |
| 4/15/2013 | 4/17/2013 | 12 | 2 | 16.4 | 44.4 | 27.8 | 31.2 | 23.6 | 19.3 |
| 4/15/2013 | 4/17/2013 | 13 | 2 | 16.5 | 59.1 | 33.0 | 29.3 | 23.1 | 19.3 |
| 4/15/2013 | 4/17/2013 | 14 | 2 | 17.1 | 45.2 | 26.8 | 29.7 | 23.4 | 19.7 |
| 4/15/2013 | 4/17/2013 | 15 | 2 | 17.3 | 56.7 | 30.6 | 31.4 | 23.5 | 19.8 |
| 4/15/2013 | 4/17/2013 | 16 | 2 | 16.9 | 42.6 | 27.6 | 29.5 | 23.1 | 19.5 |
| 4/15/2013 | 4/17/2013 | 17 | 2 | 16.8 | 49.8 | 30.8 | 31.9 | 24.1 | 19.6 |
| 4/15/2013 | 4/17/2013 | 18 | 2 | 15.3 | 49.3 | 34.1 | 33.4 | 25.8 | 22.2 |
| 4/15/2013 | 4/17/2013 | 19 | 2 | 15.1 | 47.7 | 30.8 | 30.1 | 24.1 | 20.1 |
| 4/15/2013 | 4/17/2013 | 20 | 2 | 15.6 | 37.0 | 23.5 | 25.9 | 21.1 | 18.4 |
| 4/15/2013 | 4/17/2013 | 21 | 2 | 14.5 | 61.4 | 33.0 | 25.2 | 21.8 | 18.0 |
| 4/15/2013 | 4/17/2013 | 22 | 2 | 15.2 | 35.9 | 24.3 | 24.7 | 21.5 | 20.0 |
| 4/15/2013 | 4/17/2013 | 23 | 2 | 14.8 | 40.0 | 25.0 | 27.7 | 24.4 | 19.2 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 54. PAPA018 (Mesa Road 3 lek) dBA and one-third octave band metrics, April 15-17, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/15/13 | 4/17/13 | dBA | 47 | 14.4 | 61.4 | 30.2 | 29.3 | 24.1 | 20.1 |
| 4/15/13 | 4/17/13 | 12.5 | 47 | 19.0 | 78.4 | 55.6 | 47.9 | 41.8 | 36.8 |
| 4/15/13 | 4/17/13 | 16 | 47 | 23.7 | 75.3 | 51.9 | 50.1 | 44.7 | 38.4 |
| 4/15/13 | 4/17/13 | 20 | 47 | 29.4 | 75.1 | 56.4 | 58.5 | 49.3 | 45.1 |
| 4/15/13 | 4/17/13 | 25 | 47 | 22.0 | 70.9 | 46.4 | 45.5 | 41.0 | 36.5 |
| 4/15/13 | 4/17/13 | 31.5 | 47 | 23.7 | 69.4 | 50.8 | 51.6 | 45.4 | 39.5 |
| 4/15/13 | 4/17/13 | 40 | 47 | 21.0 | 65.1 | 42.6 | 42.7 | 37.8 | 34.3 |
| 4/15/13 | 4/17/13 | 50 | 47 | 20.6 | 64.2 | 40.8 | 40.6 | 36.0 | 32.1 |
| 4/15/13 | 4/17/13 | 63 | 47 | 17.8 | 66.0 | 41.0 | 40.8 | 34.7 | 30.7 |
| 4/15/13 | 4/17/13 | 80 | 47 | 14.1 | 68.8 | 37.8 | 37.8 | 31.5 | 26.4 |
| 4/15/13 | 4/17/13 | 100 | 47 | 12.9 | 77.6 | 38.6 | 37.3 | 29.8 | 25.2 |
| 4/15/13 | 4/17/13 | 125 | 47 | 11.6 | 76.8 | 36.6 | 35.0 | 28.8 | 24.0 |
| 4/15/13 | 4/17/13 | 160 | 47 | 8.4 | 60.3 | 33.0 | 32.7 | 26.1 | 22.4 |
| 4/15/13 | 4/17/13 | 200 | 47 | 7.6 | 68.3 | 33.4 | 32.4 | 26.2 | 21.8 |
| 4/15/13 | 4/17/13 | 250 | 47 | 2.7 | 63.9 | 27.9 | 28.0 | 22.7 | 18.0 |
| 4/15/13 | 4/17/13 | 315 | 47 | -0.1 | 52.9 | 25.3 | 24.3 | 19.3 | 15.0 |
| 4/15/13 | 4/17/13 | 400 | 47 | -3.3 | 57.8 | 22.4 | 19.1 | 13.9 | 9.8 |
| 4/15/13 | 4/17/13 | 500 | 47 | -3.8 | 59.7 | 20.4 | 14.6 | 9.1 | 4.7 |
| 4/15/13 | 4/17/13 | 630 | 47 | -3.9 | 52.9 | 16.2 | 10.8 | 5.0 | 1.0 |
| 4/15/13 | 4/17/13 | 800 | 47 | -3.6 | 39.9 | 13.2 | 10.7 | 2.8 | -0.3 |
| 4/15/13 | 4/17/13 | 1000 | 47 | -2.9 | 38.3 | 12.7 | 8.3 | 0.5 | -1.1 |
| 4/15/13 | 4/17/13 | 1250 | 47 | -2.4 | 34.1 | 13.1 | 6.8 | -0.2 | -0.9 |
| 4/15/13 | 4/17/13 | 1600 | 47 | -1.5 | 35.5 | 13.0 | 3.8 | 0.2 | -0.4 |
| 4/15/13 | 4/17/13 | 2000 | 47 | -0.7 | 37.3 | 11.8 | 3.0 | 0.9 | 0.3 |
| 4/15/13 | 4/17/13 | 2500 | 47 | 0.2 | 36.9 | 9.7 | 2.6 | 1.5 | 1.1 |
| 4/15/13 | 4/17/13 | 3150 | 47 | 1.2 | 34.4 | 7.0 | 2.8 | 2.2 | 1.9 |
| 4/15/13 | 4/17/13 | 4000 | 47 | 2.2 | 43.8 | 5.9 | 3.4 | 3.0 | 2.8 |
| 4/15/13 | 4/17/13 | 5000 | 47 | 2.9 | 47.8 | 7.5 | 4.1 | 3.8 | 3.6 |
| 4/15/13 | 4/17/13 | 6300 | 47 | 2.8 | 54.3 | 10.2 | 4.7 | 4.5 | 4.4 |
| 4/15/13 | 4/17/13 | 8000 | 47 | 2.6 | 55.8 | 13.4 | 5.2 | 5.1 | 4.9 |
| 4/15/13 | 4/17/13 | 10000 | 47 | 2.7 | 36.8 | 5.9 | 5.5 | 5.3 | 5.2 |
| 4/15/13 | 4/17/13 | 12500 | 47 | 2.5 | 28.0 | 5.7 | 5.2 | 4.8 | 4.7 |
| 4/15/13 | 4/17/13 | 16000 | 47 | 1.6 | 33.5 | 3.9 | 3.2 | 2.8 | 2.6 |
| 4/15/13 | 4/17/13 | 20000 | 47 | -0.4 | 19.2 | 1.1 | 0.7 | 0.2 | 0.0 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 55. PAPA019 (Bloom Reservoir lek) hourly dBA metrics, April 15-17, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/15/2013 | 4/17/2013 | 0 | 2 | 15.1 | 37.4 | 23.7 | 25.6 | 21.5 | 17.9 |
| 4/15/2013 | 4/17/2013 | 1 | 2 | 18.7 | 42.5 | 29.4 | 29.9 | 25.9 | 23.1 |
| 4/15/2013 | 4/17/2013 | 2 | 2 | 20.6 | 38.2 | 24.7 | 26.1 | 24.2 | 23.0 |
| 4/15/2013 | 4/17/2013 | 3 | 2 | 23.0 | 43.1 | 30.0 | 32.3 | 27.8 | 25.5 |
| 4/15/2013 | 4/17/2013 | 4 | 2 | 19.2 | 44.4 | 28.8 | 30.1 | 27.9 | 25.6 |
| 4/15/2013 | 4/17/2013 | 5 | 2 | 16.2 | 60.1 | 27.0 | 26.0 | 23.4 | 21.8 |
| 4/15/2013 | 4/17/2013 | 6 | 2 | 20.6 | 37.7 | 26.2 | 27.4 | 25.3 | 23.8 |
| 4/15/2013 | 4/17/2013 | 7 | 2 | 18.5 | 39.3 | 25.7 | 27.5 | 24.4 | 21.3 |
| 4/15/2013 | 4/17/2013 | 8 | 2 | 15.6 | 43.7 | 24.0 | 24.5 | 20.3 | 18.4 |
| 4/15/2013 | 4/17/2013 | 9 | 2 | 16.5 | 38.5 | 23.4 | 26.4 | 21.5 | 18.0 |
| 4/15/2013 | 4/17/2013 | 10 | 2 | 16.1 | 41.0 | 24.8 | 27.6 | 21.4 | 18.2 |
| 4/16/2013 | 4/16/2013 | 11 | 1 | 15.9 | 36.1 | 18.9 | 20.5 | 17.9 | 16.8 |
| 4/16/2013 | 4/16/2013 | 12 | 1 | 15.5 | 42.0 | 22.2 | 24.7 | 19.2 | 16.6 |
| 4/15/2013 | 4/17/2013 | 13 | 2 | 15.7 | 55.9 | 31.2 | 27.6 | 21.2 | 17.5 |
| 4/15/2013 | 4/17/2013 | 14 | 2 | 16.2 | 43.1 | 26.2 | 27.7 | 21.4 | 17.6 |
| 4/15/2013 | 4/17/2013 | 15 | 2 | 15.5 | 52.2 | 30.0 | 32.3 | 22.5 | 17.9 |
| 4/15/2013 | 4/17/2013 | 16 | 2 | 15.6 | 47.1 | 29.1 | 30.2 | 23.1 | 18.6 |
| 4/15/2013 | 4/17/2013 | 17 | 2 | 16.6 | 51.8 | 32.1 | 34.3 | 26.2 | 20.5 |
| 4/15/2013 | 4/17/2013 | 18 | 2 | 15.7 | 53.1 | 34.1 | 32.0 | 26.1 | 22.2 |
| 4/15/2013 | 4/17/2013 | 19 | 2 | 15.9 | 48.4 | 31.0 | 30.1 | 24.3 | 19.3 |
| 4/15/2013 | 4/17/2013 | 20 | 2 | 14.9 | 53.8 | 24.8 | 26.2 | 19.7 | 17.5 |
| 4/15/2013 | 4/17/2013 | 21 | 2 | 16.0 | 61.2 | 33.2 | 26.2 | 21.0 | 17.9 |
| 4/15/2013 | 4/17/2013 | 22 | 2 | 14.7 | 35.4 | 19.0 | 21.0 | 17.4 | 15.5 |
| 4/15/2013 | 4/17/2013 | 23 | 2 | 14.9 | 29.3 | 20.0 | 22.2 | 19.4 | 16.7 |

## Appendix B. dBA and One-third Octave Metrics for PAPA Treatment Leks (cont.).

Table 56. PAPA019 (Bloom Reservoir lek) dBA and one-third octave band metrics, April 15-17, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/15/13 | 4/17/13 | dBA | 46 | 14.7 | 61.2 | 28.6 | 26.6 | 22.0 | 18.3 |
| 4/15/13 | 4/17/13 | 12.5 | 46 | 16.2 | 73.2 | 47.0 | 43.7 | 38.5 | 33.9 |
| 4/15/13 | 4/17/13 | 16 | 46 | 19.9 | 69.7 | 46.2 | 44.9 | 40.0 | 34.9 |
| 4/15/13 | 4/17/13 | 20 | 46 | 22.6 | 71.7 | 52.3 | 52.9 | 43.9 | 39.5 |
| 4/15/13 | 4/17/13 | 25 | 46 | 20.7 | 63.8 | 42.1 | 42.2 | 36.7 | 32.1 |
| 4/15/13 | 4/17/13 | 31.5 | 46 | 20.7 | 63.6 | 45.9 | 45.2 | 39.5 | 33.6 |
| 4/15/13 | 4/17/13 | 40 | 46 | 18.5 | 60.9 | 39.5 | 39.1 | 34.3 | 29.6 |
| 4/15/13 | 4/17/13 | 50 | 46 | 16.6 | 59.7 | 38.4 | 39.0 | 33.1 | 28.8 |
| 4/15/13 | 4/17/13 | 63 | 46 | 18.5 | 65.6 | 39.2 | 38.6 | 32.9 | 28.5 |
| 4/15/13 | 4/17/13 | 80 | 46 | 14.5 | 76.9 | 37.9 | 36.8 | 30.8 | 26.7 |
| 4/15/13 | 4/17/13 | 100 | 46 | 14.3 | 74.5 | 37.1 | 35.3 | 28.8 | 24.9 |
| 4/15/13 | 4/17/13 | 125 | 46 | 11.3 | 71.6 | 34.3 | 33.1 | 27.1 | 22.5 |
| 4/15/13 | 4/17/13 | 160 | 46 | 7.8 | 60.1 | 30.4 | 29.4 | 24.5 | 20.0 |
| 4/15/13 | 4/17/13 | 200 | 46 | 4.8 | 68.0 | 29.5 | 27.6 | 22.5 | 18.2 |
| 4/15/13 | 4/17/13 | 250 | 46 | 1.1 | 65.3 | 25.3 | 23.4 | 18.5 | 14.9 |
| 4/15/13 | 4/17/13 | 315 | 46 | -1.9 | 52.1 | 21.3 | 20.5 | 14.7 | 10.8 |
| 4/15/13 | 4/17/13 | 400 | 46 | -3.3 | 56.2 | 19.8 | 16.1 | 10.0 | 5.8 |
| 4/15/13 | 4/17/13 | 500 | 46 | -3.9 | 56.8 | 18.9 | 12.2 | 5.4 | 1.0 |
| 4/15/13 | 4/17/13 | 630 | 46 | -3.6 | 52.4 | 16.2 | 8.6 | 1.9 | -1.4 |
| 4/15/13 | 4/17/13 | 800 | 46 | -3.3 | 48.5 | 13.7 | 8.2 | 0.5 | -1.5 |
| 4/15/13 | 4/17/13 | 1000 | 46 | -2.4 | 50.7 | 14.4 | 7.7 | 0.2 | -1.0 |
| 4/15/13 | 4/17/13 | 1250 | 46 | -1.6 | 53.4 | 15.1 | 6.9 | 0.4 | -0.3 |
| 4/15/13 | 4/17/13 | 1600 | 46 | -0.7 | 54.4 | 14.7 | 5.9 | 1.1 | 0.5 |
| 4/15/13 | 4/17/13 | 2000 | 46 | 0.3 | 49.9 | 12.4 | 3.5 | 1.8 | 1.3 |
| 4/15/13 | 4/17/13 | 2500 | 46 | 1.3 | 43.8 | 10.2 | 3.1 | 2.5 | 2.0 |
| 4/15/13 | 4/17/13 | 3150 | 46 | 2.1 | 35.2 | 7.4 | 3.7 | 3.2 | 2.9 |
| 4/15/13 | 4/17/13 | 4000 | 46 | 2.0 | 37.0 | 5.4 | 4.3 | 3.9 | 3.6 |
| 4/15/13 | 4/17/13 | 5000 | 46 | 2.4 | 35.9 | 5.1 | 4.7 | 4.4 | 4.2 |
| 4/15/13 | 4/17/13 | 6300 | 46 | 1.4 | 37.7 | 5.1 | 4.9 | 4.7 | 4.5 |
| 4/15/13 | 4/17/13 | 8000 | 46 | 1.1 | 29.6 | 4.9 | 4.8 | 4.6 | 4.4 |
| 4/15/13 | 4/17/13 | 10000 | 46 | 0.5 | 32.1 | 4.5 | 4.5 | 4.2 | 4.0 |
| 4/15/13 | 4/17/13 | 12500 | 46 | 0.0 | 28.3 | 3.8 | 3.8 | 3.5 | 3.3 |
| 4/15/13 | 4/17/13 | 16000 | 46 | -0.4 | 26.5 | 2.9 | 2.9 | 2.5 | 2.3 |
| 4/15/13 | 4/17/13 | 20000 | 46 | -0.3 | 26.4 | 1.3 | 1.4 | 0.9 | 0.6 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites.

Table 57. PAPA201 (Injection Well 100 m) hourly dBA metrics, April 14-15, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/15/2013 | 4/15/2013 | 0 | 1 | 53.8 | 58.4 | 56.0 | 56.8 | 55.9 | 55.1 |
| 4/15/2013 | 4/15/2013 | 1 | 1 | 53.9 | 58.3 | 56.2 | 56.9 | 56.1 | 55.4 |
| 4/15/2013 | 4/15/2013 | 2 | 1 | 53.3 | 58.4 | 56.2 | 57.1 | 56.2 | 54.9 |
| 4/15/2013 | 4/15/2013 | 3 | 1 | 52.7 | 57.5 | 55.3 | 56.1 | 55.3 | 54.4 |
| 4/15/2013 | 4/15/2013 | 4 | 1 | 53.2 | 58.2 | 56.3 | 57.0 | 56.3 | 55.4 |
| 4/15/2013 | 4/15/2013 | 5 | 1 | 53.3 | 57.9 | 56.3 | 57.0 | 56.3 | 55.6 |
| 4/15/2013 | 4/15/2013 | 6 | 1 | 53.5 | 57.9 | 56.1 | 56.8 | 56.1 | 55.4 |
| 4/15/2013 | 4/15/2013 | 7 | 1 | 54.3 | 58.2 | 56.4 | 57.0 | 56.4 | 55.8 |
| 4/15/2013 | 4/15/2013 | 8 | 1 | 53.5 | 58.0 | 56.2 | 56.8 | 56.2 | 55.4 |
| 4/14/2013 | 4/15/2013 | 9 | 2 | 50.2 | 58.1 | 55.3 | 56.2 | 55.3 | 54.3 |
| 4/14/2013 | 4/15/2013 | 10 | 2 | 50.3 | 66.3 | 55.5 | 56.1 | 55.3 | 54.3 |
| 4/14/2013 | 4/15/2013 | 11 | 2 | 50.5 | 58.0 | 55.3 | 56.0 | 55.1 | 54.0 |
| 4/14/2013 | 4/15/2013 | 12 | 2 | 50.5 | 60.9 | 54.9 | 56.0 | 55.0 | 52.7 |
| 4/14/2013 | 4/14/2013 | 13 | 1 | 50.3 | 57.6 | 54.5 | 55.5 | 54.4 | 53.2 |
| 4/14/2013 | 4/14/2013 | 14 | 1 | 50.9 | 62.1 | 54.6 | 55.6 | 54.6 | 53.3 |
| 4/14/2013 | 4/14/2013 | 15 | 1 | 51.5 | 57.7 | 55.6 | 56.5 | 55.6 | 54.4 |
| 4/14/2013 | 4/14/2013 | 16 | 1 | 52.1 | 58.1 | 55.6 | 56.5 | 55.7 | 54.5 |
| 4/14/2013 | 4/14/2013 | 17 | 1 | 52.2 | 57.4 | 55.6 | 56.5 | 55.6 | 54.4 |
| 4/14/2013 | 4/14/2013 | 18 | 1 | 52.1 | 57.1 | 55.2 | 55.9 | 55.2 | 54.3 |
| 4/14/2013 | 4/14/2013 | 19 | 1 | 52.6 | 57.4 | 55.6 | 56.2 | 55.6 | 54.9 |
| 4/14/2013 | 4/14/2013 | 20 | 1 | 53.7 | 59.1 | 55.9 | 56.5 | 55.9 | 55.2 |
| 4/14/2013 | 4/14/2013 | 21 | 1 | 53.8 | 64.7 | 55.9 | 56.4 | 55.9 | 55.2 |
| 4/14/2013 | 4/14/2013 | 22 | 1 | 53.8 | 57.9 | 56.2 | 56.7 | 56.2 | 55.6 |
| 4/14/2013 | 4/14/2013 | 23 | 1 | 52.9 | 57.3 | 55.6 | 56.3 | 55.6 | 54.9 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 58. PAPA201 (Injection Well 100 m) dBA and one-third octave band metrics, April 14-15, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/14/13 | 4/15/13 | dBA | 28 | 50.2 | 66.3 | 55.6 | 56.5 | 55.8 | 54.9 |
| 4/14/13 | 4/15/13 | 12.5 | 28 | 29.0 | 76.4 | 56.2 | 50.5 | 46.0 | 42.4 |
| 4/14/13 | 4/15/13 | 16 | 28 | 33.9 | 76.6 | 54.7 | 51.1 | 47.7 | 44.7 |
| 4/14/13 | 4/15/13 | 20 | 28 | 40.0 | 74.9 | 55.4 | 54.8 | 52.0 | 48.5 |
| 4/14/13 | 4/15/13 | 25 | 28 | 43.0 | 72.6 | 54.2 | 53.9 | 51.8 | 49.6 |
| 4/14/13 | 4/15/13 | 31.5 | 28 | 44.7 | 70.7 | 56.1 | 58.0 | 55.7 | 52.4 |
| 4/14/13 | 4/15/13 | 40 | 28 | 49.2 | 77.7 | 59.3 | 61.1 | 59.1 | 56.3 |
| 4/14/13 | 4/15/13 | 50 | 28 | 49.0 | 68.2 | 60.7 | 61.8 | 60.7 | 59.4 |
| 4/14/13 | 4/15/13 | 63 | 28 | 53.9 | 78.3 | 67.7 | 69.2 | 67.6 | 65.6 |
| 4/14/13 | 4/15/13 | 80 | 28 | 55.2 | 77.2 | 65.9 | 66.2 | 65.0 | 63.9 |
| 4/14/13 | 4/15/13 | 100 | 28 | 56.4 | 79.0 | 71.8 | 73.3 | 72.4 | 71.5 |
| 4/14/13 | 4/15/13 | 125 | 28 | 50.8 | 77.7 | 60.5 | 61.9 | 60.5 | 59.2 |
| 4/14/13 | 4/15/13 | 160 | 28 | 48.5 | 73.1 | 58.4 | 59.5 | 58.4 | 57.3 |
| 4/14/13 | 4/15/13 | 200 | 28 | 45.9 | 72.8 | 57.6 | 58.8 | 57.7 | 56.5 |
| 4/14/13 | 4/15/13 | 250 | 28 | 36.9 | 62.2 | 49.0 | 50.3 | 48.9 | 47.6 |
| 4/14/13 | 4/15/13 | 315 | 28 | 37.4 | 53.6 | 48.4 | 49.9 | 48.4 | 47.0 |
| 4/14/13 | 4/15/13 | 400 | 28 | 30.6 | 50.0 | 43.7 | 45.4 | 43.7 | 42.2 |
| 4/14/13 | 4/15/13 | 500 | 28 | 27.3 | 48.7 | 38.9 | 40.5 | 38.6 | 36.5 |
| 4/14/13 | 4/15/13 | 630 | 28 | 24.8 | 47.5 | 37.6 | 39.2 | 37.0 | 34.4 |
| 4/14/13 | 4/15/13 | 800 | 28 | 17.4 | 47.0 | 33.3 | 35.3 | 32.6 | 30.0 |
| 4/14/13 | 4/15/13 | 1000 | 28 | 14.1 | 47.5 | 31.6 | 34.3 | 30.8 | 28.0 |
| 4/14/13 | 4/15/13 | 1250 | 28 | 11.7 | 47.4 | 31.6 | 33.6 | 31.1 | 28.1 |
| 4/14/13 | 4/15/13 | 1600 | 28 | 9.9 | 45.8 | 33.8 | 35.9 | 33.4 | 29.8 |
| 4/14/13 | 4/15/13 | 2000 | 28 | 8.8 | 47.0 | 32.8 | 34.8 | 32.0 | 28.2 |
| 4/14/13 | 4/15/13 | 2500 | 28 | 7.5 | 47.6 | 32.8 | 35.0 | 32.2 | 27.6 |
| 4/14/13 | 4/15/13 | 3150 | 28 | 8.0 | 46.5 | 31.0 | 34.0 | 30.7 | 25.5 |
| 4/14/13 | 4/15/13 | 4000 | 28 | 8.4 | 44.3 | 28.7 | 30.8 | 27.9 | 22.1 |
| 4/14/13 | 4/15/13 | 5000 | 28 | 7.4 | 53.0 | 26.2 | 28.1 | 24.6 | 19.4 |
| 4/14/13 | 4/15/13 | 6300 | 28 | 6.8 | 60.0 | 22.6 | 24.6 | 21.3 | 16.4 |
| 4/14/13 | 4/15/13 | 8000 | 28 | 6.1 | 37.0 | 16.5 | 19.4 | 16.6 | 12.0 |
| 4/14/13 | 4/15/13 | 10000 | 28 | 4.6 | 33.4 | 12.1 | 13.8 | 11.2 | 8.3 |
| 4/14/13 | 4/15/13 | 12500 | 28 | 3.8 | 32.7 | 8.2 | 9.9 | 7.2 | 5.9 |
| 4/14/13 | 4/15/13 | 16000 | 28 | 3.2 | 28.1 | 5.5 | 6.1 | 4.7 | 4.1 |
| 4/14/13 | 4/15/13 | 20000 | 28 | 1.8 | 23.3 | 4.0 | 3.3 | 2.8 | 2.5 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 59. PAPA202 (Injection Well 200 m) hourly dBA metrics, April 14-15, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/15/2013 | 4/15/2013 | 0 | 1 | 46.0 | 51.5 | 49.2 | 50.1 | 49.2 | 48.2 |
| 4/15/2013 | 4/15/2013 | 1 | 1 | 46.1 | 51.6 | 49.4 | 50.2 | 49.3 | 48.4 |
| 4/15/2013 | 4/15/2013 | 2 | 1 | 45.1 | 52.0 | 49.3 | 50.4 | 49.3 | 47.7 |
| 4/15/2013 | 4/15/2013 | 3 | 1 | 44.6 | 51.0 | 48.4 | 49.4 | 48.3 | 47.1 |
| 4/15/2013 | 4/15/2013 | 4 | 1 | 46.0 | 51.6 | 49.2 | 50.0 | 49.1 | 48.2 |
| 4/15/2013 | 4/15/2013 | 5 | 1 | 45.8 | 51.0 | 49.3 | 50.1 | 49.3 | 48.2 |
| 4/15/2013 | 4/15/2013 | 6 | 1 | 45.7 | 51.2 | 49.0 | 49.7 | 48.9 | 48.1 |
| 4/15/2013 | 4/15/2013 | 7 | 1 | 46.1 | 50.9 | 49.3 | 50.0 | 49.2 | 48.4 |
| 4/15/2013 | 4/15/2013 | 8 | 1 | 45.0 | 51.2 | 48.8 | 49.7 | 48.8 | 47.9 |
| 4/14/2013 | 4/15/2013 | 9 | 2 | 38.4 | 51.0 | 47.4 | 48.4 | 47.0 | 45.4 |
| 4/14/2013 | 4/15/2013 | 10 | 2 | 37.8 | 52.8 | 47.4 | 48.1 | 46.7 | 45.3 |
| 4/14/2013 | 4/15/2013 | 11 | 2 | 37.5 | 53.9 | 47.4 | 48.3 | 46.8 | 45.2 |
| 4/14/2013 | 4/15/2013 | 12 | 2 | 39.4 | 51.1 | 47.1 | 48.4 | 46.8 | 44.2 |
| 4/14/2013 | 4/14/2013 | 13 | 1 | 39.5 | 61.0 | 45.9 | 47.6 | 45.5 | 43.2 |
| 4/14/2013 | 4/14/2013 | 14 | 1 | 38.3 | 59.8 | 46.1 | 47.9 | 45.8 | 43.2 |
| 4/14/2013 | 4/14/2013 | 15 | 1 | 39.1 | 51.6 | 47.9 | 49.5 | 47.9 | 45.4 |
| 4/14/2013 | 4/14/2013 | 16 | 1 | 41.0 | 51.2 | 48.1 | 49.5 | 48.2 | 45.5 |
| 4/14/2013 | 4/14/2013 | 17 | 1 | 39.9 | 51.4 | 47.9 | 49.3 | 47.9 | 45.3 |
| 4/14/2013 | 4/14/2013 | 18 | 1 | 42.1 | 50.2 | 47.2 | 48.4 | 47.1 | 45.4 |
| 4/14/2013 | 4/14/2013 | 19 | 1 | 44.1 | 52.1 | 48.0 | 48.9 | 47.9 | 46.9 |
| 4/14/2013 | 4/14/2013 | 20 | 1 | 45.1 | 52.6 | 48.4 | 49.1 | 48.3 | 47.6 |
| 4/14/2013 | 4/14/2013 | 21 | 1 | 45.4 | 62.1 | 48.8 | 49.1 | 48.5 | 47.7 |
| 4/14/2013 | 4/14/2013 | 22 | 1 | 46.5 | 50.9 | 49.2 | 49.9 | 49.2 | 48.3 |
| 4/14/2013 | 4/14/2013 | 23 | 1 | 46.1 | 50.9 | 49.1 | 49.8 | 49.0 | 48.3 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 60. PAPA202 (Injection Well 200 m) dBA and one-third octave band metrics, April 14-15, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/14/13 | 4/15/13 | dBA | 28 | 37.5 | 62.1 | 48.2 | 49.5 | 48.5 | 47.7 |
| 4/14/13 | 4/15/13 | 12.5 | 28 | 26.5 | 74.3 | 52.8 | 47.1 | 43.2 | 39.2 |
| 4/14/13 | 4/15/13 | 16 | 28 | 28.7 | 71.7 | 50.0 | 48.6 | 44.8 | 40.4 |
| 4/14/13 | 4/15/13 | 20 | 28 | 31.9 | 73.5 | 50.2 | 52.5 | 47.3 | 43.2 |
| 4/14/13 | 4/15/13 | 25 | 28 | 37.2 | 66.9 | 47.7 | 48.3 | 46.0 | 43.4 |
| 4/14/13 | 4/15/13 | 31.5 | 28 | 39.8 | 67.6 | 50.9 | 52.9 | 50.5 | 47.1 |
| 4/14/13 | 4/15/13 | 40 | 28 | 42.8 | 71.5 | 53.2 | 55.3 | 53.3 | 50.5 |
| 4/14/13 | 4/15/13 | 50 | 28 | 44.2 | 67.8 | 55.2 | 56.5 | 55.4 | 54.1 |
| 4/14/13 | 4/15/13 | 63 | 28 | 44.2 | 76.8 | 63.1 | 64.7 | 63.2 | 61.1 |
| 4/14/13 | 4/15/13 | 80 | 28 | 43.4 | 77.9 | 59.4 | 60.9 | 59.2 | 57.7 |
| 4/14/13 | 4/15/13 | 100 | 28 | 44.7 | 79.5 | 65.4 | 67.1 | 65.9 | 64.7 |
| 4/14/13 | 4/15/13 | 125 | 28 | 35.8 | 77.0 | 53.2 | 54.7 | 53.3 | 51.8 |
| 4/14/13 | 4/15/13 | 160 | 28 | 34.2 | 70.4 | 49.7 | 51.5 | 50.2 | 47.5 |
| 4/14/13 | 4/15/13 | 200 | 28 | 30.7 | 71.6 | 47.0 | 48.9 | 47.3 | 44.4 |
| 4/14/13 | 4/15/13 | 250 | 28 | 26.0 | 59.5 | 39.1 | 40.9 | 39.0 | 36.1 |
| 4/14/13 | 4/15/13 | 315 | 28 | 23.7 | 49.9 | 37.3 | 39.4 | 37.2 | 34.3 |
| 4/14/13 | 4/15/13 | 400 | 28 | 17.9 | 49.3 | 31.7 | 33.6 | 31.1 | 27.3 |
| 4/14/13 | 4/15/13 | 500 | 28 | 11.5 | 50.8 | 26.9 | 28.8 | 26.3 | 22.4 |
| 4/14/13 | 4/15/13 | 630 | 28 | 7.9 | 44.2 | 25.1 | 26.9 | 23.8 | 19.7 |
| 4/14/13 | 4/15/13 | 800 | 28 | 3.8 | 42.6 | 22.1 | 24.6 | 21.0 | 16.8 |
| 4/14/13 | 4/15/13 | 1000 | 28 | 2.0 | 44.4 | 21.0 | 23.3 | 19.6 | 14.4 |
| 4/14/13 | 4/15/13 | 1250 | 28 | 2.5 | 40.5 | 22.2 | 25.0 | 20.8 | 14.3 |
| 4/14/13 | 4/15/13 | 1600 | 28 | 3.3 | 42.7 | 24.3 | 27.5 | 21.7 | 13.2 |
| 4/14/13 | 4/15/13 | 2000 | 28 | 3.1 | 37.7 | 21.9 | 25.7 | 19.1 | 10.2 |
| 4/14/13 | 4/15/13 | 2500 | 28 | 3.0 | 35.9 | 20.3 | 23.6 | 16.2 | 8.3 |
| 4/14/13 | 4/15/13 | 3150 | 28 | 3.7 | 35.1 | 17.5 | 20.1 | 12.7 | 7.1 |
| 4/14/13 | 4/15/13 | 4000 | 28 | 4.0 | 37.8 | 14.2 | 16.0 | 9.8 | 6.3 |
| 4/14/13 | 4/15/13 | 5000 | 28 | 4.3 | 46.0 | 10.8 | 12.1 | 7.8 | 5.7 |
| 4/14/13 | 4/15/13 | 6300 | 28 | 3.4 | 43.5 | 7.4 | 8.9 | 6.6 | 5.4 |
| 4/14/13 | 4/15/13 | 8000 | 28 | 1.9 | 60.7 | 14.2 | 6.3 | 5.4 | 5.1 |
| 4/14/13 | 4/15/13 | 10000 | 28 | 0.8 | 44.6 | 5.8 | 5.3 | 4.9 | 4.7 |
| 4/14/13 | 4/15/13 | 12500 | 28 | 0.1 | 23.9 | 4.8 | 4.9 | 4.4 | 4.3 |
| 4/14/13 | 4/15/13 | 16000 | 28 | 0.4 | 39.9 | 4.4 | 4.4 | 3.8 | 3.5 |
| 4/14/13 | 4/15/13 | 20000 | 28 | 0.7 | 21.9 | 3.4 | 3.4 | 2.6 | 2.3 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 61. PAPA203 (Well Pad, 3 wells, 50 m) hourly dBA metrics, April 15-16, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/16/2013 | 4/16/2013 | 0 | 1 | 34.2 | 45.1 | 40.2 | 42.2 | 39.8 | 37.1 |
| 4/16/2013 | 4/16/2013 | 1 | 1 | 33.7 | 40.9 | 37.7 | 39.6 | 37.3 | 35.6 |
| 4/16/2013 | 4/16/2013 | 2 | 1 | 32.5 | 42.6 | 37.4 | 39.9 | 36.6 | 34.4 |
| 4/16/2013 | 4/16/2013 | 3 | 1 | 31.9 | 40.8 | 37.1 | 39.1 | 37.0 | 33.9 |
| 4/16/2013 | 4/16/2013 | 4 | 1 | 32.6 | 41.3 | 37.8 | 39.7 | 37.6 | 35.0 |
| 4/16/2013 | 4/16/2013 | 5 | 1 | 32.7 | 41.5 | 37.4 | 39.2 | 37.2 | 35.1 |
| 4/16/2013 | 4/16/2013 | 6 | 1 | 33.3 | 41.1 | 37.2 | 38.9 | 37.0 | 35.2 |
| 4/16/2013 | 4/16/2013 | 7 | 1 | 31.8 | 41.6 | 37.7 | 39.9 | 37.4 | 34.2 |
| 4/16/2013 | 4/16/2013 | 8 | 1 | 32.3 | 47.5 | 37.9 | 40.0 | 37.3 | 34.8 |
| 4/16/2013 | 4/16/2013 | 9 | 1 | 32.0 | 44.1 | 37.4 | 39.6 | 36.9 | 34.1 |
| 4/16/2013 | 4/16/2013 | 10 | 1 | 31.9 | 40.3 | 36.8 | 38.6 | 36.7 | 33.9 |
| 4/16/2013 | 4/16/2013 | 11 | 1 | 30.8 | 53.9 | 38.2 | 39.9 | 37.1 | 34.0 |
| 4/16/2013 | 4/16/2013 | 12 | 1 | 32.7 | 44.2 | 37.9 | 39.7 | 37.6 | 35.5 |
| 4/16/2013 | 4/16/2013 | 13 | 1 | 32.5 | 41.7 | 36.8 | 38.0 | 36.8 | 35.2 |
| 4/16/2013 | 4/16/2013 | 14 | 0 | NA | NA | NA | NA | NA | NA |
| 4/16/2013 | 4/16/2013 | 15 | 0 | NA | NA | NA | NA | NA | NA |
| 4/15/2013 | 4/15/2013 | 16 | 1 | 35.1 | 44.0 | 38.0 | 39.0 | 37.9 | 36.9 |
| 4/15/2013 | 4/15/2013 | 17 | 1 | 35.6 | 53.4 | 39.9 | 41.3 | 38.9 | 37.7 |
| 4/15/2013 | 4/15/2013 | 18 | 1 | 36.0 | 49.6 | 41.2 | 42.8 | 41.1 | 38.4 |
| 4/15/2013 | 4/15/2013 | 19 | 1 | 35.9 | 44.5 | 38.9 | 39.8 | 38.7 | 37.7 |
| 4/15/2013 | 4/15/2013 | 20 | 1 | 34.6 | 47.0 | 38.7 | 39.7 | 38.3 | 37.1 |
| 4/15/2013 | 4/15/2013 | 21 | 1 | 35.2 | 59.0 | 40.4 | 40.0 | 38.5 | 37.4 |
| 4/15/2013 | 4/15/2013 | 22 | 1 | 35.4 | 43.9 | 38.8 | 40.3 | 38.5 | 37.3 |
| 4/15/2013 | 4/15/2013 | 23 | 1 | 34.2 | 42.2 | 38.3 | 40.2 | 37.9 | 36.7 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 62. PAPA203 (Well Pad, 3 wells, 50 m) dBA and one-third octave band metrics, April 15-16, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/15/13 | 4/16/13 | dBA | 22 | 30.8 | 59.0 | 38.4 | 39.8 | 37.5 | 35.4 |
| 4/15/13 | 4/16/13 | 12.5 | 22 | 29.5 | 77.5 | 55.6 | 53.6 | 47.6 | 42.3 |
| 4/15/13 | 4/16/13 | 16 | 22 | 32.2 | 76.0 | 54.0 | 53.1 | 48.9 | 44.9 |
| 4/15/13 | 4/16/13 | 20 | 22 | 39.8 | 74.3 | 55.5 | 56.4 | 53.3 | 49.2 |
| 4/15/13 | 4/16/13 | 25 | 22 | 39.3 | 70.1 | 53.1 | 54.7 | 51.3 | 48.1 |
| 4/15/13 | 4/16/13 | 31.5 | 22 | 37.7 | 66.7 | 49.1 | 50.3 | 48.0 | 45.7 |
| 4/15/13 | 4/16/13 | 40 | 22 | 39.9 | 68.7 | 54.0 | 55.4 | 53.2 | 50.0 |
| 4/15/13 | 4/16/13 | 50 | 22 | 40.6 | 66.5 | 61.4 | 63.2 | 61.1 | 56.3 |
| 4/15/13 | 4/16/13 | 63 | 22 | 32.0 | 68.3 | 55.3 | 60.2 | 46.7 | 40.8 |
| 4/15/13 | 4/16/13 | 80 | 22 | 33.2 | 63.8 | 47.2 | 51.0 | 42.6 | 40.0 |
| 4/15/13 | 4/16/13 | 100 | 22 | 34.8 | 67.8 | 44.7 | 46.2 | 44.1 | 42.3 |
| 4/15/13 | 4/16/13 | 125 | 22 | 36.3 | 68.0 | 43.0 | 43.8 | 42.1 | 40.5 |
| 4/15/13 | 4/16/13 | 160 | 22 | 36.9 | 62.3 | 44.3 | 45.3 | 43.8 | 42.1 |
| 4/15/13 | 4/16/13 | 200 | 22 | 31.9 | 66.3 | 39.0 | 39.0 | 37.7 | 36.6 |
| 4/15/13 | 4/16/13 | 250 | 22 | 26.4 | 63.8 | 37.7 | 39.4 | 37.0 | 33.4 |
| 4/15/13 | 4/16/13 | 315 | 22 | 20.8 | 55.7 | 29.2 | 29.0 | 27.4 | 26.0 |
| 4/15/13 | 4/16/13 | 400 | 22 | 18.0 | 48.4 | 28.0 | 28.6 | 27.0 | 24.9 |
| 4/15/13 | 4/16/13 | 500 | 22 | 14.1 | 48.2 | 24.1 | 23.5 | 22.0 | 20.5 |
| 4/15/13 | 4/16/13 | 630 | 22 | 9.8 | 44.7 | 20.6 | 17.9 | 16.5 | 15.3 |
| 4/15/13 | 4/16/13 | 800 | 22 | 7.1 | 39.4 | 17.4 | 15.2 | 13.2 | 11.8 |
| 4/15/13 | 4/16/13 | 1000 | 22 | 5.4 | 38.7 | 15.2 | 13.0 | 10.5 | 9.3 |
| 4/15/13 | 4/16/13 | 1250 | 22 | 3.2 | 39.7 | 14.6 | 11.9 | 9.4 | 7.8 |
| 4/15/13 | 4/16/13 | 1600 | 22 | 3.4 | 43.5 | 15.3 | 13.0 | 10.6 | 8.9 |
| 4/15/13 | 4/16/13 | 2000 | 22 | 3.3 | 44.3 | 15.3 | 13.4 | 10.1 | 8.7 |
| 4/15/13 | 4/16/13 | 2500 | 22 | 3.7 | 45.9 | 14.9 | 13.2 | 10.1 | 8.3 |
| 4/15/13 | 4/16/13 | 3150 | 22 | 3.9 | 46.1 | 13.9 | 12.5 | 9.0 | 7.2 |
| 4/15/13 | 4/16/13 | 4000 | 22 | 4.4 | 44.4 | 11.5 | 10.2 | 7.2 | 5.9 |
| 4/15/13 | 4/16/13 | 5000 | 22 | 4.3 | 40.1 | 9.4 | 8.3 | 6.0 | 5.2 |
| 4/15/13 | 4/16/13 | 6300 | 22 | 3.4 | 40.5 | 7.5 | 7.5 | 5.8 | 5.2 |
| 4/15/13 | 4/16/13 | 8000 | 22 | 2.1 | 39.2 | 6.6 | 6.3 | 5.3 | 5.0 |
| 4/15/13 | 4/16/13 | 10000 | 22 | 1.6 | 23.2 | 5.4 | 5.9 | 5.0 | 4.7 |
| 4/15/13 | 4/16/13 | 12500 | 22 | 1.3 | 18.8 | 4.7 | 4.8 | 4.4 | 4.1 |
| 4/15/13 | 4/16/13 | 16000 | 22 | 1.0 | 16.0 | 4.0 | 4.2 | 3.6 | 3.3 |
| 4/15/13 | 4/16/13 | 20000 | 22 | 1.3 | 14.1 | 2.9 | 3.0 | 2.4 | 2.1 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 63. PAPA204 (Well Pad, 3 wells, 100 m) hourly dBA metrics, April 15-16, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/16/2013 | 4/16/2013 | 0 | 1 | 28.1 | 38.7 | 33.6 | 35.5 | 33.5 | 30.4 |
| 4/16/2013 | 4/16/2013 | 1 | 1 | 27.1 | 39.2 | 32.1 | 35.1 | 30.5 | 28.9 |
| 4/16/2013 | 4/16/2013 | 2 | 1 | 26.1 | 37.3 | 32.3 | 35.7 | 30.3 | 28.0 |
| 4/16/2013 | 4/16/2013 | 3 | 1 | 26.5 | 36.6 | 31.7 | 34.2 | 30.9 | 28.6 |
| 4/16/2013 | 4/16/2013 | 4 | 1 | 27.6 | 39.7 | 32.7 | 34.8 | 31.9 | 29.9 |
| 4/16/2013 | 4/16/2013 | 5 | 1 | 27.1 | 38.7 | 31.8 | 33.9 | 31.1 | 29.1 |
| 4/16/2013 | 4/16/2013 | 6 | 1 | 27.5 | 36.3 | 31.9 | 34.1 | 31.2 | 29.5 |
| 4/16/2013 | 4/16/2013 | 7 | 1 | 25.5 | 37.1 | 32.3 | 35.4 | 30.8 | 28.1 |
| 4/16/2013 | 4/16/2013 | 8 | 1 | 25.8 | 44.8 | 32.5 | 35.1 | 31.2 | 28.8 |
| 4/16/2013 | 4/16/2013 | 9 | 1 | 24.7 | 41.8 | 31.5 | 34.5 | 29.9 | 27.3 |
| 4/16/2013 | 4/16/2013 | 10 | 1 | 24.5 | 36.8 | 30.5 | 33.1 | 29.5 | 26.6 |
| 4/16/2013 | 4/16/2013 | 11 | 1 | 23.8 | 43.3 | 31.7 | 34.2 | 30.4 | 26.8 |
| 4/16/2013 | 4/16/2013 | 12 | 1 | 26.1 | 40.8 | 32.7 | 35.4 | 31.5 | 28.6 |
| 4/16/2013 | 4/16/2013 | 13 | 1 | 24.8 | 38.7 | 30.4 | 32.1 | 30.1 | 27.9 |
| 4/15/2013 | 4/15/2013 | 14 | 0 | NA | NA | NA | NA | NA | NA |
| 4/15/2013 | 4/15/2013 | 15 | 0 | NA | NA | NA | NA | NA | NA |
| 4/15/2013 | 4/15/2013 | 16 | 1 | 27.9 | 46.7 | 35.3 | 38.0 | 33.8 | 31.1 |
| 4/15/2013 | 4/15/2013 | 17 | 1 | 30.1 | 55.6 | 40.2 | 43.3 | 38.1 | 33.8 |
| 4/15/2013 | 4/15/2013 | 18 | 1 | 32.4 | 51.2 | 40.6 | 43.6 | 39.0 | 35.7 |
| 4/15/2013 | 4/15/2013 | 19 | 1 | 30.5 | 47.4 | 36.5 | 39.1 | 35.3 | 33.1 |
| 4/15/2013 | 4/15/2013 | 20 | 1 | 28.4 | 48.2 | 34.3 | 35.9 | 32.9 | 30.9 |
| 4/15/2013 | 4/15/2013 | 21 | 1 | 29.8 | 60.7 | 38.3 | 37.6 | 34.4 | 32.0 |
| 4/15/2013 | 4/15/2013 | 22 | 1 | 29.0 | 41.6 | 33.8 | 36.0 | 32.9 | 31.0 |
| 4/15/2013 | 4/15/2013 | 23 | 1 | 28.1 | 39.0 | 32.7 | 35.8 | 31.4 | 29.9 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 64. PAPA204 (Well Pad, 3 wells, 100 m) dBA and one-third octave band metrics, April 15-16, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/15/13 | 4/16/13 | dBA | 22 | 23.8 | 60.7 | 34.8 | 35.4 | 31.3 | 29.3 |
| 4/15/13 | 4/16/13 | 12.5 | 22 | 28.0 | 78.3 | 60.1 | 55.9 | 49.6 | 43.6 |
| 4/15/13 | 4/16/13 | 16 | 22 | 32.5 | 79.7 | 59.6 | 53.2 | 49.8 | 45.5 |
| 4/15/13 | 4/16/13 | 20 | 22 | 38.0 | 77.9 | 57.3 | 56.2 | 52.8 | 48.9 |
| 4/15/13 | 4/16/13 | 25 | 22 | 37.3 | 72.0 | 53.3 | 54.1 | 50.1 | 46.4 |
| 4/15/13 | 4/16/13 | 31.5 | 22 | 34.7 | 68.6 | 49.3 | 49.1 | 46.7 | 43.6 |
| 4/15/13 | 4/16/13 | 40 | 22 | 36.4 | 66.7 | 49.3 | 49.8 | 47.4 | 45.2 |
| 4/15/13 | 4/16/13 | 50 | 22 | 35.8 | 66.5 | 55.3 | 57.0 | 54.9 | 50.0 |
| 4/15/13 | 4/16/13 | 63 | 22 | 29.5 | 65.8 | 51.8 | 56.4 | 45.7 | 38.3 |
| 4/15/13 | 4/16/13 | 80 | 22 | 30.9 | 60.9 | 44.4 | 48.9 | 39.7 | 37.0 |
| 4/15/13 | 4/16/13 | 100 | 22 | 30.4 | 61.2 | 40.4 | 41.3 | 38.8 | 36.9 |
| 4/15/13 | 4/16/13 | 125 | 22 | 29.7 | 68.9 | 39.5 | 40.6 | 38.4 | 36.3 |
| 4/15/13 | 4/16/13 | 160 | 22 | 27.5 | 62.3 | 36.1 | 36.8 | 34.6 | 32.8 |
| 4/15/13 | 4/16/13 | 200 | 22 | 24.4 | 66.9 | 34.2 | 32.6 | 31.1 | 29.6 |
| 4/15/13 | 4/16/13 | 250 | 22 | 18.4 | 66.4 | 32.0 | 31.7 | 29.7 | 26.9 |
| 4/15/13 | 4/16/13 | 315 | 22 | 10.1 | 57.3 | 26.8 | 24.1 | 21.2 | 18.3 |
| 4/15/13 | 4/16/13 | 400 | 22 | 5.9 | 52.7 | 24.7 | 19.0 | 15.3 | 13.0 |
| 4/15/13 | 4/16/13 | 500 | 22 | 2.5 | 50.4 | 22.9 | 14.2 | 10.5 | 8.0 |
| 4/15/13 | 4/16/13 | 630 | 22 | -0.1 | 45.2 | 20.5 | 10.6 | 6.5 | 4.2 |
| 4/15/13 | 4/16/13 | 800 | 22 | -0.4 | 38.6 | 18.1 | 10.7 | 7.4 | 4.2 |
| 4/15/13 | 4/16/13 | 1000 | 22 | -0.3 | 39.8 | 17.3 | 10.3 | 7.5 | 4.7 |
| 4/15/13 | 4/16/13 | 1250 | 22 | 0.0 | 36.5 | 18.4 | 10.9 | 8.1 | 4.7 |
| 4/15/13 | 4/16/13 | 1600 | 22 | 0.9 | 37.7 | 19.1 | 9.9 | 7.8 | 5.1 |
| 4/15/13 | 4/16/13 | 2000 | 22 | 1.4 | 39.3 | 18.9 | 10.7 | 8.2 | 5.1 |
| 4/15/13 | 4/16/13 | 2500 | 22 | 2.4 | 39.7 | 17.8 | 10.2 | 7.7 | 5.2 |
| 4/15/13 | 4/16/13 | 3150 | 22 | 3.1 | 39.4 | 15.5 | 9.0 | 6.2 | 4.9 |
| 4/15/13 | 4/16/13 | 4000 | 22 | 3.9 | 37.0 | 12.2 | 6.4 | 5.4 | 4.9 |
| 4/15/13 | 4/16/13 | 5000 | 22 | 4.6 | 33.4 | 9.5 | 6.0 | 5.5 | 5.2 |
| 4/15/13 | 4/16/13 | 6300 | 22 | 4.9 | 33.2 | 8.0 | 6.2 | 5.7 | 5.5 |
| 4/15/13 | 4/16/13 | 8000 | 22 | 4.7 | 29.3 | 7.3 | 6.3 | 5.7 | 5.5 |
| 4/15/13 | 4/16/13 | 10000 | 22 | 4.3 | 24.6 | 6.4 | 5.9 | 5.4 | 5.2 |
| 4/15/13 | 4/16/13 | 12500 | 22 | 3.9 | 25.8 | 5.6 | 5.3 | 4.7 | 4.4 |
| 4/15/13 | 4/16/13 | 16000 | 22 | 3.0 | 24.6 | 4.5 | 4.3 | 3.6 | 3.4 |
| 4/15/13 | 4/16/13 | 20000 | 22 | 1.6 | 21.8 | 3.1 | 2.9 | 2.2 | 1.9 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 65. PAPA205 (Central Gathering Facility, with generator, 255 m) hourly dBA metrics, April 16-17, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/17/2013 | 4/17/2013 | 0 | 1 | 33.0 | 46.3 | 36.9 | 38.6 | 36.4 | 34.9 |
| 4/17/2013 | 4/17/2013 | 1 | 1 | 31.2 | 45.0 | 35.7 | 37.3 | 35.2 | 33.5 |
| 4/17/2013 | 4/17/2013 | 2 | 1 | 31.3 | 40.7 | 36.7 | 38.1 | 36.7 | 34.4 |
| 4/17/2013 | 4/17/2013 | 3 | 1 | 32.1 | 50.5 | 39.0 | 42.1 | 36.8 | 34.7 |
| 4/17/2013 | 4/17/2013 | 4 | 1 | 29.9 | 41.9 | 33.6 | 35.0 | 33.2 | 31.6 |
| 4/17/2013 | 4/17/2013 | 5 | 1 | 32.1 | 39.9 | 35.0 | 36.0 | 35.0 | 33.7 |
| 4/17/2013 | 4/17/2013 | 6 | 1 | 33.1 | 44.1 | 36.5 | 37.9 | 36.2 | 35.0 |
| 4/17/2013 | 4/17/2013 | 7 | 1 | 25.5 | 37.6 | 31.8 | 33.8 | 31.5 | 28.5 |
| 4/17/2013 | 4/17/2013 | 8 | 1 | 25.0 | 40.8 | 30.3 | 32.0 | 29.9 | 28.1 |
| 4/17/2013 | 4/17/2013 | 9 | 1 | 25.5 | 44.1 | 31.4 | 33.5 | 30.3 | 28.4 |
| 4/16/2013 | 4/16/2013 | 10 | 0 | NA | NA | NA | NA | NA | NA |
| 4/16/2013 | 4/16/2013 | 11 | 0 | NA | NA | NA | NA | NA | NA |
| 4/16/2013 | 4/16/2013 | 12 | 0 | NA | NA | NA | NA | NA | NA |
| 4/16/2013 | 4/16/2013 | 13 | 0 | NA | NA | NA | NA | NA | NA |
| 4/16/2013 | 4/16/2013 | 14 | 0 | NA | NA | NA | NA | NA | NA |
| 4/16/2013 | 4/16/2013 | 15 | 0 | NA | NA | NA | NA | NA | NA |
| 4/16/2013 | 4/16/2013 | 16 | 0 | NA | NA | NA | NA | NA | NA |
| 4/16/2013 | 4/16/2013 | 17 | 1 | 30.5 | 67.8 | 38.2 | 36.2 | 34.2 | 32.6 |
| 4/16/2013 | 4/16/2013 | 18 | 1 | 32.1 | 43.6 | 35.9 | 37.3 | 35.6 | 34.1 |
| 4/16/2013 | 4/16/2013 | 19 | 1 | 31.5 | 41.7 | 36.1 | 37.8 | 35.7 | 34.2 |
| 4/16/2013 | 4/16/2013 | 20 | 1 | 33.5 | 41.5 | 37.6 | 39.3 | 37.2 | 35.6 |
| 4/16/2013 | 4/16/2013 | 21 | 1 | 35.1 | 44.2 | 39.6 | 40.6 | 39.6 | 38.2 |
| 4/16/2013 | 4/16/2013 | 22 | 1 | 33.8 | 43.4 | 37.3 | 38.7 | 37.0 | 35.6 |
| 4/16/2013 | 4/16/2013 | 23 | 1 | 32.4 | 46.2 | 38.4 | 40.4 | 37.9 | 35.5 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 66. PAPA205 (Central Gathering Facility, with generator, 255 m) dBA and one-third octave band metrics, April 16-17, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/16/13 | 4/17/13 | dBA | 17 | 25.0 | 67.8 | 36.6 | 37.8 | 35.7 | 34.2 |
| 4/16/13 | 4/17/13 | 12.5 | 17 | 32.1 | 71.1 | 53.4 | 54.7 | 53.0 | 51.6 |
| 4/16/13 | 4/17/13 | 16 | 17 | 32.6 | 71.5 | 51.2 | 53.3 | 48.1 | 44.5 |
| 4/16/13 | 4/17/13 | 20 | 17 | 39.8 | 74.6 | 61.1 | 66.4 | 56.2 | 51.1 |
| 4/16/13 | 4/17/13 | 25 | 17 | 39.6 | 69.1 | 52.4 | 52.7 | 50.5 | 48.2 |
| 4/16/13 | 4/17/13 | 31.5 | 17 | 38.6 | 78.9 | 66.4 | 68.9 | 64.8 | 58.4 |
| 4/16/13 | 4/17/13 | 40 | 17 | 35.4 | 64.3 | 50.1 | 52.0 | 49.1 | 46.0 |
| 4/16/13 | 4/17/13 | 50 | 17 | 32.0 | 64.7 | 49.5 | 51.6 | 49.7 | 47.5 |
| 4/16/13 | 4/17/13 | 63 | 17 | 36.0 | 62.7 | 52.4 | 54.1 | 51.1 | 48.0 |
| 4/16/13 | 4/17/13 | 80 | 17 | 35.1 | 60.8 | 52.3 | 54.3 | 52.4 | 47.1 |
| 4/16/13 | 4/17/13 | 100 | 17 | 28.8 | 60.8 | 43.8 | 45.5 | 43.5 | 41.1 |
| 4/16/13 | 4/17/13 | 125 | 17 | 27.4 | 62.3 | 41.6 | 42.7 | 40.3 | 37.6 |
| 4/16/13 | 4/17/13 | 160 | 17 | 24.6 | 55.9 | 35.5 | 36.8 | 33.8 | 30.8 |
| 4/16/13 | 4/17/13 | 200 | 17 | 22.0 | 54.5 | 33.9 | 34.6 | 30.7 | 28.3 |
| 4/16/13 | 4/17/13 | 250 | 17 | 17.3 | 54.4 | 32.9 | 34.5 | 30.6 | 27.7 |
| 4/16/13 | 4/17/13 | 315 | 17 | 12.0 | 56.1 | 31.8 | 34.0 | 29.8 | 26.6 |
| 4/16/13 | 4/17/13 | 400 | 17 | 8.8 | 61.7 | 30.2 | 31.4 | 27.4 | 23.5 |
| 4/16/13 | 4/17/13 | 500 | 17 | 3.0 | 60.4 | 25.5 | 26.4 | 22.9 | 19.5 |
| 4/16/13 | 4/17/13 | 630 | 17 | -0.1 | 59.9 | 21.7 | 22.9 | 19.8 | 14.3 |
| 4/16/13 | 4/17/13 | 800 | 17 | -0.1 | 56.3 | 19.8 | 21.7 | 17.8 | 12.7 |
| 4/16/13 | 4/17/13 | 1000 | 17 | 0.9 | 54.3 | 20.2 | 22.3 | 17.8 | 14.0 |
| 4/16/13 | 4/17/13 | 1250 | 17 | 0.9 | 49.6 | 20.9 | 20.7 | 16.6 | 12.2 |
| 4/16/13 | 4/17/13 | 1600 | 17 | 1.1 | 50.9 | 18.8 | 19.1 | 15.1 | 11.7 |
| 4/16/13 | 4/17/13 | 2000 | 17 | 1.5 | 50.5 | 15.2 | 14.8 | 11.2 | 7.6 |
| 4/16/13 | 4/17/13 | 2500 | 17 | 2.2 | 51.6 | 12.4 | 10.7 | 6.9 | 4.7 |
| 4/16/13 | 4/17/13 | 3150 | 17 | 2.9 | 53.5 | 10.6 | 6.2 | 4.7 | 4.0 |
| 4/16/13 | 4/17/13 | 4000 | 17 | 3.8 | 53.4 | 10.2 | 5.1 | 4.7 | 4.4 |
| 4/16/13 | 4/17/13 | 5000 | 17 | 4.5 | 52.8 | 10.6 | 5.6 | 5.2 | 5.0 |
| 4/16/13 | 4/17/13 | 6300 | 17 | 5.0 | 50.4 | 8.3 | 5.9 | 5.6 | 5.4 |
| 4/16/13 | 4/17/13 | 8000 | 17 | 4.8 | 45.7 | 7.2 | 5.7 | 5.6 | 5.4 |
| 4/16/13 | 4/17/13 | 10000 | 17 | 4.5 | 44.4 | 6.2 | 5.4 | 5.2 | 5.0 |
| 4/16/13 | 4/17/13 | 12500 | 17 | 3.9 | 40.2 | 4.9 | 4.6 | 4.4 | 4.2 |
| 4/16/13 | 4/17/13 | 16000 | 17 | 2.8 | 34.8 | 3.6 | 3.5 | 3.3 | 3.1 |
| 4/16/13 | 4/17/13 | 20000 | 17 | 1.4 | 36.1 | 2.3 | 2.2 | 1.9 | 1.8 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 67. PAPA206 (Central Gathering Facility, with generator, 555 m) hourly dBA metrics, April 16-17, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/17/2013 | 4/17/2013 | 0 | 1 | 33.0 | 44.2 | 36.7 | 38.6 | 36.2 | 34.8 |
| 4/17/2013 | 4/17/2013 | 1 | 1 | 33.1 | 46.7 | 37.5 | 39.4 | 36.9 | 35.2 |
| 4/17/2013 | 4/17/2013 | 2 | 1 | 34.2 | 42.4 | 38.1 | 39.6 | 37.9 | 36.0 |
| 4/17/2013 | 4/17/2013 | 3 | 1 | 34.4 | 53.5 | 41.5 | 44.8 | 38.6 | 36.4 |
| 4/17/2013 | 4/17/2013 | 4 | 1 | 33.1 | 44.9 | 36.5 | 38.3 | 35.8 | 34.8 |
| 4/17/2013 | 4/17/2013 | 5 | 1 | 34.1 | 39.6 | 36.4 | 37.9 | 36.0 | 35.2 |
| 4/17/2013 | 4/17/2013 | 6 | 1 | 35.6 | 43.7 | 38.1 | 39.2 | 37.9 | 36.8 |
| 4/17/2013 | 4/17/2013 | 7 | 1 | 31.6 | 50.5 | 37.4 | 39.0 | 35.9 | 34.1 |
| 4/17/2013 | 4/17/2013 | 8 | 1 | 31.1 | 44.5 | 36.7 | 38.7 | 36.1 | 33.8 |
| 4/17/2013 | 4/17/2013 | 9 | 1 | 31.3 | 43.8 | 37.2 | 39.6 | 36.5 | 33.9 |
| 4/17/2013 | 4/17/2013 | 10 | 0 | NA | NA | NA | NA | NA | NA |
| 4/17/2013 | 4/17/2013 | 11 | 0 | NA | NA | NA | NA | NA | NA |
| 4/17/2013 | 4/17/2013 | 12 | 0 | NA | NA | NA | NA | NA | NA |
| 4/17/2013 | 4/17/2013 | 13 | 0 | NA | NA | NA | NA | NA | NA |
| 4/17/2013 | 4/17/2013 | 14 | 0 | NA | NA | NA | NA | NA | NA |
| 4/17/2013 | 4/17/2013 | 15 | 0 | NA | NA | NA | NA | NA | NA |
| 4/17/2013 | 4/17/2013 | 16 | 0 | NA | NA | NA | NA | NA | NA |
| 4/17/2013 | 4/17/2013 | 17 | 0 | NA | NA | NA | NA | NA | NA |
| 4/16/2013 | 4/16/2013 | 18 | 1 | 36.6 | 47.0 | 41.0 | 42.9 | 40.5 | 38.6 |
| 4/16/2013 | 4/16/2013 | 19 | 1 | 37.7 | 50.1 | 41.6 | 43.5 | 41.0 | 39.2 |
| 4/16/2013 | 4/16/2013 | 20 | 1 | 37.2 | 45.2 | 41.5 | 42.9 | 41.3 | 39.7 |
| 4/16/2013 | 4/16/2013 | 21 | 1 | 38.5 | 44.9 | 41.7 | 42.7 | 41.6 | 40.5 |
| 4/16/2013 | 4/16/2013 | 22 | 1 | 34.4 | 41.8 | 37.8 | 39.4 | 37.4 | 36.1 |
| 4/16/2013 | 4/16/2013 | 23 | 1 | 33.7 | 47.3 | 38.2 | 40.2 | 37.4 | 35.7 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 68. PAPA206 (Central Gathering Facility, with generator, 555 m) dBA and one-third octave band metrics, April 16-17, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/16/13 | 4/17/13 | dBA | 16 | 31.1 | 53.5 | 39.1 | 39.5 | 37.4 | 35.9 |
| 4/16/13 | 4/17/13 | 12.5 | 16 | 33.9 | 69.7 | 59.2 | 60.5 | 59.5 | 58.4 |
| 4/16/13 | 4/17/13 | 16 | 16 | 35.6 | 69.4 | 52.2 | 54.4 | 49.1 | 45.5 |
| 4/16/13 | 4/17/13 | 20 | 16 | 44.2 | 76.0 | 62.8 | 67.1 | 58.6 | 53.5 |
| 4/16/13 | 4/17/13 | 25 | 16 | 42.3 | 64.7 | 57.1 | 58.5 | 56.8 | 54.2 |
| 4/16/13 | 4/17/13 | 31.5 | 16 | 42.8 | 74.4 | 63.3 | 66.3 | 62.5 | 57.9 |
| 4/16/13 | 4/17/13 | 40 | 16 | 40.9 | 63.2 | 52.0 | 53.5 | 51.6 | 49.5 |
| 4/16/13 | 4/17/13 | 50 | 16 | 38.1 | 66.0 | 53.1 | 55.8 | 53.4 | 50.8 |
| 4/16/13 | 4/17/13 | 63 | 16 | 42.1 | 67.1 | 54.0 | 55.1 | 53.0 | 51.2 |
| 4/16/13 | 4/17/13 | 80 | 16 | 43.2 | 60.9 | 51.8 | 52.4 | 50.6 | 49.2 |
| 4/16/13 | 4/17/13 | 100 | 16 | 36.2 | 60.5 | 46.8 | 47.6 | 45.3 | 43.3 |
| 4/16/13 | 4/17/13 | 125 | 16 | 34.9 | 58.5 | 45.8 | 47.4 | 43.7 | 41.6 |
| 4/16/13 | 4/17/13 | 160 | 16 | 30.0 | 57.3 | 42.0 | 43.6 | 39.5 | 37.3 |
| 4/16/13 | 4/17/13 | 200 | 16 | 29.6 | 59.3 | 39.0 | 41.4 | 37.2 | 34.0 |
| 4/16/13 | 4/17/13 | 250 | 16 | 24.6 | 52.7 | 35.8 | 38.0 | 34.6 | 31.3 |
| 4/16/13 | 4/17/13 | 315 | 16 | 23.3 | 51.7 | 35.1 | 36.5 | 33.4 | 30.7 |
| 4/16/13 | 4/17/13 | 400 | 16 | 18.8 | 51.4 | 34.3 | 34.9 | 30.8 | 27.8 |
| 4/16/13 | 4/17/13 | 500 | 16 | 9.9 | 45.6 | 28.1 | 28.0 | 25.0 | 22.0 |
| 4/16/13 | 4/17/13 | 630 | 16 | 3.3 | 36.5 | 22.1 | 23.7 | 20.6 | 17.6 |
| 4/16/13 | 4/17/13 | 800 | 16 | 1.9 | 33.9 | 20.3 | 22.3 | 19.1 | 15.9 |
| 4/16/13 | 4/17/13 | 1000 | 16 | 3.7 | 42.1 | 24.3 | 23.1 | 19.7 | 16.8 |
| 4/16/13 | 4/17/13 | 1250 | 16 | 3.7 | 41.3 | 23.2 | 20.2 | 17.2 | 14.7 |
| 4/16/13 | 4/17/13 | 1600 | 16 | 2.9 | 36.9 | 20.1 | 18.2 | 14.6 | 12.2 |
| 4/16/13 | 4/17/13 | 2000 | 16 | 2.9 | 35.8 | 17.7 | 15.7 | 11.4 | 8.6 |
| 4/16/13 | 4/17/13 | 2500 | 16 | 2.7 | 38.4 | 12.8 | 11.2 | 7.2 | 5.5 |
| 4/16/13 | 4/17/13 | 3150 | 16 | 2.8 | 48.9 | 15.0 | 10.1 | 4.6 | 4.0 |
| 4/16/13 | 4/17/13 | 4000 | 16 | 3.4 | 42.9 | 8.2 | 6.9 | 4.3 | 4.0 |
| 4/16/13 | 4/17/13 | 5000 | 16 | 3.2 | 33.5 | 5.7 | 5.2 | 4.7 | 4.5 |
| 4/16/13 | 4/17/13 | 6300 | 16 | 3.3 | 33.6 | 5.5 | 5.3 | 5.0 | 4.8 |
| 4/16/13 | 4/17/13 | 8000 | 16 | 3.3 | 38.1 | 6.3 | 5.3 | 5.0 | 4.8 |
| 4/16/13 | 4/17/13 | 10000 | 16 | 2.6 | 19.0 | 4.7 | 4.9 | 4.7 | 4.5 |
| 4/16/13 | 4/17/13 | 12500 | 16 | 2.7 | 17.7 | 4.1 | 4.3 | 4.1 | 3.9 |
| 4/16/13 | 4/17/13 | 16000 | 16 | 2.5 | 15.6 | 3.4 | 3.6 | 3.3 | 3.1 |
| 4/16/13 | 4/17/13 | 20000 | 16 | 1.5 | 11.3 | 2.2 | 2.3 | 2.1 | 1.8 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 69. PAPA207 (Drill Rig, pad 9-24, 2300 m) hourly dBA metrics, April 5-7, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/5/2013 | 4/7/2013 | 0 | 2 | 24.9 | 55.2 | 41.1 | 39.9 | 36.2 | 33.1 |
| 4/5/2013 | 4/7/2013 | 1 | 2 | 25.0 | 51.4 | 34.3 | 34.7 | 31.8 | 29.6 |
| 4/5/2013 | 4/7/2013 | 2 | 2 | 24.8 | 54.9 | 33.6 | 34.1 | 30.8 | 28.9 |
| 4/5/2013 | 4/7/2013 | 3 | 2 | 26.0 | 56.4 | 34.1 | 34.8 | 30.9 | 27.9 |
| 4/5/2013 | 4/7/2013 | 4 | 2 | 26.6 | 58.0 | 35.2 | 34.5 | 31.9 | 30.2 |
| 4/5/2013 | 4/7/2013 | 5 | 2 | 28.6 | 57.7 | 35.0 | 35.6 | 33.2 | 31.4 |
| 4/5/2013 | 4/7/2013 | 6 | 2 | 28.3 | 58.9 | 37.8 | 38.8 | 35.5 | 32.1 |
| 4/5/2013 | 4/7/2013 | 7 | 2 | 24.6 | 61.1 | 33.5 | 35.4 | 31.5 | 28.3 |
| 4/5/2013 | 4/7/2013 | 8 | 2 | 24.7 | 48.1 | 33.3 | 35.6 | 31.7 | 27.7 |
| 4/5/2013 | 4/7/2013 | 9 | 2 | 19.9 | 54.8 | 31.2 | 32.7 | 27.7 | 25.2 |
| 4/5/2013 | 4/7/2013 | 10 | 2 | 20.5 | 60.9 | 31.6 | 30.9 | 26.8 | 24.7 |
| 4/5/2013 | 4/7/2013 | 11 | 2 | 21.0 | 50.2 | 28.0 | 29.4 | 25.8 | 23.3 |
| 4/5/2013 | 4/7/2013 | 12 | 2 | 20.8 | 46.6 | 28.3 | 30.4 | 25.9 | 23.3 |
| 4/5/2013 | 4/7/2013 | 13 | 2.0 | 21.1 | 47.7 | 30.3 | 32.2 | 27.1 | 24.3 |
| 4/5/2013 | 4/7/2013 | 14 | 2.0 | 20.3 | 52.7 | 33.2 | 34.8 | 27.9 | 24.6 |
| 4/5/2013 | 4/7/2013 | 15 | 2.0 | 22.1 | 51.5 | 32.1 | 33.9 | 27.2 | 24.7 |
| 4/5/2013 | 4/7/2013 | 16 | 1.0 | 20.6 | 47.5 | 29.8 | 33.2 | 27.2 | 23.3 |
| 4/5/2013 | 4/7/2013 | 17 | 2.0 | 21.3 | 68.7 | 40.0 | 34.6 | 29.4 | 26.2 |
| 4/5/2013 | 4/7/2013 | 18 | 2.0 | 22.3 | 55.3 | 34.3 | 33.7 | 29.9 | 27.1 |
| 4/5/2013 | 4/7/2013 | 19 | 2.0 | 22.2 | 51.3 | 32.9 | 35.1 | 30.7 | 26.2 |
| 4/5/2013 | 4/7/2013 | 20 | 2.0 | 26.0 | 54.6 | 34.4 | 36.3 | 32.4 | 29.9 |
| 4/5/2013 | 4/7/2013 | 21 | 2.0 | 21.8 | 49.6 | 33.2 | 34.1 | 30.3 | 27.0 |
| 4/5/2013 | 4/7/2013 | 22 | 2.0 | 21.5 | 49.6 | 32.6 | 33.1 | 30.4 | 27.7 |
| 4/5/2013 | 4/7/2013 | 23 | 2.0 | 26.0 | 55.9 | 37.5 | 39.3 | 33.1 | 30.4 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 70. PAPA207 (Drill Rig, pad 9-24, 2300 m) dBA and one-third octave band metrics, April 5-7, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/5/13 | 4/7/13 | dBA | 47 | 19.9 | 68.7 | 34.9 | 34.8 | 30.4 | 27.2 |
| 4/5/13 | 4/7/13 | 12.5 | 47 | 25.1 | 78.3 | 50.9 | 49.4 | 44.0 | 38.5 |
| 4/5/13 | 4/7/13 | 16 | 47 | 29.3 | 74.2 | 50.7 | 49.5 | 45.8 | 41.9 |
| 4/5/13 | 4/7/13 | 20 | 47 | 34.5 | 72.2 | 54.7 | 55.0 | 51.1 | 47.4 |
| 4/5/13 | 4/7/13 | 25 | 47 | 32.3 | 68.5 | 52.4 | 53.2 | 48.7 | 44.3 |
| 4/5/13 | 4/7/13 | 31.5 | 47 | 34.8 | 69.3 | 57.1 | 60.2 | 54.6 | 49.8 |
| 4/5/13 | 4/7/13 | 40 | 47 | 30.2 | 64.1 | 46.3 | 48.1 | 45.4 | 42.8 |
| 4/5/13 | 4/7/13 | 50 | 47 | 30.8 | 63.0 | 47.1 | 49.2 | 46.0 | 42.5 |
| 4/5/13 | 4/7/13 | 63 | 47 | 31.4 | 71.5 | 45.3 | 46.4 | 43.3 | 40.2 |
| 4/5/13 | 4/7/13 | 80 | 47 | 25.4 | 69.9 | 42.8 | 44.2 | 39.2 | 36.1 |
| 4/5/13 | 4/7/13 | 100 | 47 | 22.8 | 71.7 | 44.6 | 42.0 | 37.4 | 34.1 |
| 4/5/13 | 4/7/13 | 125 | 47 | 19.8 | 63.9 | 40.2 | 39.8 | 35.8 | 32.2 |
| 4/5/13 | 4/7/13 | 160 | 47 | 15.9 | 66.2 | 37.8 | 37.1 | 32.5 | 29.6 |
| 4/5/13 | 4/7/13 | 200 | 47 | 14.7 | 60.5 | 36.5 | 35.4 | 31.1 | 27.5 |
| 4/5/13 | 4/7/13 | 250 | 47 | 11.4 | 61.1 | 33.1 | 32.8 | 28.5 | 25.1 |
| 4/5/13 | 4/7/13 | 315 | 47 | 9.1 | 59.0 | 30.2 | 29.9 | 25.4 | 21.8 |
| 4/5/13 | 4/7/13 | 400 | 47 | 7.1 | 60.1 | 28.2 | 28.8 | 23.1 | 18.3 |
| 4/5/13 | 4/7/13 | 500 | 47 | 2.3 | 65.3 | 25.3 | 22.9 | 17.3 | 12.5 |
| 4/5/13 | 4/7/13 | 630 | 47 | 0.6 | 63.5 | 23.5 | 21.2 | 15.0 | 9.9 |
| 4/5/13 | 4/7/13 | 800 | 47 | 0.1 | 56.9 | 21.1 | 20.4 | 14.1 | 8.7 |
| 4/5/13 | 4/7/13 | 1000 | 47 | 0.0 | 55.1 | 19.3 | 19.2 | 12.0 | 7.9 |
| 4/5/13 | 4/7/13 | 1250 | 47 | 0.0 | 57.6 | 17.2 | 15.6 | 9.7 | 6.0 |
| 4/5/13 | 4/7/13 | 1600 | 47 | 0.2 | 56.6 | 14.5 | 10.9 | 5.4 | 2.9 |
| 4/5/13 | 4/7/13 | 2000 | 47 | 0.8 | 54.1 | 12.9 | 7.0 | 3.1 | 2.1 |
| 4/5/13 | 4/7/13 | 2500 | 47 | 1.4 | 52.4 | 12.5 | 3.4 | 2.7 | 2.3 |
| 4/5/13 | 4/7/13 | 3150 | 47 | 2.2 | 59.1 | 13.5 | 3.8 | 3.2 | 3.0 |
| 4/5/13 | 4/7/13 | 4000 | 47 | 3.0 | 50.4 | 10.8 | 4.6 | 3.9 | 3.6 |
| 4/5/13 | 4/7/13 | 5000 | 47 | 2.8 | 57.8 | 14.6 | 5.2 | 4.4 | 4.2 |
| 4/5/13 | 4/7/13 | 6300 | 47 | 1.4 | 56.5 | 12.4 | 4.8 | 4.6 | 4.4 |
| 4/5/13 | 4/7/13 | 8000 | 47 | 0.6 | 51.0 | 9.4 | 4.6 | 4.5 | 4.4 |
| 4/5/13 | 4/7/13 | 10000 | 47 | -0.1 | 51.0 | 8.2 | 4.2 | 4.1 | 4.0 |
| 4/5/13 | 4/7/13 | 12500 | 47 | -0.4 | 50.7 | 7.1 | 3.5 | 3.4 | 3.3 |
| 4/5/13 | 4/7/13 | 16000 | 47 | 0.0 | 51.2 | 6.0 | 2.5 | 2.3 | 2.2 |
| 4/5/13 | 4/7/13 | 20000 | 47 | 0.2 | 55.9 | 6.3 | 0.8 | 0.7 | 0.6 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 71. PAPA208 (Drill Rig, pad 9-24, 300 m) hourly dBA metrics, April 5-7, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/5/2013 | 4/7/2013 | 0 | 2 | 47.5 | 61.6 | 56.3 | 57.4 | 55.6 | 53.0 |
| 4/5/2013 | 4/7/2013 | 1 | 2 | 45.6 | 60.8 | 52.7 | 55.2 | 51.1 | 48.4 |
| 4/5/2013 | 4/7/2013 | 2 | 2 | 44.6 | 61.2 | 52.0 | 54.3 | 51.2 | 48.6 |
| 4/5/2013 | 4/7/2013 | 3 | 2 | 43.8 | 63.8 | 51.1 | 52.1 | 50.3 | 48.0 |
| 4/5/2013 | 4/7/2013 | 4 | 2 | 47.6 | 62.4 | 51.8 | 53.3 | 51.5 | 50.0 |
| 4/5/2013 | 4/7/2013 | 5 | 2 | 47.2 | 61.8 | 53.0 | 54.6 | 52.7 | 50.9 |
| 4/5/2013 | 4/7/2013 | 6 | 2 | 50.3 | 84.5 | 53.9 | 54.2 | 53.0 | 51.8 |
| 4/5/2013 | 4/7/2013 | 7 | 2 | 47.5 | 59.5 | 52.1 | 53.5 | 51.7 | 50.5 |
| 4/5/2013 | 4/7/2013 | 8 | 2 | 47.3 | 57.4 | 51.9 | 53.2 | 51.6 | 50.1 |
| 4/5/2013 | 4/7/2013 | 9 | 2 | 49.7 | 59.7 | 52.3 | 53.3 | 52.1 | 51.2 |
| 4/5/2013 | 4/7/2013 | 10 | 2 | 43.4 | 58.9 | 51.4 | 52.8 | 51.0 | 48.6 |
| 4/5/2013 | 4/7/2013 | 11 | 2 | 43.1 | 60.9 | 51.1 | 52.0 | 50.4 | 48.1 |
| 4/5/2013 | 4/7/2013 | 12 | 2 | 43.9 | 58.2 | 51.5 | 53.1 | 51.3 | 48.3 |
| 4/5/2013 | 4/7/2013 | 13 | 2 | 47.2 | 60.2 | 53.1 | 54.8 | 52.8 | 50.9 |
| 4/6/2013 | 4/6/2013 | 14 | 1 | 46.6 | 64.2 | 53.3 | 54.9 | 53.1 | 49.9 |
| 4/6/2013 | 4/6/2013 | 15 | 1 | 50.1 | 66.5 | 53.3 | 54.1 | 53.0 | 52.0 |
| 4/6/2013 | 4/6/2013 | 16 | 1 | 46.4 | 57.5 | 51.3 | 54.1 | 50.0 | 48.2 |
| 4/6/2013 | 4/6/2013 | 17 | 1 | 45.4 | 64.7 | 51.2 | 53.0 | 51.0 | 48.3 |
| 4/5/2013 | 4/7/2013 | 18 | 2 | 48.9 | 58.7 | 52.5 | 53.6 | 52.3 | 51.2 |
| 4/5/2013 | 4/7/2013 | 19 | 2 | 48.9 | 61.9 | 53.7 | 55.0 | 53.3 | 52.0 |
| 4/5/2013 | 4/7/2013 | 20 | 2 | 51.6 | 64.8 | 55.6 | 56.7 | 55.3 | 54.1 |
| 4/5/2013 | 4/7/2013 | 21 | 2 | 51.8 | 63.5 | 55.2 | 56.2 | 55.0 | 53.7 |
| 4/5/2013 | 4/7/2013 | 22 | 2 | 52.5 | 63.5 | 57.0 | 57.8 | 56.4 | 55.2 |
| 4/5/2013 | 4/7/2013 | 23 | 2 | 51.5 | 65.0 | 57.7 | 59.8 | 57.3 | 54.0 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 72. PAPA208 (Drill Rig, pad 9-24, 300 m) dBA and one-third octave band metrics, April 5-7, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/5/13 | 4/7/13 | dBA | 44 | 43.1 | 84.5 | 53.7 | 54.2 | 52.5 | 51.0 |
| 4/5/13 | 4/7/13 | 12.5 | 44 | 29.9 | 76.7 | 51.6 | 51.4 | 47.3 | 43.2 |
| 4/5/13 | 4/7/13 | 16 | 44 | 35.8 | 73.2 | 52.3 | 53.8 | 49.8 | 46.0 |
| 4/5/13 | 4/7/13 | 20 | 44 | 39.6 | 74.9 | 56.5 | 58.1 | 54.7 | 51.4 |
| 4/5/13 | 4/7/13 | 25 | 44 | 41.0 | 73.7 | 54.4 | 55.5 | 52.2 | 49.6 |
| 4/5/13 | 4/7/13 | 31.5 | 44 | 43.8 | 76.5 | 67.4 | 70.4 | 66.3 | 61.0 |
| 4/5/13 | 4/7/13 | 40 | 44 | 46.5 | 74.7 | 59.1 | 61.3 | 58.6 | 55.5 |
| 4/5/13 | 4/7/13 | 50 | 44 | 54.4 | 78.0 | 66.2 | 67.8 | 65.9 | 64.0 |
| 4/5/13 | 4/7/13 | 63 | 44 | 53.0 | 78.7 | 65.2 | 66.8 | 64.8 | 62.4 |
| 4/5/13 | 4/7/13 | 80 | 44 | 50.6 | 77.4 | 65.8 | 67.2 | 65.1 | 62.9 |
| 4/5/13 | 4/7/13 | 100 | 44 | 35.9 | 77.8 | 66.4 | 67.2 | 65.0 | 62.9 |
| 4/5/13 | 4/7/13 | 125 | 44 | 44.1 | 77.0 | 62.2 | 62.8 | 60.6 | 58.1 |
| 4/5/13 | 4/7/13 | 160 | 44 | 41.1 | 79.1 | 58.5 | 58.2 | 56.2 | 54.2 |
| 4/5/13 | 4/7/13 | 200 | 44 | 38.1 | 71.7 | 55.1 | 54.2 | 52.0 | 50.0 |
| 4/5/13 | 4/7/13 | 250 | 44 | 33.5 | 62.3 | 46.6 | 47.8 | 45.5 | 43.1 |
| 4/5/13 | 4/7/13 | 315 | 44 | 24.5 | 59.8 | 43.6 | 45.9 | 42.3 | 39.4 |
| 4/5/13 | 4/7/13 | 400 | 44 | 21.6 | 59.3 | 44.3 | 47.5 | 43.7 | 39.7 |
| 4/5/13 | 4/7/13 | 500 | 44 | 17.7 | 55.1 | 36.4 | 37.3 | 33.2 | 30.1 |
| 4/5/13 | 4/7/13 | 630 | 44 | 15.7 | 55.6 | 35.5 | 37.2 | 32.0 | 28.2 |
| 4/5/13 | 4/7/13 | 800 | 44 | 13.4 | 57.5 | 34.4 | 36.8 | 30.5 | 25.7 |
| 4/5/13 | 4/7/13 | 1000 | 44 | 12.0 | 56.4 | 34.5 | 36.3 | 30.8 | 25.2 |
| 4/5/13 | 4/7/13 | 1250 | 44 | 11.3 | 56.6 | 35.2 | 36.2 | 30.9 | 24.9 |
| 4/5/13 | 4/7/13 | 1600 | 44 | 11.2 | 62.6 | 35.9 | 37.9 | 32.1 | 24.7 |
| 4/5/13 | 4/7/13 | 2000 | 44 | 10.8 | 57.3 | 36.4 | 38.3 | 32.6 | 25.4 |
| 4/5/13 | 4/7/13 | 2500 | 44 | 8.0 | 52.9 | 33.4 | 35.7 | 29.6 | 21.9 |
| 4/5/13 | 4/7/13 | 3150 | 44 | 5.5 | 53.1 | 28.7 | 30.0 | 24.9 | 16.9 |
| 4/5/13 | 4/7/13 | 4000 | 44 | 4.6 | 55.3 | 23.8 | 25.2 | 18.9 | 11.8 |
| 4/5/13 | 4/7/13 | 5000 | 44 | 4.3 | 53.1 | 17.7 | 17.1 | 11.7 | 7.4 |
| 4/5/13 | 4/7/13 | 6300 | 44 | 4.4 | 47.9 | 11.0 | 10.3 | 6.6 | 5.5 |
| 4/5/13 | 4/7/13 | 8000 | 44 | 4.2 | 35.3 | 7.1 | 5.6 | 5.2 | 5.0 |
| 4/5/13 | 4/7/13 | 10000 | 44 | 3.8 | 32.2 | 6.4 | 5.0 | 4.8 | 4.7 |
| 4/5/13 | 4/7/13 | 12500 | 44 | 3.4 | 31.8 | 6.0 | 4.7 | 4.6 | 4.5 |
| 4/5/13 | 4/7/13 | 16000 | 44 | 3.1 | 32.3 | 5.2 | 3.9 | 3.8 | 3.7 |
| 4/5/13 | 4/7/13 | 20000 | 44 | 1.6 | 30.8 | 3.4 | 2.5 | 2.3 | 2.2 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 73. PAPA209 (Highway 191, 100 m) hourly dBA metrics, April 17-18, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 04/18/13 | 04/18/13 | 0 | 1 | 15.5 | 48.8 | 23.2 | 19.0 | 17.0 | 16.1 |
| 04/18/13 | 04/18/13 | 1 | 1 | 15.3 | 47.2 | 23.1 | 18.4 | 16.8 | 15.8 |
| 04/18/13 | 04/18/13 | 2 | 1 | 14.8 | 46.1 | 21.1 | 16.7 | 15.4 | 15.1 |
| 04/18/13 | 04/18/13 | 3 | 1 | 15.1 | 45.0 | 19.6 | 17.5 | 16.3 | 15.7 |
| 04/18/13 | 04/18/13 | 4 | 1 | 15.8 | 53.0 | 32.9 | 26.0 | 18.0 | 16.6 |
| 04/18/13 | 04/18/13 | 5 | 1 | 16.8 | 58.1 | 41.5 | 45.7 | 26.4 | 18.0 |
| 04/18/13 | 04/18/13 | 6 | 1 | 16.7 | 64.0 | 48.0 | 52.7 | 40.7 | 24.2 |
| 04/18/13 | 04/18/13 | 7 | 1 | 17.3 | 63.8 | 45.1 | 48.9 | 34.1 | 21.4 |
| 04/18/13 | 04/18/13 | 8 | 1 | 18.6 | 55.5 | 33.7 | 34.9 | 24.9 | 20.6 |
| 04/18/13 | 04/18/13 | 9 | 1 | 18.8 | 52.2 | 32.5 | 34.7 | 24.5 | 21.0 |
| 04/18/13 | 04/18/13 | 10 | 1 | 19.1 | 60.2 | 35.6 | 34.8 | 25.8 | 22.2 |
| 04/18/13 | 04/18/13 | 11 | 1 | 20.1 | 59.5 | 37.5 | 37.8 | 27.2 | 22.6 |
| 04/18/13 | 04/18/13 | 12 | 1 | 18.5 | 59.2 | 39.7 | 42.1 | 28.3 | 21.6 |
| 04/17/13 | 04/17/13 | 13 | 0 | NA | NA | NA | NA | NA | NA |
| 04/17/13 | 04/17/13 | 14 | 1 | 18.2 | 60.8 | 43.5 | 47.3 | 31.9 | 23.0 |
| 04/17/13 | 04/17/13 | 15 | 1 | 20.0 | 64.2 | 45.2 | 46.9 | 32.4 | 23.9 |
| 04/17/13 | 04/17/13 | 16 | 1 | 23.4 | 64.0 | 43.5 | 46.9 | 34.1 | 26.9 |
| 04/17/13 | 04/17/13 | 17 | 1 | 23.4 | 65.1 | 45.1 | 48.7 | 35.7 | 27.8 |
| 04/17/13 | 04/17/13 | 18 | 1 | 23.8 | 59.8 | 42.5 | 46.0 | 35.0 | 28.3 |
| 04/17/13 | 04/17/13 | 19 | 1 | 20.0 | 58.0 | 38.0 | 37.7 | 26.3 | 22.7 |
| 04/17/13 | 04/17/13 | 20 | 1 | 16.1 | 54.7 | 31.4 | 31.4 | 20.5 | 17.5 |
| 04/17/13 | 04/17/13 | 21 | 1 | 15.8 | 45.3 | 26.0 | 28.0 | 18.6 | 16.7 |
| 04/17/13 | 04/17/13 | 22 | 1 | 14.9 | 47.1 | 24.9 | 24.3 | 16.3 | 15.4 |
| 04/17/13 | 04/17/13 | 23 | 1 | 15.5 | 41.3 | 22.8 | 21.3 | 18.0 | 16.5 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 74. PAPA209 (Highway 191, 100 m) dBA and one-third octave band metrics, April 17-18, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/17/13 | 4/18/13 | dBA | 23 | 14.8 | 65.1 | 40.7 | 34.9 | 25.8 | 21.0 |
| 4/17/13 | 4/18/13 | 12.5 | 23 | 24.7 | 77.2 | 51.8 | 47.3 | 42.1 | 37.9 |
| 4/17/13 | 4/18/13 | 16 | 23 | 27.6 | 71.7 | 48.6 | 47.1 | 42.8 | 39.1 |
| 4/17/13 | 4/18/13 | 20 | 23 | 31.3 | 71.1 | 49.6 | 51.6 | 47.2 | 43.5 |
| 4/17/13 | 4/18/13 | 25 | 23 | 21.6 | 71.7 | 45.1 | 48.2 | 41.2 | 35.4 |
| 4/17/13 | 4/18/13 | 31.5 | 23 | 20.8 | 75.3 | 47.0 | 48.9 | 41.8 | 35.8 |
| 4/17/13 | 4/18/13 | 40 | 23 | 18.6 | 73.2 | 44.5 | 48.1 | 38.7 | 31.7 |
| 4/17/13 | 4/18/13 | 50 | 23 | 16.5 | 70.7 | 44.9 | 48.4 | 35.9 | 30.2 |
| 4/17/13 | 4/18/13 | 63 | 23 | 16.3 | 82.1 | 50.0 | 47.9 | 35.2 | 30.1 |
| 4/17/13 | 4/18/13 | 80 | 23 | 12.4 | 83.4 | 49.6 | 43.8 | 33.7 | 29.0 |
| 4/17/13 | 4/18/13 | 100 | 23 | 10.7 | 78.1 | 48.1 | 39.7 | 31.0 | 27.3 |
| 4/17/13 | 4/18/13 | 125 | 23 | 9.3 | 80.5 | 46.7 | 35.0 | 29.7 | 25.5 |
| 4/17/13 | 4/18/13 | 160 | 23 | 6.7 | 78.2 | 42.8 | 31.8 | 26.1 | 22.6 |
| 4/17/13 | 4/18/13 | 200 | 23 | 4.9 | 73.5 | 38.6 | 30.7 | 23.5 | 19.9 |
| 4/17/13 | 4/18/13 | 250 | 23 | 1.8 | 66.4 | 33.1 | 26.6 | 20.2 | 16.2 |
| 4/17/13 | 4/18/13 | 315 | 23 | 0.1 | 56.8 | 27.9 | 23.0 | 15.9 | 12.2 |
| 4/17/13 | 4/18/13 | 400 | 23 | -2.9 | 54.2 | 26.4 | 20.6 | 13.5 | 8.4 |
| 4/17/13 | 4/18/13 | 500 | 23 | -3.3 | 53.6 | 27.8 | 21.0 | 10.5 | 4.5 |
| 4/17/13 | 4/18/13 | 630 | 23 | -3.2 | 61.0 | 30.4 | 23.3 | 11.7 | 3.3 |
| 4/17/13 | 4/18/13 | 800 | 23 | -2.5 | 58.3 | 32.2 | 24.1 | 12.2 | 2.5 |
| 4/17/13 | 4/18/13 | 1000 | 23 | -2.1 | 59.4 | 32.0 | 23.6 | 11.9 | 1.4 |
| 4/17/13 | 4/18/13 | 1250 | 23 | -1.3 | 59.1 | 30.8 | 22.9 | 9.3 | 1.3 |
| 4/17/13 | 4/18/13 | 1600 | 23 | -0.2 | 53.7 | 28.5 | 20.6 | 6.7 | 1.3 |
| 4/17/13 | 4/18/13 | 2000 | 23 | 0.8 | 51.4 | 25.1 | 16.2 | 4.1 | 1.7 |
| 4/17/13 | 4/18/13 | 2500 | 23 | 1.5 | 46.8 | 21.8 | 11.9 | 3.5 | 2.4 |
| 4/17/13 | 4/18/13 | 3150 | 23 | 2.5 | 47.1 | 18.4 | 8.6 | 4.1 | 3.2 |
| 4/17/13 | 4/18/13 | 4000 | 23 | 3.3 | 45.1 | 14.1 | 6.9 | 4.2 | 3.9 |
| 4/17/13 | 4/18/13 | 5000 | 23 | 3.9 | 44.3 | 10.5 | 7.0 | 4.7 | 4.5 |
| 4/17/13 | 4/18/13 | 6300 | 23 | 4.2 | 41.2 | 8.2 | 6.4 | 5.0 | 4.7 |
| 4/17/13 | 4/18/13 | 8000 | 23 | 3.8 | 38.0 | 6.7 | 5.9 | 4.9 | 4.8 |
| 4/17/13 | 4/18/13 | 10000 | 23 | 3.6 | 36.1 | 5.8 | 5.1 | 4.6 | 4.5 |
| 4/17/13 | 4/18/13 | 12500 | 23 | 3.5 | 35.5 | 5.1 | 4.7 | 4.1 | 3.9 |
| 4/17/13 | 4/18/13 | 16000 | 23 | 2.6 | 32.4 | 4.4 | 3.8 | 3.3 | 3.1 |
| 4/17/13 | 4/18/13 | 20000 | 23 | 1.2 | 32.9 | 3.1 | 2.4 | 1.9 | 1.8 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 75. PAPA210 (Highway 191, 200 m) hourly dBA metrics, April 17-18, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 04/18/13 | 04/18/13 | 0 | 1 | 15.9 | 40.4 | 20.3 | 19.4 | 17.3 | 16.4 |
| 04/18/13 | 04/18/13 | 1 | 1 | 15.5 | 48.0 | 23.8 | 18.7 | 17.1 | 16.1 |
| 04/18/13 | 04/18/13 | 2 | 1 | 15.2 | 37.4 | 18.1 | 17.1 | 15.8 | 15.5 |
| 04/18/13 | 04/18/13 | 3 | 1 | 15.5 | 38.0 | 19.1 | 18.0 | 16.6 | 16.0 |
| 04/18/13 | 04/18/13 | 4 | 1 | 16.2 | 46.9 | 27.8 | 26.3 | 18.4 | 17.0 |
| 04/18/13 | 04/18/13 | 5 | 1 | 16.9 | 51.9 | 37.0 | 41.6 | 25.9 | 18.3 |
| 04/18/13 | 04/18/13 | 6 | 1 | 17.0 | 55.7 | 43.2 | 47.6 | 39.0 | 23.9 |
| 04/18/13 | 04/18/13 | 7 | 1 | 17.5 | 55.9 | 41.8 | 46.5 | 33.6 | 21.9 |
| 04/18/13 | 04/18/13 | 8 | 1 | 18.9 | 45.0 | 29.0 | 32.6 | 24.1 | 20.5 |
| 04/18/13 | 04/18/13 | 9 | 1 | 19.3 | 45.8 | 28.3 | 29.2 | 24.0 | 21.0 |
| 04/18/13 | 04/18/13 | 10 | 1 | 20.0 | 49.2 | 29.3 | 30.7 | 24.9 | 22.0 |
| 04/18/13 | 04/18/13 | 11 | 1 | 20.8 | 49.4 | 30.7 | 32.6 | 26.6 | 22.9 |
| 04/18/13 | 04/18/13 | 12 | 1 | 18.8 | 51.5 | 34.2 | 37.2 | 27.3 | 21.3 |
| 04/17/13 | 04/17/13 | 13 | 0 | NA | NA | NA | NA | NA | NA |
| 04/17/13 | 04/17/13 | 14 | 1 | 18.3 | 53.6 | 38.8 | 42.9 | 32.0 | 22.9 |
| 04/17/13 | 04/17/13 | 15 | 1 | 19.8 | 56.9 | 39.3 | 42.0 | 31.1 | 23.6 |
| 04/17/13 | 04/17/13 | 16 | 1 | 23.2 | 56.1 | 37.2 | 40.6 | 32.0 | 26.7 |
| 04/17/13 | 04/17/13 | 17 | 1 | 24.2 | 55.9 | 39.8 | 43.7 | 34.8 | 27.7 |
| 04/17/13 | 04/17/13 | 18 | 1 | 23.9 | 56.0 | 39.6 | 43.2 | 35.5 | 29.0 |
| 04/17/13 | 04/17/13 | 19 | 1 | 20.7 | 57.5 | 35.9 | 34.7 | 26.5 | 23.2 |
| 04/17/13 | 04/17/13 | 20 | 1 | 16.4 | 51.1 | 29.4 | 29.8 | 20.7 | 17.8 |
| 04/17/13 | 04/17/13 | 21 | 1 | 16.1 | 44.0 | 24.5 | 27.7 | 19.0 | 17.1 |
| 04/17/13 | 04/17/13 | 22 | 1 | 15.4 | 42.7 | 22.0 | 23.8 | 16.7 | 15.8 |
| 04/17/13 | 04/17/13 | 23 | 1 | 15.9 | 41.3 | 22.3 | 21.8 | 18.4 | 16.9 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 76. PAPA210 (Highway 191, 200 m) dBA and one-third octave band metrics, April 17-18, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/17/13 | 4/18/13 | dBA | 23 | 15.2 | 57.5 | 36.1 | 32.6 | 24.9 | 21.0 |
| 4/17/13 | 4/18/13 | 12.5 | 23 | 27.2 | 79.5 | 54.9 | 46.8 | 42.1 | 37.9 |
| 4/17/13 | 4/18/13 | 16 | 23 | 27.6 | 76.9 | 49.8 | 46.4 | 42.7 | 39.2 |
| 4/17/13 | 4/18/13 | 20 | 23 | 31.2 | 72.2 | 49.4 | 50.8 | 46.6 | 43.4 |
| 4/17/13 | 4/18/13 | 25 | 23 | 20.8 | 68.6 | 44.5 | 46.4 | 40.7 | 35.2 |
| 4/17/13 | 4/18/13 | 31.5 | 23 | 20.5 | 70.1 | 45.7 | 47.4 | 41.3 | 35.7 |
| 4/17/13 | 4/18/13 | 40 | 23 | 18.0 | 67.8 | 42.5 | 45.3 | 37.4 | 31.7 |
| 4/17/13 | 4/18/13 | 50 | 23 | 16.7 | 63.9 | 41.9 | 43.1 | 34.9 | 30.1 |
| 4/17/13 | 4/18/13 | 63 | 23 | 16.2 | 71.4 | 43.8 | 40.3 | 33.9 | 30.2 |
| 4/17/13 | 4/18/13 | 80 | 23 | 13.4 | 76.3 | 44.9 | 38.5 | 32.7 | 28.7 |
| 4/17/13 | 4/18/13 | 100 | 23 | 12.5 | 74.1 | 43.9 | 34.8 | 30.4 | 27.4 |
| 4/17/13 | 4/18/13 | 125 | 23 | 10.0 | 73.0 | 41.4 | 33.5 | 29.1 | 24.8 |
| 4/17/13 | 4/18/13 | 160 | 23 | 6.5 | 68.9 | 36.1 | 31.1 | 25.9 | 21.7 |
| 4/17/13 | 4/18/13 | 200 | 23 | 5.3 | 67.1 | 32.1 | 29.2 | 23.0 | 19.2 |
| 4/17/13 | 4/18/13 | 250 | 23 | 2.1 | 61.2 | 27.4 | 25.5 | 19.4 | 15.6 |
| 4/17/13 | 4/18/13 | 315 | 23 | -0.3 | 50.3 | 23.9 | 21.7 | 15.3 | 12.0 |
| 4/17/13 | 4/18/13 | 400 | 23 | -2.4 | 50.5 | 23.9 | 17.3 | 12.4 | 8.2 |
| 4/17/13 | 4/18/13 | 500 | 23 | -2.8 | 50.4 | 25.6 | 18.2 | 10.4 | 4.8 |
| 4/17/13 | 4/18/13 | 630 | 23 | -2.6 | 53.6 | 28.0 | 19.9 | 11.2 | 3.6 |
| 4/17/13 | 4/18/13 | 800 | 23 | -2.3 | 54.5 | 28.8 | 20.1 | 11.8 | 2.4 |
| 4/17/13 | 4/18/13 | 1000 | 23 | -1.7 | 51.5 | 27.5 | 20.4 | 10.8 | 1.6 |
| 4/17/13 | 4/18/13 | 1250 | 23 | -1.0 | 53.9 | 25.8 | 19.1 | 8.7 | 1.7 |
| 4/17/13 | 4/18/13 | 1600 | 23 | 0.0 | 48.2 | 23.0 | 16.6 | 5.9 | 1.4 |
| 4/17/13 | 4/18/13 | 2000 | 23 | 1.0 | 42.9 | 19.4 | 12.6 | 3.5 | 1.8 |
| 4/17/13 | 4/18/13 | 2500 | 23 | 1.9 | 44.0 | 16.2 | 9.5 | 3.8 | 2.6 |
| 4/17/13 | 4/18/13 | 3150 | 23 | 2.8 | 43.7 | 12.2 | 7.6 | 4.1 | 3.5 |
| 4/17/13 | 4/18/13 | 4000 | 23 | 3.7 | 41.4 | 9.0 | 7.1 | 4.6 | 4.3 |
| 4/17/13 | 4/18/13 | 5000 | 23 | 4.5 | 37.4 | 7.3 | 6.1 | 5.2 | 5.0 |
| 4/17/13 | 4/18/13 | 6300 | 23 | 4.7 | 41.3 | 7.7 | 6.1 | 5.6 | 5.4 |
| 4/17/13 | 4/18/13 | 8000 | 23 | 4.9 | 35.4 | 6.9 | 6.0 | 5.7 | 5.5 |
| 4/17/13 | 4/18/13 | 10000 | 23 | 4.7 | 33.9 | 6.3 | 5.6 | 5.3 | 5.1 |
| 4/17/13 | 4/18/13 | 12500 | 23 | 3.8 | 33.6 | 5.6 | 4.9 | 4.4 | 4.3 |
| 4/17/13 | 4/18/13 | 16000 | 23 | 2.7 | 31.1 | 4.6 | 3.9 | 3.4 | 3.2 |
| 4/17/13 | 4/18/13 | 20000 | 23 | 1.2 | 34.7 | 3.2 | 2.4 | 1.9 | 1.7 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 77. PAPA211 (Well heads, 3, and injection well, with generator, 100 m) hourly dBA metrics, April 18-21, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/18/2013 | 4/21/2013 | 0 | 3 | 42.2 | 53.3 | 47.2 | 48.5 | 46.3 | 45.0 |
| 4/18/2013 | 4/21/2013 | 1 | 3 | 43.2 | 54.0 | 48.1 | 49.8 | 48.0 | 46.5 |
| 4/18/2013 | 4/21/2013 | 2 | 3 | 43.5 | 56.4 | 48.4 | 49.8 | 47.5 | 45.9 |
| 4/18/2013 | 4/21/2013 | 3 | 3 | 44.1 | 54.7 | 49.3 | 51.6 | 49.3 | 46.8 |
| 4/18/2013 | 4/21/2013 | 4 | 3 | 43.2 | 56.9 | 50.9 | 53.1 | 51.8 | 50.4 |
| 4/18/2013 | 4/21/2013 | 5 | 3 | 45.1 | 56.1 | 50.7 | 53.1 | 50.0 | 47.5 |
| 4/18/2013 | 4/21/2013 | 6 | 3 | 41.3 | 57.2 | 49.8 | 50.7 | 48.6 | 46.3 |
| 4/18/2013 | 4/21/2013 | 7 | 3 | 42.8 | 56.5 | 47.8 | 50.1 | 46.3 | 44.8 |
| 4/18/2013 | 4/21/2013 | 8 | 3 | 40.7 | 59.5 | 45.6 | 46.1 | 45.1 | 44.0 |
| 4/18/2013 | 4/21/2013 | 9 | 3 | 38.8 | 57.2 | 44.7 | 46.0 | 44.4 | 42.7 |
| 4/18/2013 | 4/21/2013 | 10 | 3 | 34.4 | 53.2 | 44.3 | 46.4 | 44.5 | 42.4 |
| 4/18/2013 | 4/21/2013 | 11 | 3 | 34.8 | 49.7 | 43.3 | 45.0 | 43.0 | 40.5 |
| 4/18/2013 | 4/21/2013 | 12 | 3 | 32.1 | 50.4 | 41.7 | 43.8 | 41.4 | 38.1 |
| 4/18/2013 | 4/21/2013 | 13 | 3 | 32.7 | 58.3 | 42.0 | 44.4 | 41.5 | 37.8 |
| 4/18/2013 | 4/21/2013 | 14 | 3 | 30.6 | 50.6 | 42.0 | 44.2 | 42.2 | 39.5 |
| 4/18/2013 | 4/21/2013 | 15 | 3 | 35.6 | 54.5 | 42.8 | 44.6 | 42.3 | 40.0 |
| 4/18/2013 | 4/21/2013 | 16 | 3 | 35.8 | 58.1 | 43.7 | 45.5 | 42.4 | 39.9 |
| 4/18/2013 | 4/21/2013 | 17 | 3 | 37.2 | 57.8 | 43.9 | 46.1 | 43.1 | 41.1 |
| 4/18/2013 | 4/21/2013 | 18 | 3 | 38.9 | 51.4 | 44.1 | 45.1 | 43.6 | 42.3 |
| 4/18/2013 | 4/21/2013 | 19 | 3 | 39.1 | 51.4 | 45.1 | 45.9 | 44.6 | 43.5 |
| 4/18/2013 | 4/21/2013 | 20 | 3 | 42.3 | 51.0 | 45.6 | 46.8 | 45.6 | 44.4 |
| 4/18/2013 | 4/21/2013 | 21 | 3 | 42.7 | 53.2 | 47.0 | 47.0 | 45.7 | 44.8 |
| 4/18/2013 | 4/21/2013 | 22 | 3 | 43.2 | 59.6 | 50.1 | 53.6 | 46.3 | 45.2 |
| 4/18/2013 | 4/21/2013 | 23 | 3 | 42.2 | 54.4 | 46.4 | 48.4 | 46.1 | 45.1 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 78. PAPA211 (Well heads, 3, and injection well, with generator, 200 m) dBA and one-third octave band metrics, April 18-21, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/18/13 | 4/21/13 | dBA | 72 | 30.6 | 59.6 | 46.9 | 46.7 | 45.5 | 44.3 |
| 4/18/13 | 4/21/13 | 12.5 | 72 | 25.6 | 73.4 | 50.4 | 46.5 | 42.8 | 38.4 |
| 4/18/13 | 4/21/13 | 16 | 72 | 34.0 | 71.6 | 52.5 | 54.1 | 50.1 | 46.2 |
| 4/18/13 | 4/21/13 | 20 | 72 | 38.2 | 77.9 | 61.9 | 63.3 | 56.0 | 52.0 |
| 4/18/13 | 4/21/13 | 25 | 72 | 32.8 | 68.0 | 49.4 | 50.8 | 47.3 | 44.0 |
| 4/18/13 | 4/21/13 | 31.5 | 72 | 38.9 | 72.1 | 53.6 | 55.4 | 51.7 | 47.9 |
| 4/18/13 | 4/21/13 | 40 | 72 | 38.9 | 75.1 | 53.2 | 54.0 | 52.5 | 50.9 |
| 4/18/13 | 4/21/13 | 50 | 72 | 37.8 | 77.5 | 52.3 | 54.0 | 50.7 | 48.1 |
| 4/18/13 | 4/21/13 | 63 | 72 | 35.9 | 77.0 | 48.5 | 49.7 | 47.6 | 45.8 |
| 4/18/13 | 4/21/13 | 80 | 72 | 32.9 | 71.6 | 48.4 | 49.7 | 48.0 | 46.1 |
| 4/18/13 | 4/21/13 | 100 | 72 | 33.3 | 69.7 | 49.1 | 50.3 | 48.6 | 47.0 |
| 4/18/13 | 4/21/13 | 125 | 72 | 34.2 | 69.3 | 55.5 | 57.2 | 55.3 | 53.1 |
| 4/18/13 | 4/21/13 | 160 | 72 | 31.3 | 67.9 | 49.2 | 50.1 | 48.8 | 47.5 |
| 4/18/13 | 4/21/13 | 200 | 72 | 26.9 | 66.2 | 47.0 | 48.2 | 47.0 | 45.5 |
| 4/18/13 | 4/21/13 | 250 | 72 | 28.4 | 63.0 | 47.2 | 48.9 | 47.2 | 45.3 |
| 4/18/13 | 4/21/13 | 315 | 72 | 22.7 | 62.0 | 41.7 | 42.3 | 41.1 | 39.3 |
| 4/18/13 | 4/21/13 | 400 | 72 | 19.9 | 50.3 | 37.3 | 39.1 | 37.1 | 34.7 |
| 4/18/13 | 4/21/13 | 500 | 72 | 17.2 | 53.5 | 30.2 | 32.1 | 29.3 | 27.0 |
| 4/18/13 | 4/21/13 | 630 | 72 | 9.6 | 51.8 | 24.0 | 24.7 | 22.3 | 19.9 |
| 4/18/13 | 4/21/13 | 800 | 72 | 8.1 | 48.8 | 27.5 | 26.0 | 22.3 | 18.7 |
| 4/18/13 | 4/21/13 | 1000 | 72 | 6.8 | 44.2 | 26.7 | 24.8 | 20.3 | 16.9 |
| 4/18/13 | 4/21/13 | 1250 | 72 | 8.5 | 52.9 | 32.1 | 28.5 | 23.5 | 19.3 |
| 4/18/13 | 4/21/13 | 1600 | 72 | 6.9 | 49.7 | 31.5 | 28.4 | 22.7 | 18.0 |
| 4/18/13 | 4/21/13 | 2000 | 72 | 6.3 | 51.1 | 33.6 | 28.8 | 23.5 | 18.7 |
| 4/18/13 | 4/21/13 | 2500 | 72 | 5.2 | 54.6 | 32.4 | 27.7 | 22.8 | 17.3 |
| 4/18/13 | 4/21/13 | 3150 | 72 | 6.3 | 52.8 | 36.1 | 32.3 | 26.1 | 20.9 |
| 4/18/13 | 4/21/13 | 4000 | 72 | 4.5 | 51.3 | 26.7 | 22.7 | 17.3 | 12.2 |
| 4/18/13 | 4/21/13 | 5000 | 72 | 2.7 | 52.7 | 19.6 | 16.5 | 12.0 | 7.8 |
| 4/18/13 | 4/21/13 | 6300 | 72 | 1.6 | 50.2 | 15.8 | 12.3 | 8.4 | 6.3 |
| 4/18/13 | 4/21/13 | 8000 | 72 | 0.5 | 56.6 | 12.0 | 7.9 | 5.9 | 5.2 |
| 4/18/13 | 4/21/13 | 10000 | 72 | -0.6 | 44.5 | 6.3 | 6.2 | 5.1 | 4.8 |
| 4/18/13 | 4/21/13 | 12500 | 72 | -1.0 | 36.2 | 4.8 | 4.6 | 4.2 | 4.1 |
| 4/18/13 | 4/21/13 | 16000 | 72 | -1.0 | 31.1 | 4.1 | 3.8 | 3.4 | 3.3 |
| 4/18/13 | 4/21/13 | 20000 | 72 | -0.3 | 31.5 | 3.0 | 2.3 | 2.1 | 1.9 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 79. PAPA212 (Well heads, 3, and injection well, with generator, 200 m) hourly dBA metrics, April 18-21, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/18/2013 | 4/21/2013 | 0 | 3 | 35.0 | 45.8 | 40.1 | 42.0 | 39.0 | 37.5 |
| 4/18/2013 | 4/21/2013 | 1 | 3 | 36.0 | 47.7 | 41.1 | 42.6 | 40.5 | 39.2 |
| 4/18/2013 | 4/21/2013 | 2 | 3 | 35.6 | 50.3 | 41.9 | 44.7 | 41.2 | 38.7 |
| 4/18/2013 | 4/21/2013 | 3 | 3 | 36.4 | 49.3 | 42.4 | 43.5 | 40.9 | 38.8 |
| 4/18/2013 | 4/21/2013 | 4 | 3 | 34.9 | 51.0 | 43.7 | 44.8 | 42.9 | 41.2 |
| 4/18/2013 | 4/21/2013 | 5 | 3 | 36.9 | 48.5 | 43.1 | 45.1 | 43.0 | 40.8 |
| 4/18/2013 | 4/21/2013 | 6 | 3 | 35.2 | 51.0 | 42.1 | 42.1 | 40.4 | 38.7 |
| 4/18/2013 | 4/21/2013 | 7 | 3 | 35.1 | 51.1 | 40.5 | 44.2 | 39.0 | 37.4 |
| 4/18/2013 | 4/21/2013 | 8 | 3 | 32.3 | 50.2 | 38.6 | 39.4 | 37.8 | 36.4 |
| 4/18/2013 | 4/21/2013 | 9 | 2 | 29.7 | 51.2 | 37.4 | 38.9 | 37.1 | 35.1 |
| 4/18/2013 | 4/21/2013 | 10 | 2 | 28.8 | 45.2 | 37.2 | 39.4 | 36.8 | 33.8 |
| 4/18/2013 | 4/21/2013 | 11 | 2 | 27.0 | 54.6 | 36.0 | 38.2 | 34.9 | 31.9 |
| 4/18/2013 | 4/21/2013 | 12 | 2 | 26.4 | 47.7 | 34.8 | 37.4 | 33.2 | 30.1 |
| 4/18/2013 | 4/21/2013 | 13 | 2 | 25.9 | 56.0 | 36.4 | 38.1 | 33.6 | 30.4 |
| 4/18/2013 | 4/21/2013 | 14 | 2 | 26.8 | 55.1 | 35.8 | 38.3 | 34.5 | 30.8 |
| 4/18/2013 | 4/21/2013 | 15 | 2 | 27.5 | 53.7 | 37.3 | 39.7 | 34.8 | 31.7 |
| 4/18/2013 | 4/21/2013 | 16 | 3 | 26.7 | 57.9 | 38.0 | 41.1 | 36.4 | 32.7 |
| 4/18/2013 | 4/21/2013 | 17 | 3 | 28.3 | 55.0 | 39.1 | 41.6 | 37.8 | 33.7 |
| 4/18/2013 | 4/21/2013 | 18 | 3 | 30.0 | 51.0 | 38.2 | 39.7 | 36.5 | 34.4 |
| 4/18/2013 | 4/21/2013 | 19 | 3 | 30.4 | 53.0 | 39.5 | 39.0 | 37.0 | 35.6 |
| 4/18/2013 | 4/21/2013 | 20 | 3 | 34.6 | 49.0 | 39.1 | 40.5 | 38.4 | 37.0 |
| 4/18/2013 | 4/21/2013 | 21 | 3 | 35.5 | 46.2 | 39.5 | 41.4 | 39.1 | 37.7 |
| 4/18/2013 | 4/21/2013 | 22 | 3 | 35.8 | 51.6 | 42.2 | 45.2 | 39.5 | 37.9 |
| 4/18/2013 | 4/21/2013 | 23 | 3 | 34.8 | 48.3 | 39.3 | 41.0 | 39.0 | 37.8 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 80. PAPA212 (Well heads, 3, and injection well, with generator, 200 m) dBA and one-third octave band metrics, April 18-21, 2013, 0000-2300.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/18/13 | 4/21/13 | dBA | 65 | 25.9 | 57.9 | 40.2 | 41.4 | 38.6 | 37.0 |
| 4/18/13 | 4/21/13 | 12.5 | 65 | 24.1 | 77.9 | 53.6 | 46.4 | 43.2 | 38.1 |
| 4/18/13 | 4/21/13 | 16 | 65 | 32.5 | 76.9 | 53.9 | 54.0 | 48.2 | 44.3 |
| 4/18/13 | 4/21/13 | 20 | 65 | 36.2 | 77.1 | 62.1 | 63.4 | 57.4 | 52.3 |
| 4/18/13 | 4/21/13 | 25 | 65 | 31.8 | 72.0 | 48.8 | 49.3 | 45.9 | 42.4 |
| 4/18/13 | 4/21/13 | 31.5 | 65 | 33.6 | 68.2 | 51.9 | 54.3 | 50.3 | 45.7 |
| 4/18/13 | 4/21/13 | 40 | 65 | 33.9 | 70.0 | 49.7 | 51.0 | 48.8 | 46.5 |
| 4/18/13 | 4/21/13 | 50 | 65 | 34.0 | 70.6 | 48.7 | 50.5 | 47.1 | 44.7 |
| 4/18/13 | 4/21/13 | 63 | 65 | 32.5 | 69.5 | 46.1 | 47.9 | 45.1 | 42.7 |
| 4/18/13 | 4/21/13 | 80 | 65 | 31.2 | 69.8 | 44.8 | 46.0 | 44.1 | 41.7 |
| 4/18/13 | 4/21/13 | 100 | 65 | 29.9 | 66.3 | 44.9 | 46.5 | 44.4 | 42.7 |
| 4/18/13 | 4/21/13 | 125 | 65 | 28.4 | 63.0 | 50.7 | 52.7 | 50.4 | 48.2 |
| 4/18/13 | 4/21/13 | 160 | 65 | 27.1 | 65.0 | 43.9 | 45.4 | 43.9 | 42.3 |
| 4/18/13 | 4/21/13 | 200 | 65 | 24.2 | 98.9 | 46.6 | 41.5 | 40.2 | 38.4 |
| 4/18/13 | 4/21/13 | 250 | 65 | 22.0 | 61.3 | 36.0 | 37.6 | 35.0 | 32.8 |
| 4/18/13 | 4/21/13 | 315 | 65 | 16.8 | 54.5 | 30.3 | 30.7 | 27.8 | 25.4 |
| 4/18/13 | 4/21/13 | 400 | 65 | 11.1 | 47.3 | 26.6 | 27.4 | 23.5 | 20.8 |
| 4/18/13 | 4/21/13 | 500 | 65 | 7.0 | 51.7 | 26.0 | 26.3 | 21.4 | 17.7 |
| 4/18/13 | 4/21/13 | 630 | 65 | 2.4 | 50.8 | 22.3 | 22.7 | 16.9 | 13.1 |
| 4/18/13 | 4/21/13 | 800 | 65 | 1.9 | 45.7 | 23.9 | 23.4 | 17.7 | 12.6 |
| 4/18/13 | 4/21/13 | 1000 | 65 | 1.9 | 39.1 | 22.9 | 23.4 | 16.4 | 11.1 |
| 4/18/13 | 4/21/13 | 1250 | 65 | 3.3 | 44.4 | 26.6 | 25.9 | 18.1 | 12.9 |
| 4/18/13 | 4/21/13 | 1600 | 65 | 3.2 | 43.2 | 26.9 | 26.6 | 17.8 | 12.4 |
| 4/18/13 | 4/21/13 | 2000 | 65 | 3.2 | 45.5 | 25.4 | 26.3 | 15.6 | 10.5 |
| 4/18/13 | 4/21/13 | 2500 | 65 | 3.4 | 44.8 | 23.0 | 25.2 | 14.1 | 8.6 |
| 4/18/13 | 4/21/13 | 3150 | 65 | 4.7 | 47.0 | 27.0 | 24.2 | 17.3 | 11.7 |
| 4/18/13 | 4/21/13 | 4000 | 65 | 4.4 | 47.7 | 17.7 | 17.7 | 9.2 | 6.3 |
| 4/18/13 | 4/21/13 | 5000 | 65 | 4.0 | 54.2 | 13.8 | 10.8 | 6.5 | 5.7 |
| 4/18/13 | 4/21/13 | 6300 | 65 | 3.5 | 43.1 | 8.6 | 7.9 | 6.0 | 5.7 |
| 4/18/13 | 4/21/13 | 8000 | 65 | 1.4 | 43.4 | 6.7 | 6.1 | 5.7 | 5.5 |
| 4/18/13 | 4/21/13 | 10000 | 65 | 1.3 | 29.5 | 5.7 | 5.4 | 5.3 | 5.1 |
| 4/18/13 | 4/21/13 | 12500 | 65 | 1.1 | 28.7 | 4.9 | 4.6 | 4.5 | 4.4 |
| 4/18/13 | 4/21/13 | 16000 | 65 | 1.1 | 27.1 | 4.0 | 3.6 | 3.5 | 3.3 |
| 4/18/13 | 4/21/13 | 20000 | 65 | 1.5 | 22.8 | 2.8 | 2.2 | 2.1 | 2.0 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 81. PAPA213 (Gobbler's Knob, north side, liquid stabilizing facility and central gathering facility, 150 m) hourly dBA metrics, April 22-24, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/22/2013 | 4/24/2013 | 0 | 2 | 35.3 | 55.9 | 45.9 | 48.7 | 44.9 | 40.6 |
| 4/22/2013 | 4/24/2013 | 1 | 2 | 35.9 | 54.3 | 43.8 | 45.4 | 42.8 | 40.6 |
| 4/22/2013 | 4/24/2013 | 2 | 2 | 34.6 | 52.7 | 44.4 | 46.3 | 43.6 | 40.3 |
| 4/22/2013 | 4/24/2013 | 3 | 2 | 34.4 | 54.8 | 47.4 | 45.8 | 44.1 | 41.3 |
| 4/22/2013 | 4/24/2013 | 4 | 2 | 34.3 | 55.3 | 46.1 | 46.5 | 43.1 | 41.3 |
| 4/22/2013 | 4/24/2013 | 5 | 2 | 37.3 | 54.3 | 45.9 | 47.7 | 45.5 | 41.5 |
| 4/22/2013 | 4/24/2013 | 6 | 2 | 37.4 | 53.7 | 45.5 | 47.8 | 44.9 | 41.4 |
| 4/22/2013 | 4/24/2013 | 7 | 2 | 37.5 | 57.6 | 47.1 | 49.2 | 46.6 | 42.9 |
| 4/22/2013 | 4/24/2013 | 8 | 2 | 36.5 | 53.6 | 44.9 | 47.6 | 44.1 | 40.6 |
| 4/22/2013 | 4/24/2013 | 9 | 2 | 35.2 | 69.5 | 46.5 | 46.6 | 42.4 | 38.7 |
| 4/22/2013 | 4/24/2013 | 10 | 2 | 36.2 | 58.4 | 47.1 | 46.7 | 43.9 | 40.1 |
| 4/22/2013 | 4/24/2013 | 11 | 2 | 37.7 | 61.0 | 50.1 | 49.4 | 46.9 | 44.9 |
| 4/22/2013 | 4/24/2013 | 12 | 2 | 38.9 | 75.7 | 50.3 | 49.5 | 44.8 | 42.6 |
| 4/22/2013 | 4/24/2013 | 13 | 2 | 33.9 | 55.3 | 43.8 | 45.7 | 43.5 | 40.3 |
| 4/22/2013 | 4/24/2013 | 14 | 2 | 33.7 | 57.1 | 42.2 | 43.8 | 40.8 | 38.3 |
| 4/22/2013 | 4/24/2013 | 15 | 2 | 34.3 | 62.0 | 43.3 | 44.8 | 41.2 | 38.7 |
| 4/22/2013 | 4/24/2013 | 16 | 2 | 34.2 | 64.5 | 44.4 | 45.7 | 42.5 | 39.5 |
| 4/22/2013 | 4/24/2013 | 17 | 2 | 33.9 | 61.6 | 44.3 | 46.4 | 43.4 | 40.1 |
| 4/22/2013 | 4/24/2013 | 18 | 2 | 36.4 | 58.8 | 43.1 | 44.6 | 41.7 | 40.0 |
| 4/22/2013 | 4/24/2013 | 19 | 2 | 37.5 | 63.2 | 44.0 | 45.1 | 42.5 | 40.7 |
| 4/22/2013 | 4/24/2013 | 20 | 2 | 38.7 | 54.6 | 44.2 | 46.5 | 43.2 | 41.6 |
| 4/22/2013 | 4/24/2013 | 21 | 2 | 37.4 | 55.8 | 46.6 | 48.1 | 44.9 | 43.2 |
| 4/22/2013 | 4/24/2013 | 22 | 2 | 36.0 | 53.8 | 46.0 | 48.5 | 45.0 | 40.1 |
| 4/22/2013 | 4/24/2013 | 23 | 2 | 34.5 | 54.2 | 45.5 | 48.4 | 44.5 | 39.7 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 82. PAPA213 (Gobbler's Knob, north side, liquid stabilizing facility and central gathering facility, 150 m) dBA and one-third octave band metrics, April 22-24, 2013.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/22/13 | 4/24/13 | dBA | 48 | 33.7 | 75.7 | 46.0 | 46.9 | 43.8 | 40.3 |
| 4/22/13 | 4/24/13 | 12.5 | 48 | 36.4 | 75.2 | 55.3 | 56.8 | 53.2 | 49.7 |
| 4/22/13 | 4/24/13 | 16 | 48 | 44.7 | 75.9 | 59.4 | 61.6 | 57.4 | 54.4 |
| 4/22/13 | 4/24/13 | 20 | 48 | 46.1 | 74.6 | 61.8 | 64.3 | 60.7 | 57.6 |
| 4/22/13 | 4/24/13 | 25 | 48 | 47.3 | 76.3 | 61.5 | 63.2 | 59.7 | 56.5 |
| 4/22/13 | 4/24/13 | 31.5 | 48 | 45.5 | 75.7 | 61.4 | 63.0 | 59.7 | 56.7 |
| 4/22/13 | 4/24/13 | 40 | 48 | 47.7 | 77.6 | 62.7 | 64.9 | 61.2 | 58.3 |
| 4/22/13 | 4/24/13 | 50 | 48 | 50.9 | 74.8 | 64.4 | 66.5 | 63.8 | 61.1 |
| 4/22/13 | 4/24/13 | 63 | 48 | 45.1 | 78.7 | 58.6 | 60.2 | 56.6 | 53.5 |
| 4/22/13 | 4/24/13 | 80 | 48 | 38.9 | 76.5 | 60.2 | 62.7 | 59.8 | 55.2 |
| 4/22/13 | 4/24/13 | 100 | 48 | 29.6 | 82.4 | 54.7 | 54.8 | 51.2 | 47.6 |
| 4/22/13 | 4/24/13 | 125 | 48 | 25.7 | 85.0 | 51.9 | 51.3 | 45.3 | 41.5 |
| 4/22/13 | 4/24/13 | 160 | 48 | 22.2 | 73.1 | 49.0 | 47.0 | 42.1 | 38.4 |
| 4/22/13 | 4/24/13 | 200 | 48 | 20.4 | 71.8 | 44.9 | 43.5 | 38.5 | 35.2 |
| 4/22/13 | 4/24/13 | 250 | 48 | 16.7 | 65.1 | 40.9 | 41.1 | 35.6 | 31.8 |
| 4/22/13 | 4/24/13 | 315 | 48 | 14.6 | 60.7 | 37.0 | 37.3 | 32.3 | 28.7 |
| 4/22/13 | 4/24/13 | 400 | 48 | 10.4 | 64.8 | 33.1 | 34.3 | 29.5 | 25.3 |
| 4/22/13 | 4/24/13 | 500 | 48 | 10.5 | 57.0 | 29.5 | 29.0 | 25.6 | 22.2 |
| 4/22/13 | 4/24/13 | 630 | 48 | 9.9 | 56.6 | 28.0 | 27.9 | 23.5 | 19.1 |
| 4/22/13 | 4/24/13 | 800 | 48 | 7.6 | 61.7 | 29.2 | 28.2 | 23.3 | 18.0 |
| 4/22/13 | 4/24/13 | 1000 | 48 | 10.4 | 65.2 | 33.0 | 31.4 | 26.6 | 20.0 |
| 4/22/13 | 4/24/13 | 1250 | 48 | 9.7 | 67.8 | 33.9 | 32.5 | 27.4 | 19.6 |
| 4/22/13 | 4/24/13 | 1600 | 48 | 7.8 | 68.8 | 33.1 | 31.6 | 25.5 | 17.9 |
| 4/22/13 | 4/24/13 | 2000 | 48 | 5.5 | 68.7 | 31.5 | 28.6 | 22.3 | 15.3 |
| 4/22/13 | 4/24/13 | 2500 | 48 | 4.4 | 66.0 | 30.6 | 26.1 | 19.9 | 14.0 |
| 4/22/13 | 4/24/13 | 3150 | 48 | 3.4 | 58.6 | 23.2 | 20.7 | 14.0 | 7.7 |
| 4/22/13 | 4/24/13 | 4000 | 48 | 3.4 | 49.6 | 16.8 | 13.5 | 9.0 | 4.8 |
| 4/22/13 | 4/24/13 | 5000 | 48 | 3.9 | 42.9 | 11.2 | 8.8 | 5.7 | 4.7 |
| 4/22/13 | 4/24/13 | 6300 | 48 | 4.1 | 36.9 | 6.9 | 5.3 | 4.9 | 4.6 |
| 4/22/13 | 4/24/13 | 8000 | 48 | 4.1 | 38.1 | 6.5 | 4.9 | 4.7 | 4.5 |
| 4/22/13 | 4/24/13 | 10000 | 48 | 3.6 | 40.7 | 6.1 | 4.5 | 4.3 | 4.2 |
| 4/22/13 | 4/24/13 | 12500 | 48 | 2.8 | 38.3 | 5.8 | 4.1 | 3.7 | 3.5 |
| 4/22/13 | 4/24/13 | 16000 | 48 | 1.7 | 29.7 | 5.1 | 3.2 | 2.8 | 2.5 |
| 4/22/13 | 4/24/13 | 20000 | 48 | 0.1 | 29.1 | 3.6 | 1.7 | 1.3 | 0.9 |

## Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).

Table 83. PAPA214 (North Anticline Road, east side, 50 m from centerline) hourly dBA metrics, April 22-23, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/23/2013 | 4/23/2013 | 0 | 1 | 20.8 | 61.0 | 36.6 | 33.4 | 24.8 | 22.7 |
| 4/23/2013 | 4/23/2013 | 1 | 1 | 21.5 | 58.0 | 35.9 | 30.6 | 24.5 | 23.1 |
| 4/23/2013 | 4/23/2013 | 2 | 1 | 21.5 | 59.6 | 35.2 | 27.1 | 24.5 | 23.0 |
| 4/23/2013 | 4/23/2013 | 3 | 1 | 21.0 | 55.5 | 33.8 | 29.6 | 24.5 | 23.0 |
| 4/23/2013 | 4/23/2013 | 4 | 1 | 22.2 | 58.2 | 37.6 | 39.0 | 26.7 | 24.2 |
| 4/23/2013 | 4/23/2013 | 5 | 1 | 24.6 | 66.0 | 43.4 | 45.6 | 31.7 | 27.2 |
| 4/23/2013 | 4/23/2013 | 6 | 1 | 24.9 | 66.5 | 44.1 | 46.0 | 30.2 | 27.0 |
| 4/23/2013 | 4/23/2013 | 7 | 1 | 25.4 | 64.6 | 44.8 | 47.2 | 33.2 | 27.6 |
| 4/23/2013 | 4/23/2013 | 8 | 1 | 23.4 | 60.7 | 39.4 | 42.5 | 29.8 | 25.7 |
| 4/22/2013 | 4/22/2013 | 9 | 1 | 29.4 | 75.8 | 50.6 | 51.3 | 37.2 | 31.5 |
| 4/22/2013 | 4/22/2013 | 10 | 1 | 29.2 | 67.6 | 48.6 | 50.8 | 35.3 | 31.2 |
| 4/22/2013 | 4/22/2013 | 11 | 1 | 31.4 | 66.1 | 47.0 | 49.0 | 36.5 | 34.1 |
| 4/22/2013 | 4/22/2013 | 12 | 1 | 27.2 | 79.2 | 50.1 | 47.0 | 34.5 | 29.9 |
| 4/22/2013 | 4/22/2013 | 13 | 1 | 24.4 | 54.7 | 38.6 | 42.2 | 31.1 | 27.1 |
| 4/22/2013 | 4/22/2013 | 14 | 1 | 24.2 | 59.6 | 42.8 | 47.7 | 32.4 | 27.2 |
| 4/22/2013 | 4/22/2013 | 15 | 1 | 23.6 | 58.8 | 40.1 | 42.5 | 28.9 | 25.5 |
| 4/22/2013 | 4/22/2013 | 16 | 1 | 22.2 | 56.3 | 35.7 | 36.8 | 26.2 | 24.0 |
| 4/22/2013 | 4/22/2013 | 17 | 1 | 21.9 | 64.8 | 39.7 | 40.3 | 27.0 | 24.0 |
| 4/22/2013 | 4/22/2013 | 18 | 1 | 21.8 | 57.7 | 37.8 | 39.3 | 25.7 | 23.4 |
| 4/22/2013 | 4/22/2013 | 19 | 1 | 21.2 | 57.1 | 38.3 | 39.4 | 25.5 | 23.5 |
| 4/22/2013 | 4/22/2013 | 20 | 1 | 21.7 | 56.8 | 37.8 | 36.2 | 25.2 | 23.5 |
| 4/22/2013 | 4/22/2013 | 21 | 1 | 20.9 | 71.3 | 44.0 | 36.4 | 25.3 | 23.0 |
| 4/22/2013 | 4/22/2013 | 22 | 1 | 21.2 | 52.7 | 32.1 | 27.9 | 24.2 | 22.6 |
| 4/22/2013 | 4/22/2013 | 23 | 1 | 20.0 | 60.3 | 37.5 | 35.5 | 23.6 | 21.8 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 84. PAPA214 (North Anticline Road, east side, 50 m from centerline) dBA and one-third octave band metrics, April 22-23, 2013.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/22/13 | 4/23/13 | dBA | 24 | 20.0 | 79.2 | 43.6 | 39.9 | 26.9 | 24.1 |
| 4/22/13 | 4/23/13 | 12.5 | 24 | 28.7 | 76.1 | 52.7 | 54.1 | 48.0 | 42.9 |
| 4/22/13 | 4/23/13 | 16 | 24 | 35.0 | 78.6 | 53.8 | 55.4 | 52.1 | 48.9 |
| 4/22/13 | 4/23/13 | 20 | 24 | 45.2 | 74.7 | 60.3 | 62.4 | 59.6 | 56.6 |
| 4/22/13 | 4/23/13 | 25 | 24 | 36.8 | 79.5 | 52.0 | 53.8 | 49.6 | 46.6 |
| 4/22/13 | 4/23/13 | 31.5 | 24 | 35.5 | 75.6 | 50.5 | 52.2 | 47.5 | 44.4 |
| 4/22/13 | 4/23/13 | 40 | 24 | 37.3 | 79.0 | 52.7 | 54.2 | 50.6 | 46.6 |
| 4/22/13 | 4/23/13 | 50 | 24 | 40.1 | 82.7 | 54.5 | 55.0 | 50.7 | 47.5 |
| 4/22/13 | 4/23/13 | 63 | 24 | 30.4 | 85.1 | 54.5 | 54.6 | 43.2 | 38.7 |
| 4/22/13 | 4/23/13 | 80 | 24 | 24.8 | 84.8 | 55.2 | 53.3 | 36.9 | 34.2 |
| 4/22/13 | 4/23/13 | 100 | 24 | 15.8 | 83.0 | 51.6 | 46.5 | 29.5 | 26.2 |
| 4/22/13 | 4/23/13 | 125 | 24 | 11.0 | 83.6 | 47.9 | 36.9 | 25.9 | 21.6 |
| 4/22/13 | 4/23/13 | 160 | 24 | 8.6 | 79.7 | 46.6 | 32.6 | 22.1 | 17.4 |
| 4/22/13 | 4/23/13 | 200 | 24 | 6.5 | 77.2 | 43.3 | 29.4 | 19.8 | 16.3 |
| 4/22/13 | 4/23/13 | 250 | 24 | 3.1 | 73.8 | 39.9 | 25.5 | 16.3 | 12.4 |
| 4/22/13 | 4/23/13 | 315 | 24 | 4.5 | 69.9 | 36.3 | 21.7 | 17.8 | 14.9 |
| 4/22/13 | 4/23/13 | 400 | 24 | 2.1 | 66.4 | 31.0 | 18.4 | 12.8 | 10.1 |
| 4/22/13 | 4/23/13 | 500 | 24 | 1.5 | 63.7 | 28.1 | 17.9 | 11.3 | 8.5 |
| 4/22/13 | 4/23/13 | 630 | 24 | 1.9 | 63.6 | 27.8 | 19.1 | 12.4 | 9.0 |
| 4/22/13 | 4/23/13 | 800 | 24 | 2.1 | 64.0 | 28.5 | 20.8 | 13.5 | 9.0 |
| 4/22/13 | 4/23/13 | 1000 | 24 | 2.6 | 65.1 | 29.1 | 22.1 | 12.2 | 8.1 |
| 4/22/13 | 4/23/13 | 1250 | 24 | 1.9 | 67.4 | 29.7 | 23.7 | 11.5 | 6.9 |
| 4/22/13 | 4/23/13 | 1600 | 24 | 1.9 | 67.8 | 30.0 | 24.6 | 9.1 | 5.9 |
| 4/22/13 | 4/23/13 | 2000 | 24 | 1.9 | 67.2 | 30.0 | 23.7 | 6.3 | 4.4 |
| 4/22/13 | 4/23/13 | 2500 | 24 | 2.5 | 66.4 | 28.8 | 22.5 | 5.3 | 4.2 |
| 4/22/13 | 4/23/13 | 3150 | 24 | 3.3 | 62.9 | 27.1 | 20.7 | 5.0 | 4.2 |
| 4/22/13 | 4/23/13 | 4000 | 24 | 3.9 | 63.2 | 24.7 | 18.0 | 5.1 | 4.6 |
| 4/22/13 | 4/23/13 | 5000 | 24 | 4.5 | 62.6 | 23.7 | 14.9 | 5.5 | 5.2 |
| 4/22/13 | 4/23/13 | 6300 | 24 | 5.0 | 58.9 | 19.2 | 11.0 | 5.8 | 5.5 |
| 4/22/13 | 4/23/13 | 8000 | 24 | 5.1 | 57.0 | 16.2 | 8.2 | 5.8 | 5.6 |
| 4/22/13 | 4/23/13 | 10000 | 24 | 4.7 | 53.2 | 13.5 | 7.0 | 5.5 | 5.3 |
| 4/22/13 | 4/23/13 | 12500 | 24 | 3.9 | 50.8 | 10.7 | 5.8 | 4.7 | 4.5 |
| 4/22/13 | 4/23/13 | 16000 | 24 | 2.7 | 50.3 | 10.0 | 4.5 | 3.8 | 3.5 |
| 4/22/13 | 4/23/13 | 20000 | 24 | 1.4 | 49.6 | 8.0 | 3.0 | 2.4 | 2.1 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 85. PAPA215 (Mesa pad 3-27, 21 wells, with intermittent generator, 200 m) hourly dBA metrics, April 23-24, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/24/2013 | 4/24/2013 | 0 | 1 | 40.3 | 58.9 | 49.0 | 52.1 | 47.4 | 44.1 |
| 4/24/2013 | 4/24/2013 | 1 | 1 | 37.1 | 52.6 | 44.2 | 46.8 | 43.1 | 40.4 |
| 4/24/2013 | 4/24/2013 | 2 | 1 | 37.3 | 60.2 | 47.0 | 50.3 | 43.3 | 40.0 |
| 4/24/2013 | 4/24/2013 | 3 | 1 | 38.3 | 56.7 | 42.2 | 43.9 | 41.3 | 39.8 |
| 4/24/2013 | 4/24/2013 | 4 | 1 | 37.6 | 47.5 | 41.1 | 42.5 | 40.7 | 39.4 |
| 4/24/2013 | 4/24/2013 | 5 | 1 | 36.7 | 56.2 | 41.1 | 41.3 | 40.1 | 38.7 |
| 4/24/2013 | 4/24/2013 | 6 | 1 | 32.2 | 48.9 | 37.8 | 40.3 | 36.5 | 33.8 |
| 4/24/2013 | 4/24/2013 | 7 | 1 | 32.6 | 45.1 | 35.8 | 37.1 | 35.4 | 34.1 |
| 4/24/2013 | 4/24/2013 | 8 | 1 | 29.1 | 43.0 | 33.5 | 35.0 | 33.2 | 31.5 |
| 4/23/2013 | 4/23/2013 | 9 | 1 | 32.5 | 50.7 | 37.1 | 37.7 | 36.2 | 34.6 |
| 4/23/2013 | 4/23/2013 | 10 | 1 | 33.9 | 45.3 | 39.8 | 42.5 | 39.0 | 36.4 |
| 4/23/2013 | 4/23/2013 | 11 | 1 | 37.0 | 49.1 | 44.6 | 46.9 | 44.4 | 40.8 |
| 4/23/2013 | 4/23/2013 | 12 | 1 | 36.9 | 56.5 | 45.0 | 47.3 | 44.7 | 40.3 |
| 4/23/2013 | 4/23/2013 | 13 | 1 | 36.1 | 49.3 | 44.9 | 47.2 | 44.7 | 40.4 |
| 4/23/2013 | 4/23/2013 | 14 | 1 | 34.9 | 49.8 | 44.6 | 47.1 | 44.2 | 40.3 |
| 4/23/2013 | 4/23/2013 | 15 | 1 | 35.8 | 58.3 | 45.1 | 47.4 | 44.4 | 40.9 |
| 4/23/2013 | 4/23/2013 | 16 | 1 | 36.0 | 51.5 | 45.6 | 48.0 | 45.0 | 41.4 |
| 4/23/2013 | 4/23/2013 | 17 | 1 | 36.2 | 50.1 | 45.2 | 47.5 | 44.8 | 41.5 |
| 4/23/2013 | 4/23/2013 | 18 | 1 | 39.7 | 52.2 | 47.6 | 49.6 | 47.3 | 44.6 |
| 4/23/2013 | 4/23/2013 | 19 | 1 | 43.6 | 52.0 | 47.5 | 48.9 | 47.3 | 45.6 |
| 4/23/2013 | 4/23/2013 | 20 | 1 | 44.0 | 53.5 | 47.6 | 48.6 | 47.4 | 46.5 |
| 4/23/2013 | 4/23/2013 | 21 | 1 | 44.6 | 56.5 | 49.9 | 51.6 | 49.5 | 48.0 |
| 4/23/2013 | 4/23/2013 | 22 | 1 | 45.5 | 57.1 | 48.7 | 49.8 | 48.3 | 47.1 |
| 4/23/2013 | 4/23/2013 | 23 | 1 | 41.9 | 60.9 | 46.6 | 47.9 | 45.8 | 44.4 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 86. PAPA215 (Mesa pad 3-27, 21 wells, with intermittent generator, 200 m) dBA and one-third octave band metrics, April 23-24, 2013.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/23/13 | 4/24/13 | dBA | 24 | 29.1 | 60.9 | 45.4 | 47.3 | 44.4 | 40.4 |
| 4/23/13 | 4/24/13 | 12.5 | 24 | 31.5 | 73.6 | 49.9 | 50.7 | 45.9 | 42.3 |
| 4/23/13 | 4/24/13 | 16 | 24 | 37.2 | 73.8 | 51.5 | 53.7 | 50.1 | 46.7 |
| 4/23/13 | 4/24/13 | 20 | 24 | 41.8 | 75.5 | 64.2 | 65.7 | 60.5 | 56.2 |
| 4/23/13 | 4/24/13 | 25 | 24 | 36.1 | 72.5 | 48.6 | 50.6 | 47.5 | 44.7 |
| 4/23/13 | 4/24/13 | 31.5 | 24 | 39.5 | 68.9 | 51.4 | 53.2 | 50.6 | 47.7 |
| 4/23/13 | 4/24/13 | 40 | 24 | 42.3 | 73.3 | 55.0 | 54.6 | 51.3 | 49.1 |
| 4/23/13 | 4/24/13 | 50 | 24 | 43.8 | 80.8 | 55.8 | 56.1 | 52.7 | 50.0 |
| 4/23/13 | 4/24/13 | 63 | 24 | 40.5 | 81.6 | 59.1 | 55.5 | 52.0 | 48.0 |
| 4/23/13 | 4/24/13 | 80 | 24 | 38.5 | 76.8 | 61.7 | 63.9 | 61.4 | 54.4 |
| 4/23/13 | 4/24/13 | 100 | 24 | 35.7 | 79.9 | 52.6 | 53.3 | 50.5 | 48.0 |
| 4/23/13 | 4/24/13 | 125 | 24 | 23.9 | 75.1 | 51.5 | 51.3 | 48.0 | 45.6 |
| 4/23/13 | 4/24/13 | 160 | 24 | 22.7 | 71.7 | 47.2 | 47.3 | 44.5 | 42.0 |
| 4/23/13 | 4/24/13 | 200 | 24 | 25.5 | 65.9 | 47.4 | 47.8 | 43.8 | 40.4 |
| 4/23/13 | 4/24/13 | 250 | 24 | 21.7 | 61.8 | 44.6 | 45.2 | 41.5 | 37.3 |
| 4/23/13 | 4/24/13 | 315 | 24 | 18.0 | 60.1 | 40.5 | 40.1 | 36.1 | 32.7 |
| 4/23/13 | 4/24/13 | 400 | 24 | 14.7 | 58.5 | 37.3 | 36.7 | 31.8 | 28.4 |
| 4/23/13 | 4/24/13 | 500 | 24 | 9.4 | 56.2 | 32.4 | 32.3 | 27.2 | 23.5 |
| 4/23/13 | 4/24/13 | 630 | 24 | 5.3 | 55.9 | 29.2 | 29.2 | 24.4 | 21.1 |
| 4/23/13 | 4/24/13 | 800 | 24 | 2.8 | 48.9 | 27.1 | 27.8 | 23.5 | 19.1 |
| 4/23/13 | 4/24/13 | 1000 | 24 | 2.2 | 44.8 | 25.8 | 26.8 | 22.4 | 17.9 |
| 4/23/13 | 4/24/13 | 1250 | 24 | 2.1 | 43.3 | 24.0 | 24.9 | 20.4 | 15.9 |
| 4/23/13 | 4/24/13 | 1600 | 24 | 1.5 | 39.1 | 20.9 | 22.7 | 18.7 | 14.0 |
| 4/23/13 | 4/24/13 | 2000 | 24 | 1.6 | 32.0 | 15.8 | 17.4 | 12.6 | 9.1 |
| 4/23/13 | 4/24/13 | 2500 | 24 | 2.2 | 39.9 | 13.0 | 11.3 | 8.2 | 6.2 |
| 4/23/13 | 4/24/13 | 3150 | 24 | 2.8 | 34.4 | 10.9 | 8.8 | 6.5 | 5.3 |
| 4/23/13 | 4/24/13 | 4000 | 24 | 3.6 | 50.7 | 9.4 | 6.2 | 5.3 | 4.9 |
| 4/23/13 | 4/24/13 | 5000 | 24 | 4.3 | 52.4 | 11.1 | 5.6 | 5.2 | 5.0 |
| 4/23/13 | 4/24/13 | 6300 | 24 | 4.6 | 46.0 | 7.1 | 5.7 | 5.5 | 5.3 |
| 4/23/13 | 4/24/13 | 8000 | 24 | 4.7 | 27.9 | 5.6 | 5.7 | 5.5 | 5.3 |
| 4/23/13 | 4/24/13 | 10000 | 24 | 4.6 | 28.1 | 5.3 | 5.4 | 5.1 | 5.0 |
| 4/23/13 | 4/24/13 | 12500 | 24 | 4.0 | 20.5 | 4.6 | 4.8 | 4.5 | 4.4 |
| 4/23/13 | 4/24/13 | 16000 | 24 | 3.1 | 20.8 | 3.8 | 3.8 | 3.6 | 3.5 |
| 4/23/13 | 4/24/13 | 20000 | 24 | 1.7 | 16.2 | 2.6 | 2.8 | 2.4 | 2.2 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 87. PAPA216 (Drill rig, pad 5-19, 435 m) hourly dBA metrics, April 23-24, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/24/2013 | 4/24/2013 | 0 | 1 | 35.5 | 58.9 | 41.0 | 42.2 | 40.4 | 38.2 |
| 4/24/2013 | 4/24/2013 | 1 | 1 | 37.4 | 58.4 | 42.0 | 42.7 | 41.3 | 39.8 |
| 4/24/2013 | 4/24/2013 | 2 | 1 | 37.6 | 52.9 | 42.5 | 43.8 | 42.0 | 40.4 |
| 4/24/2013 | 4/24/2013 | 3 | 1 | 40.3 | 62.9 | 44.5 | 45.5 | 43.9 | 42.3 |
| 4/24/2013 | 4/24/2013 | 4 | 1 | 39.7 | 61.8 | 44.5 | 45.2 | 43.6 | 41.9 |
| 4/24/2013 | 4/24/2013 | 5 | 1 | 40.7 | 65.9 | 46.1 | 46.0 | 44.5 | 43.2 |
| 4/24/2013 | 4/24/2013 | 6 | 1 | 41.4 | 65.1 | 46.3 | 45.9 | 44.3 | 43.0 |
| 4/24/2013 | 4/24/2013 | 7 | 1 | 40.1 | 49.0 | 43.4 | 44.6 | 43.2 | 41.9 |
| 4/24/2013 | 4/24/2013 | 8 | 1 | 35.9 | 53.9 | 41.5 | 43.4 | 41.2 | 38.4 |
| 4/24/2013 | 4/24/2013 | 9 | 1 | 34.0 | 49.6 | 39.0 | 40.6 | 38.6 | 36.9 |
| 4/24/2013 | 4/24/2013 | 10 | 1 | NA | NA | NA | NA | NA | NA |
| 4/23/2013 | 4/23/2013 | 11 | 1 | 29.9 | 49.6 | 36.9 | 39.1 | 36.2 | 33.7 |
| 4/23/2013 | 4/23/2013 | 12 | 1 | 30.3 | 61.6 | 39.0 | 40.5 | 37.9 | 34.4 |
| 4/23/2013 | 4/23/2013 | 13 | 1 | 35.5 | 45.0 | 40.5 | 42.0 | 40.3 | 38.6 |
| 4/23/2013 | 4/23/2013 | 14 | 1 | 38.1 | 51.8 | 41.8 | 43.0 | 41.4 | 40.0 |
| 4/23/2013 | 4/23/2013 | 15 | 1 | 35.5 | 53.3 | 42.7 | 44.4 | 42.5 | 39.0 |
| 4/23/2013 | 4/23/2013 | 16 | 1 | 36.1 | 55.9 | 41.9 | 44.1 | 41.2 | 38.8 |
| 4/23/2013 | 4/23/2013 | 17 | 1 | 35.3 | 58.4 | 41.4 | 41.8 | 39.5 | 37.6 |
| 4/23/2013 | 4/23/2013 | 18 | 1 | 34.0 | 44.9 | 39.5 | 41.0 | 39.2 | 37.6 |
| 4/23/2013 | 4/23/2013 | 19 | 1 | 35.8 | 44.4 | 39.0 | 40.2 | 38.8 | 37.5 |
| 4/23/2013 | 4/23/2013 | 20 | 1 | 36.7 | 45.6 | 39.9 | 41.0 | 39.7 | 38.6 |
| 4/23/2013 | 4/23/2013 | 21 | 1 | 37.1 | 49.5 | 40.6 | 41.8 | 40.2 | 38.8 |
| 4/23/2013 | 4/23/2013 | 22 | 1 | 36.9 | 51.7 | 41.2 | 42.4 | 40.7 | 39.3 |
| 4/23/2013 | 4/23/2013 | 23 | 1 | 38.5 | 49.4 | 41.5 | 42.5 | 41.2 | 40.1 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 88. PAPA216 (Drill rig, pad 5-19, 435 m) dBA and one-third octave band metrics, April 23-24, 2013.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/23/13 | 4/24/13 | dBA | 23 | 29.9 | 65.9 | 42.2 | 42.5 | 41.2 | 38.8 |
| 4/23/13 | 4/24/13 | 12.5 | 23 | 32.2 | 71.0 | 49.0 | 50.7 | 46.4 | 42.1 |
| 4/23/13 | 4/24/13 | 16 | 23 | 37.9 | 69.8 | 52.5 | 54.6 | 51.4 | 47.7 |
| 4/23/13 | 4/24/13 | 20 | 23 | 47.5 | 73.9 | 65.0 | 68.0 | 64.7 | 59.9 |
| 4/23/13 | 4/24/13 | 25 | 23 | 43.7 | 75.0 | 60.9 | 64.1 | 57.4 | 53.2 |
| 4/23/13 | 4/24/13 | 31.5 | 23 | 52.9 | 82.4 | 72.3 | 74.6 | 70.3 | 64.4 |
| 4/23/13 | 4/24/13 | 40 | 23 | 44.3 | 68.2 | 58.1 | 59.7 | 57.5 | 55.7 |
| 4/23/13 | 4/24/13 | 50 | 23 | 40.8 | 69.4 | 57.5 | 58.6 | 55.2 | 52.7 |
| 4/23/13 | 4/24/13 | 63 | 23 | 36.8 | 73.4 | 62.8 | 64.4 | 61.6 | 58.3 |
| 4/23/13 | 4/24/13 | 80 | 23 | 31.2 | 73.9 | 55.4 | 57.4 | 54.2 | 51.0 |
| 4/23/13 | 4/24/13 | 100 | 23 | 28.0 | 76.8 | 52.2 | 54.1 | 51.7 | 49.1 |
| 4/23/13 | 4/24/13 | 125 | 23 | 25.3 | 71.5 | 43.5 | 44.8 | 43.2 | 40.1 |
| 4/23/13 | 4/24/13 | 160 | 23 | 23.0 | 64.4 | 42.7 | 40.9 | 38.2 | 35.8 |
| 4/23/13 | 4/24/13 | 200 | 23 | 21.0 | 65.2 | 38.1 | 37.3 | 34.4 | 31.8 |
| 4/23/13 | 4/24/13 | 250 | 23 | 16.8 | 62.4 | 35.0 | 34.4 | 30.7 | 27.5 |
| 4/23/13 | 4/24/13 | 315 | 23 | 16.8 | 57.9 | 34.5 | 35.2 | 31.1 | 27.5 |
| 4/23/13 | 4/24/13 | 400 | 23 | 14.8 | 53.4 | 32.8 | 33.2 | 29.0 | 25.2 |
| 4/23/13 | 4/24/13 | 500 | 23 | 8.8 | 53.8 | 27.5 | 27.0 | 22.3 | 18.5 |
| 4/23/13 | 4/24/13 | 630 | 23 | 8.9 | 54.0 | 26.3 | 25.1 | 20.7 | 17.4 |
| 4/23/13 | 4/24/13 | 800 | 23 | 7.8 | 50.4 | 25.5 | 25.3 | 21.5 | 17.4 |
| 4/23/13 | 4/24/13 | 1000 | 23 | 7.6 | 49.3 | 24.5 | 24.1 | 20.4 | 16.9 |
| 4/23/13 | 4/24/13 | 1250 | 23 | 7.7 | 45.9 | 24.6 | 22.6 | 19.5 | 16.7 |
| 4/23/13 | 4/24/13 | 1600 | 23 | 7.0 | 44.8 | 24.6 | 21.0 | 18.3 | 15.5 |
| 4/23/13 | 4/24/13 | 2000 | 23 | 4.4 | 51.3 | 20.0 | 17.2 | 13.7 | 10.5 |
| 4/23/13 | 4/24/13 | 2500 | 23 | 3.7 | 37.9 | 15.0 | 15.1 | 10.3 | 7.5 |
| 4/23/13 | 4/24/13 | 3150 | 23 | 3.4 | 44.0 | 10.8 | 8.8 | 5.9 | 4.9 |
| 4/23/13 | 4/24/13 | 4000 | 23 | 3.6 | 41.9 | 7.9 | 5.8 | 4.7 | 4.4 |
| 4/23/13 | 4/24/13 | 5000 | 23 | 4.0 | 40.6 | 7.2 | 5.1 | 4.7 | 4.5 |
| 4/23/13 | 4/24/13 | 6300 | 23 | 4.3 | 37.7 | 5.6 | 5.1 | 4.9 | 4.7 |
| 4/23/13 | 4/24/13 | 8000 | 23 | 4.4 | 39.5 | 5.4 | 5.0 | 4.8 | 4.7 |
| 4/23/13 | 4/24/13 | 10000 | 23 | 4.1 | 36.0 | 4.9 | 4.7 | 4.6 | 4.4 |
| 4/23/13 | 4/24/13 | 12500 | 23 | 3.5 | 28.9 | 4.3 | 4.2 | 4.1 | 3.9 |
| 4/23/13 | 4/24/13 | 16000 | 23 | 2.7 | 27.6 | 3.6 | 3.5 | 3.3 | 3.2 |
| 4/23/13 | 4/24/13 | 20000 | 23 | 1.5 | 24.9 | 2.5 | 2.5 | 2.2 | 1.9 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 89. PAPA217 (Johan compressor station, 140 m ESE) hourly dBA metrics, April 23-24, 2013.

| Date Start | Date End | Hour | N. Hrs. | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/24/2013 | 4/24/2013 | 0 | 1 | 49.6 | 68.9 | 51.9 | 52.0 | 51.2 | 50.5 |
| 4/24/2013 | 4/24/2013 | 1 | 1 | 49.2 | 55.9 | 51.3 | 52.2 | 51.1 | 50.4 |
| 4/24/2013 | 4/24/2013 | 2 | 1 | 49.2 | 60.0 | 51.3 | 51.8 | 51.0 | 50.4 |
| 4/24/2013 | 4/24/2013 | 3 | 1 | 48.7 | 59.0 | 51.0 | 51.8 | 50.8 | 49.9 |
| 4/24/2013 | 4/24/2013 | 4 | 1 | 49.0 | 54.5 | 51.0 | 51.8 | 50.8 | 50.0 |
| 4/24/2013 | 4/24/2013 | 5 | 1 | 48.6 | 59.2 | 50.6 | 51.5 | 50.4 | 49.6 |
| 4/24/2013 | 4/24/2013 | 6 | 1 | 48.5 | 56.8 | 50.7 | 51.5 | 50.6 | 49.8 |
| 4/24/2013 | 4/24/2013 | 7 | 1 | 48.3 | 63.7 | 50.6 | 51.5 | 50.4 | 49.5 |
| 4/24/2013 | 4/24/2013 | 8 | 1 | 48.2 | 54.5 | 50.4 | 51.3 | 50.2 | 49.4 |
| 4/24/2013 | 4/24/2013 | 9 | 1 | 47.6 | 62.1 | 50.1 | 50.9 | 49.8 | 49.0 |
| 4/24/2013 | 4/24/2013 | 10 | 1 | 48.1 | 55.8 | 50.8 | 51.8 | 50.6 | 49.6 |
| 4/23/2013 | 4/23/2013 | 11 | 1 | NA | NA | NA | NA | NA | NA |
| 4/23/2013 | 4/23/2013 | 12 | 1 | 46.1 | 60.9 | 51.7 | 54.5 | 50.4 | 47.7 |
| 4/23/2013 | 4/23/2013 | 13 | 1 | 48.8 | 59.5 | 54.8 | 56.1 | 55.0 | 50.5 |
| 4/23/2013 | 4/23/2013 | 14 | 1 | 48.7 | 60.8 | 55.9 | 58.2 | 56.3 | 50.4 |
| 4/23/2013 | 4/23/2013 | 15 | 1 | 48.6 | 66.8 | 55.0 | 58.2 | 53.6 | 50.5 |
| 4/23/2013 | 4/23/2013 | 16 | 1 | 49.2 | 58.3 | 51.1 | 51.9 | 51.0 | 50.2 |
| 4/23/2013 | 4/23/2013 | 17 | 1 | 48.9 | 58.1 | 50.9 | 51.8 | 50.8 | 50.0 |
| 4/23/2013 | 4/23/2013 | 18 | 1 | 48.9 | 56.0 | 51.0 | 51.9 | 50.8 | 50.0 |
| 4/23/2013 | 4/23/2013 | 19 | 1 | 48.9 | 55.0 | 51.0 | 51.8 | 50.9 | 50.1 |
| 4/23/2013 | 4/23/2013 | 20 | 1 | 49.6 | 54.4 | 51.2 | 51.8 | 51.2 | 50.6 |
| 4/23/2013 | 4/23/2013 | 21 | 1 | 49.1 | 64.5 | 51.2 | 51.7 | 50.9 | 50.3 |
| 4/23/2013 | 4/23/2013 | 22 | 1 | 49.7 | 65.0 | 51.9 | 52.3 | 51.5 | 50.9 |
| 4/23/2013 | 4/23/2013 | 23 | 1 | 50.0 | 60.9 | 51.8 | 52.3 | 51.5 | 50.9 |

**Appendix C. dBA and One-third Octave Metrics for PAPA Noise Source Sites (cont.).**

Table 90. PAPA217 (Johan compressor station, 140 m ESE) dBA and one-third octave band metrics, April 23-24, 2013.

| Date Start | Date End | dBA/Freq | N. Hrs | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|---|
| 4/23/13 | 4/24/13 | dBA | 23 | 46.1 | 68.9 | 51.9 | 51.8 | 50.9 | 50.1 |
| 4/23/13 | 4/24/13 | 12.5 | 23 | 41.8 | 73.7 | 56.2 | 58.1 | 54.8 | 50.9 |
| 4/23/13 | 4/24/13 | 16 | 23 | 47.6 | 78.1 | 62.6 | 64.5 | 61.3 | 57.2 |
| 4/23/13 | 4/24/13 | 20 | 23 | 49.4 | 78.8 | 66.2 | 68.9 | 64.5 | 60.6 |
| 4/23/13 | 4/24/13 | 25 | 23 | 48.6 | 78.6 | 59.9 | 61.6 | 59.3 | 56.9 |
| 4/23/13 | 4/24/13 | 31.5 | 23 | 52.6 | 76.7 | 62.8 | 64.6 | 62.3 | 59.9 |
| 4/23/13 | 4/24/13 | 40 | 23 | 52.9 | 79.2 | 60.6 | 61.6 | 59.9 | 58.0 |
| 4/23/13 | 4/24/13 | 50 | 23 | 55.5 | 82.7 | 64.4 | 64.5 | 62.9 | 61.1 |
| 4/23/13 | 4/24/13 | 63 | 23 | 56.2 | 81.2 | 64.3 | 65.3 | 64.0 | 62.6 |
| 4/23/13 | 4/24/13 | 80 | 23 | 57.9 | 80.5 | 65.5 | 66.2 | 64.9 | 63.6 |
| 4/23/13 | 4/24/13 | 100 | 23 | 53.0 | 75.4 | 63.5 | 62.9 | 61.4 | 60.0 |
| 4/23/13 | 4/24/13 | 125 | 23 | 49.1 | 71.1 | 57.8 | 58.5 | 56.9 | 55.1 |
| 4/23/13 | 4/24/13 | 160 | 23 | 47.9 | 75.8 | 56.4 | 55.8 | 54.5 | 53.4 |
| 4/23/13 | 4/24/13 | 200 | 23 | 41.5 | 67.2 | 54.7 | 55.5 | 54.2 | 52.4 |
| 4/23/13 | 4/24/13 | 250 | 23 | 41.2 | 63.4 | 50.9 | 51.7 | 50.1 | 48.7 |
| 4/23/13 | 4/24/13 | 315 | 23 | 32.2 | 63.6 | 42.1 | 42.1 | 40.3 | 38.5 |
| 4/23/13 | 4/24/13 | 400 | 23 | 28.7 | 55.9 | 37.3 | 37.8 | 35.7 | 34.1 |
| 4/23/13 | 4/24/13 | 500 | 23 | 26.3 | 57.3 | 34.8 | 35.7 | 33.6 | 31.9 |
| 4/23/13 | 4/24/13 | 630 | 23 | 22.4 | 56.0 | 30.9 | 31.9 | 30.0 | 27.9 |
| 4/23/13 | 4/24/13 | 800 | 23 | 19.5 | 52.3 | 28.8 | 30.0 | 27.3 | 25.1 |
| 4/23/13 | 4/24/13 | 1000 | 23 | 19.7 | 55.9 | 30.6 | 32.1 | 29.4 | 27.0 |
| 4/23/13 | 4/24/13 | 1250 | 23 | 21.5 | 60.0 | 33.1 | 35.2 | 32.0 | 29.3 |
| 4/23/13 | 4/24/13 | 1600 | 23 | 22.8 | 60.9 | 36.0 | 38.5 | 34.9 | 31.8 |
| 4/23/13 | 4/24/13 | 2000 | 23 | 21.3 | 60.9 | 33.7 | 35.1 | 32.5 | 30.0 |
| 4/23/13 | 4/24/13 | 2500 | 23 | 22.2 | 57.0 | 33.2 | 34.4 | 32.4 | 30.0 |
| 4/23/13 | 4/24/13 | 3150 | 23 | 18.0 | 59.7 | 30.1 | 31.1 | 29.3 | 26.5 |
| 4/23/13 | 4/24/13 | 4000 | 23 | 14.7 | 52.9 | 26.2 | 27.3 | 25.5 | 23.1 |
| 4/23/13 | 4/24/13 | 5000 | 23 | 10.7 | 56.4 | 21.5 | 22.2 | 20.0 | 17.8 |
| 4/23/13 | 4/24/13 | 6300 | 23 | 6.8 | 55.7 | 16.7 | 15.2 | 13.6 | 11.6 |
| 4/23/13 | 4/24/13 | 8000 | 23 | 5.4 | 49.1 | 11.1 | 9.8 | 8.5 | 7.3 |
| 4/23/13 | 4/24/13 | 10000 | 23 | 5.2 | 42.8 | 7.7 | 6.9 | 6.3 | 5.9 |
| 4/23/13 | 4/24/13 | 12500 | 23 | 4.4 | 40.6 | 6.6 | 5.2 | 5.0 | 4.8 |
| 4/23/13 | 4/24/13 | 16000 | 23 | 2.3 | 33.9 | 4.1 | 3.0 | 2.9 | 2.7 |
| 4/23/13 | 4/24/13 | 20000 | 23 | -0.1 | 30.6 | 2.1 | 0.6 | 0.5 | 0.3 |

## Appendix D. Influence of Fleece Windscreen on Decibel Data.

In the PAPA area, high winds, animals, and human activity are common. In order to minimize the influence of wind on the decibel data and to protect the equipment, we used a second windscreen in addition to the standard 90 mm foam windscreen. The additional windscreen was made of thin fleece material placed over a 0.4 m (15 in) high and 0.3 m (12 in) wide wire cylindrical cage (Figures 7-8). This approach is similar to the dual-stage windscreen used in noise measurement systems in remote and windy areas of national parks (Miller et al. 1997, Lee et al. 2006).

In order to test the influence of the fleece windscreen on decibel data, we collected data simultaneously using two LD 831 sound level meters at the Big John lek from April 7-10, 2013. One system had the standard 90 mm foam windscreen only and the other system had the 90 mm foam windscreen plus the fleece and wire cage windscreen (Figures 7-8). We tested the influence of the additional windscreen on dBA and one-third octave band decibel data, both daily and for all days, and found the influence to be minimal.

For daily $L_{50}$ dBA levels, the mean difference was 0.0 dBA (min = -0.1, max = +0.2); for daily $L_{90}$ dBA levels, the mean difference was +0.1 dBA (min = +0.3; max = 0.0). For daily $L_{eq}$ levels, the mean difference was -1.5 dBA (min = -2.8; max = -0.1) (Table 92). Overall, for all days, $L_{eq}$ dBA was slightly higher for the system with the foam only windscreen, $L_{90}$ dBA was slightly higher for the system with the foam/fleece windscreen, and $L_{50}$ dBA was the same for both systems.

$L_{50}$ one-third octave band frequency levels were on average +0.1 dB different (min = -1.8; max = +2.1) between the two windscreens; $L_{90}$ levels were on average +0.3 dB different (min = -1.4; max = +2.5); and $L_{eq}$ levels were on average -1.6 dB different (min = -4.5; max = +0.9) (Tables 93-94; Figures 9-13). For all metrics, the largest differences were at low (<40 Hz) or high frequencies (>4000 Hz).

Normally, the addition of windscreen material over a microphone results in lower decibel levels at high frequencies. However, this comparison revealed that the addition of the fleece windscreen did not always result in lower levels for this system, and frequently this system had higher levels. These small differences in dBA levels, with each system occasionally higher or lower, suggest that differences in dBA and dB levels were likely due to localized effects related to wind through vegetation, the presence of insects or other acoustic phenomena. All of the dBA level differences and most of the dB level differences were within the precision limits of the instruments.

**Appendix D. Influence of Fleece Windscreen on Decibel Data (cont.).**

In addition to providing extra wind protection, the fleece cover also protected the 90 mm foam windscreen from disturbance by mammals in the area. In previous long-term measurements in remote locations, mammals such as deer, moose, bear, and small rodents frequently chewed on or removed the foam windscreen from the microphone, resulting in unusable decibel data. Using the fleece material and cylindrical cage over the microphone prevented damage to the microphones and foam windscreens due to animals. A third benefit of the fleece material was security. We used a camouflage colored fleece material that was similar to the sage land cover, and this made the acoustic systems harder to see. At several measurement locations, acoustic systems were near roads and human activity, and thus susceptible to disturbance or theft. The use of camouflage fleece material minimized the risk of this issue.



Figure 7. Windscreen made of fleece material placed over a 0.4 m (15 in) high and 0.3 m (12 in) wide wire cylindrical cage.

**Appendix D. Influence of Fleece Windscreen on Decibel Data (cont.).**



Figure 8. Data collection with LD 831 systems using two different types of windscreens, foam only and foam/fleece, both microphones 0.3 m high, 2.0 m apart.

**Appendix D. Influence of Fleece Windscreen on Decibel Data (cont.).**

Table 91. PAPA101 (foam only windscreen) and PAPA102 (foam/fleece windscreen) $L_{10}$, $L_{50}$, $L_{90}$, and $L_{eq}$ dBA metrics, April 7-10, 2013, 0000-2400.

| | Foam | Foam/Fleece | |
|---|---|---|---|
| L10 | PAPA101 | PAPA102 | Difference |
| 4/7/2013 | 25.3 | 25.3 | 0.0 |
| 4/8/2013 | 25.6 | 25.9 | 0.3 |
| 4/9/2013 | 25.3 | 24.3 | -1.0 |
| 4/10/2013 | 26.9 | 26.2 | -0.7 |
| Mean | 25.8 | 25.4 | |

| L50 | PAPA101 | PAPA102 | Difference |
|---|---|---|---|
| 4/7/2013 | 21.2 | 21.2 | 0.0 |
| 4/8/2013 | 21.9 | 22.1 | 0.2 |
| 4/9/2013 | 18.3 | 18.2 | -0.1 |
| 4/10/2013 | 21.0 | 20.9 | -0.1 |
| Mean | 20.6 | 20.6 | |

| L90 | PAPA101 | PAPA102 | Difference |
|---|---|---|---|
| 4/7/2013 | 19.0 | 19.1 | 0.1 |
| 4/8/2013 | 19.7 | 19.9 | 0.2 |
| 4/9/2013 | 16.1 | 16.4 | 0.3 |
| 4/10/2013 | 18.6 | 18.6 | 0.0 |
| Mean | 18.4 | 18.5 | |

| Leq | PAPA101 | PAPA102 | Difference |
|---|---|---|---|
| 4/7/2013 | 28.0 | 26.3 | -1.7 |
| 4/8/2013 | 35.0 | 32.2 | -2.8 |
| 4/9/2013 | 25.6 | 24.4 | -1.2 |
| 4/10/2013 | 31.0 | 30.9 | -0.1 |
| Mean | 29.9 | 28.5 | |

**Appendix D. Influence of Fleece Windscreen on Decibel Data (cont.).**

Table 92. PAPA101 (foam only windscreen), dBA and one-third octave band levels, April 7-10, 2013.

| Freq./dBA | NHours | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|
| dBA | 96 | 13.9 | 67.6 | 31.3 | 25.9 | 21.2 | 18.0 |
| 20 | 96 | 17.2 | 75.3 | 52.3 | 51.2 | 45.5 | 40.3 |
| 25 | 96 | 17.8 | 74.5 | 49.0 | 44.6 | 39.0 | 34.6 |
| 31.5 | 96 | 16.2 | 71.4 | 47.0 | 44.7 | 39.2 | 34.6 |
| 40 | 96 | 13.2 | 70.7 | 44.2 | 39.3 | 34.6 | 31.0 |
| 50 | 96 | 11.1 | 74.7 | 41.6 | 36.8 | 32.4 | 29.1 |
| 63 | 96 | 10.0 | 81.6 | 40.1 | 36.2 | 31.4 | 28.4 |
| 80 | 96 | 9.0 | 82.2 | 39.2 | 35.1 | 30.0 | 26.6 |
| 100 | 96 | 5.7 | 86.2 | 38.3 | 32.9 | 28.4 | 25.4 |
| 125 | 96 | 4.3 | 74.4 | 34.4 | 31.4 | 26.5 | 22.9 |
| 160 | 96 | 1.7 | 69.3 | 31.7 | 30.6 | 24.7 | 20.3 |
| 200 | 96 | -0.7 | 71.6 | 29.3 | 27.6 | 21.5 | 17.0 |
| 250 | 96 | -1.9 | 64.0 | 26.8 | 24.6 | 18.5 | 13.6 |
| 315 | 96 | -3.0 | 56.1 | 23.9 | 21.5 | 14.7 | 9.5 |
| 400 | 96 | -4.2 | 57.7 | 21.2 | 17.1 | 10.2 | 4.5 |
| 500 | 96 | -4.2 | 53.7 | 19.3 | 14.6 | 7.3 | 0.5 |
| 630 | 96 | -4.2 | 46.2 | 16.9 | 7.6 | 1.4 | -1.6 |
| 800 | 96 | -4.0 | 45.7 | 15.0 | 6.0 | -0.3 | -2.0 |
| 1000 | 96 | -3.3 | 41.4 | 14.6 | 5.5 | -0.6 | -1.7 |
| 1250 | 96 | -2.6 | 38.3 | 14.2 | 4.8 | -0.3 | -1.2 |
| 1600 | 96 | -1.7 | 38.5 | 14.1 | 3.6 | 0.2 | -0.5 |
| 2000 | 96 | -0.8 | 38.2 | 13.5 | 3.8 | 0.9 | 0.3 |
| 2500 | 96 | 0.2 | 40.5 | 12.0 | 3.9 | 1.6 | 1.2 |
| 3150 | 96 | 0.3 | 42.3 | 10.3 | 3.7 | 2.5 | 2.1 |
| 4000 | 96 | -0.2 | 44.3 | 9.9 | 4.2 | 3.4 | 3.1 |
| 5000 | 96 | -0.4 | 46.1 | 10.6 | 4.9 | 4.2 | 3.9 |
| 6300 | 96 | -0.7 | 45.7 | 10.8 | 5.5 | 5.0 | 4.7 |
| 8000 | 96 | -0.9 | 46.0 | 11.1 | 5.9 | 5.5 | 5.3 |
| 10000 | 96 | -0.7 | 45.6 | 11.0 | 6.1 | 5.7 | 5.4 |
| 12500 | 96 | -0.9 | 44.7 | 9.8 | 5.5 | 5.0 | 4.6 |
| 16000 | 96 | -1.1 | 44.8 | 8.2 | 4.1 | 3.1 | 2.6 |
| 20000 | 96 | -1.0 | 41.3 | 4.9 | 3.1 | 0.7 | 0.1 |

**Appendix D. Influence of Fleece Windscreen on Decibel Data (cont.).**

Table 93. PAPA102 (foam/fleece windscreen), dBA and one-third octave band levels, April 7-10, 2013.

| Freq./dBA | NHours | LMin | LMax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|
| dBA | 93 | 14.6 | 68.5 | 29.5 | 25.3 | 20.9 | 18.4 |
| 20 | 93 | 16.9 | 74.7 | 49.4 | 48.9 | 43.7 | 39.3 |
| 25 | 93 | 17.5 | 70.5 | 44.6 | 41.5 | 37.3 | 33.8 |
| 31.5 | 93 | 16.4 | 67.5 | 43.0 | 42.5 | 37.8 | 33.2 |
| 40 | 93 | 14.1 | 65.9 | 39.7 | 37.3 | 34.0 | 30.8 |
| 50 | 93 | 11.3 | 75.1 | 37.5 | 35.3 | 32.0 | 28.8 |
| 63 | 93 | 9.3 | 80.8 | 37.6 | 34.7 | 30.9 | 28.0 |
| 80 | 93 | 8.7 | 84.1 | 37.7 | 33.9 | 29.1 | 26.2 |
| 100 | 93 | 5.4 | 84.5 | 38.1 | 32.4 | 28.0 | 25.2 |
| 125 | 93 | 3.3 | 72.7 | 33.5 | 31.0 | 26.6 | 23.0 |
| 160 | 93 | 1.1 | 69.5 | 30.7 | 30.4 | 24.4 | 20.4 |
| 200 | 93 | -0.8 | 69.4 | 28.1 | 27.1 | 21.2 | 16.9 |
| 250 | 93 | -2.8 | 66.8 | 25.3 | 23.0 | 17.7 | 12.5 |
| 315 | 93 | -3.4 | 58.2 | 23.2 | 20.7 | 14.5 | 9.0 |
| 400 | 93 | -4.1 | 58.5 | 21.0 | 16.4 | 10.1 | 4.6 |
| 500 | 93 | -4.1 | 51.2 | 18.9 | 13.9 | 6.3 | 0.3 |
| 630 | 93 | -3.7 | 48.4 | 16.4 | 5.9 | 1.3 | -1.3 |
| 800 | 93 | -3.0 | 47.2 | 14.3 | 5.0 | 0.1 | -1.1 |
| 1000 | 93 | -2.3 | 43.3 | 14.1 | 5.0 | 0.5 | -0.6 |
| 1250 | 93 | -1.3 | 40.3 | 14.3 | 4.8 | 1.0 | 0.1 |
| 1600 | 93 | -0.4 | 37.8 | 15.0 | 4.1 | 1.7 | 0.9 |
| 2000 | 93 | 0.6 | 38.5 | 14.0 | 4.0 | 2.4 | 1.8 |
| 2500 | 93 | 1.5 | 39.6 | 12.6 | 4.3 | 3.1 | 2.6 |
| 3150 | 93 | 2.6 | 40.4 | 10.6 | 4.7 | 3.8 | 3.4 |
| 4000 | 93 | 0.6 | 42.4 | 9.1 | 5.2 | 4.5 | 4.1 |
| 5000 | 93 | 0.0 | 48.7 | 8.8 | 5.6 | 5.0 | 4.7 |
| 6300 | 93 | 0.0 | 42.6 | 8.2 | 5.7 | 5.3 | 5.1 |
| 8000 | 93 | -0.3 | 39.2 | 7.9 | 5.7 | 5.4 | 5.1 |
| 10000 | 93 | -0.5 | 38.4 | 7.2 | 5.5 | 5.2 | 4.9 |
| 12500 | 93 | -0.7 | 36.9 | 6.3 | 5.1 | 4.7 | 4.4 |
| 16000 | 93 | -0.5 | 34.1 | 5.5 | 4.5 | 3.9 | 3.6 |
| 20000 | 93 | -0.2 | 30.9 | 4.2 | 3.7 | 2.8 | 2.6 |

**Appendix D. Influence of Fleece Windscreen on Decibel Data (cont.).**

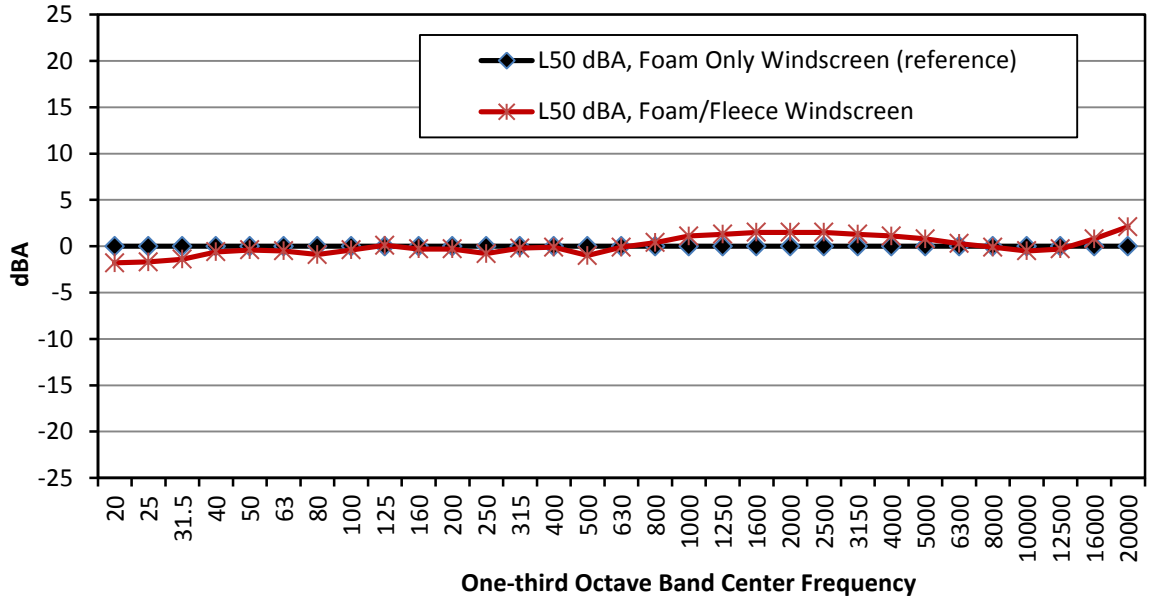



Figure 9. Difference in $L_{50}$ dB levels, 20-20,000 Hz, PAPA101, foam windscreen (reference) and PAPA102, foam/fleece windscreen, April 7-10, 2014 (93 hours).

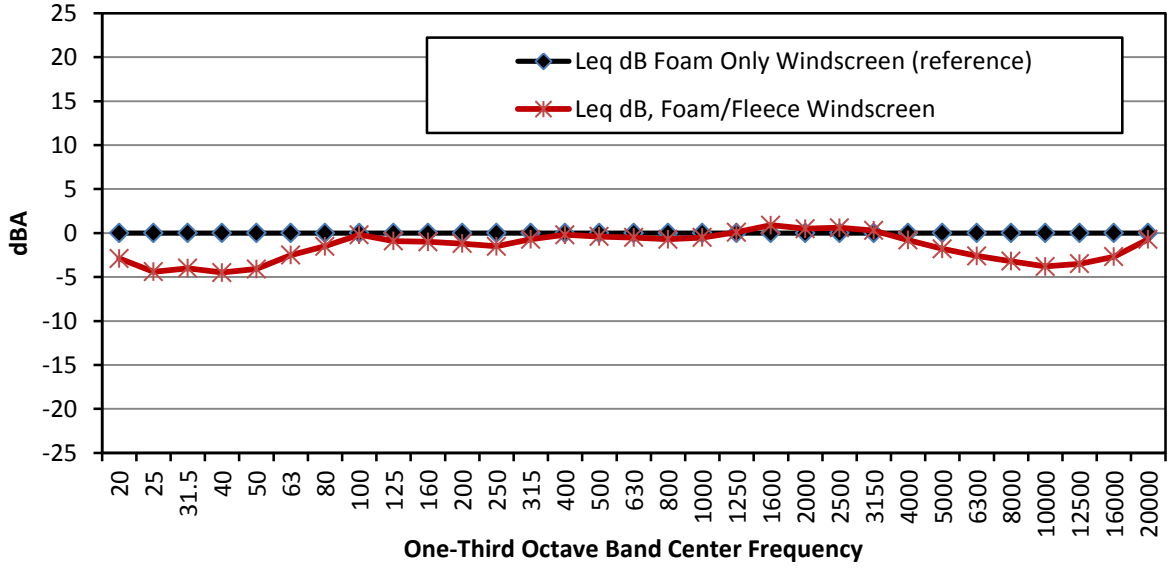



Figure 10. Difference in $L_{eq}$ dB levels, 20-20,000 Hz, PAPA101, foam windscreen (reference) and PAPA102, foam/fleece windscreen, April 7-10, 2014 (93 hours).

**Appendix E. Influence of Microphone Height, 1.5 m v. 0.3 m, on dB Data**.

In order to test the influence of microphone height on decibel data, we collected data simultaneously using two LD 831 sound level meters. One system had the microphone at 1.5 m and the other system had the microphone at 0.3 m. We compared the $L_{eq}$, $L_{10}$, $L_{50}$, $L_{90}$, $L_{min}$ and $L_{max}$ dBA metrics for 1 hour on March 13, 2013 (prior to deployment in Wyoming). All metrics of the 1.5 m microphone were slightly higher than metrics of the 0.3 m microphone (Table 92).

Table 94. Influence of microphone height (1.5 m versus 0.3 m) on dBA metrics, March 13, 2013, 1200 hour.

| | Mic at 1.5 m | Mic at 0.3 m | Difference. |
|---|---|---|---|
| Date | 20130313 | 20130313 | |
| Hour | 1200 | 1200 | |
| Leq | 41.0 | 38.4 | 2.6 |
| L10 | 37.5 | 36.0 | 1.5 |
| L50 | 29.3 | 28.8 | 0.5 |
| L90 | 26.4 | 25.3 | 1.1 |
| Lmin | 25.0 | 24.0 | 1.0 |
| Lmax | 73.7 | 68.9 | 4.8 |

## Appendix F. Acoustic Primer.

*Basic Acoustics*

Acoustics is the science of sound. *Sound* can be defined as a pressure variation in air or other media that is within the hearing range of a given species. This pressure variation has two components: amplitude and frequency.

*Frequency* is the number of times per second that the sine wave of sound repeats itself. It is expressed in cycles per second, or Hertz (Hz). The frequency of a sound determines the tone of a sound (e.g., most aircraft are low frequencies, and most bird calls are high frequencies). Different species of animals hear sounds over a wide range of frequencies. For humans with normal hearing, this range is 20 Hz to 20,000 Hz. Some animals hear better at low frequencies, others at very high frequencies. However, all animals can hear a wide range of frequencies, thus several sounds can be heard at the same time (NPS 2005).

*Amplitude* is the relative strength of sound waves, which we perceive as loudness or volume. Amplitude is measured in decibels (dB), which refer to the sound pressure level or intensity. The lower threshold of human hearing is 0 dB. Moderate levels of sound (a normal speaking voice, for example) are less than 60 dB. Decibels work on a logarithmic scale, so an increase of 10 dB causes a doubling of perceived loudness and represents a ten-fold increase in sound level (Crocker, 1997).

The acoustical environment is made up of many sounds, and the way animals experience the acoustical environment depends on interactions between the *frequencies* and *amplitudes* of all the sounds. Sound levels are often adjusted (*weighted*) to match the hearing abilities of a given animal. Humans with normal hearing can hear frequencies between 20 Hz and 20,000 Hz, and amplitude as low as 0 dB at 1,000 Hz. Sound levels adjusted for human hearing are expressed as dBA. In Figure 14, sound level thresholds by frequency for humans and some bird species are shown (Fay 1988). We do not have such data for Greater Sage-grouse, but it is likely that thresholds by frequency are similar to other birds.

**Appendix F. Acoustic Primer (cont.).**

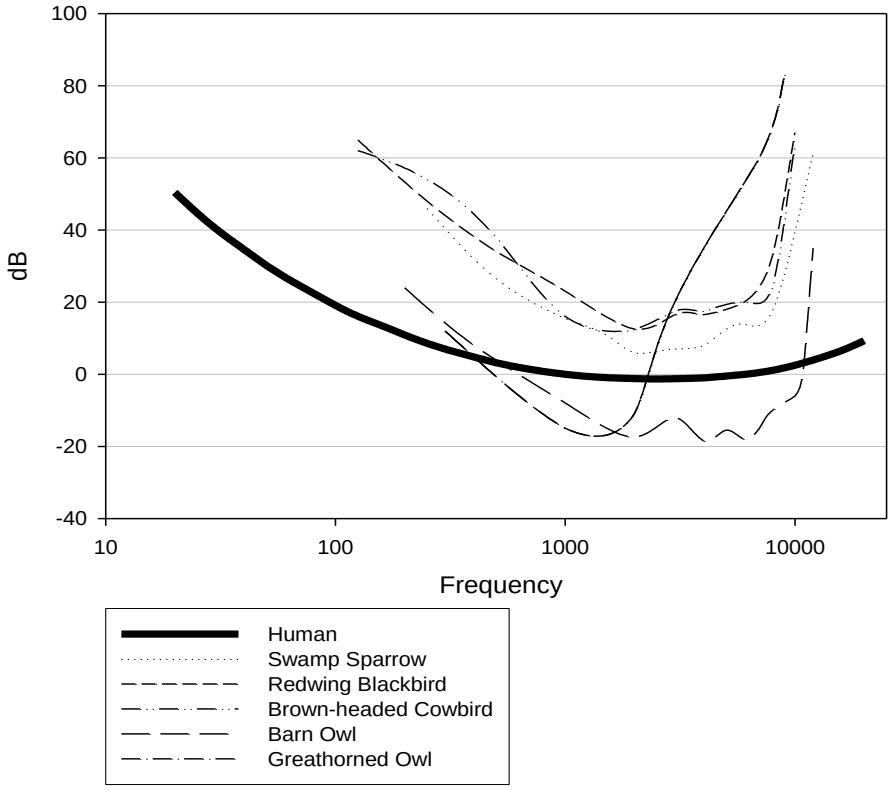



Figure 11. Sound level thresholds by frequency in hearing of humans and bird species.

*Visualizing Sounds*

Two common methods to visual acoustic data are shown in Figures 15-17. All figures are from recordings at PAPA017 (Oil Road Fork lek). In Figure 15, a 15-second segment of mechanical, Greater Sage-grouse, and coyote sounds is shown. This is called a "spectrogram." The spectrogram plots time along the x-axis and frequency along the y-axis. In this example, only frequencies between 20-5000 Hz are shown. Mechanical sounds are highest at the lower frequencies (<100 Hz), Greater Sage-grouse sounds are highest at frequencies <500 Hz, and coyote sounds dominate at 600 Hz and 1300 Hz. While the Greater Sage-grouse sounds are spread over several frequencies, the coyote sounds are specific to a few frequencies. In Figure 16, a 1-second snapshot of 1/3 octave band data (A-weighted) is shown, with the three sound sources visible at about the same frequencies as in Figure 15 but without as much detail. In this view of a 1-second snapshot, frequency is plotted along the x-axis and amplitude (loudness) is plotted along the y-axis. As in Figure 15, only frequencies between 20-5000 Hz are shown. A more detailed 1-second snapshot is shown in Figure 17. This view shows a narrower band frequency analysis, with finer detail for each frequency. This snapshot corresponds to the 15-second period in Figure 15, with mechanical sounds at about 70 Hz, Greater Sage-grouse sounds at 300-500 Hz, and coyote sounds at about 600 Hz and 1300 Hz.

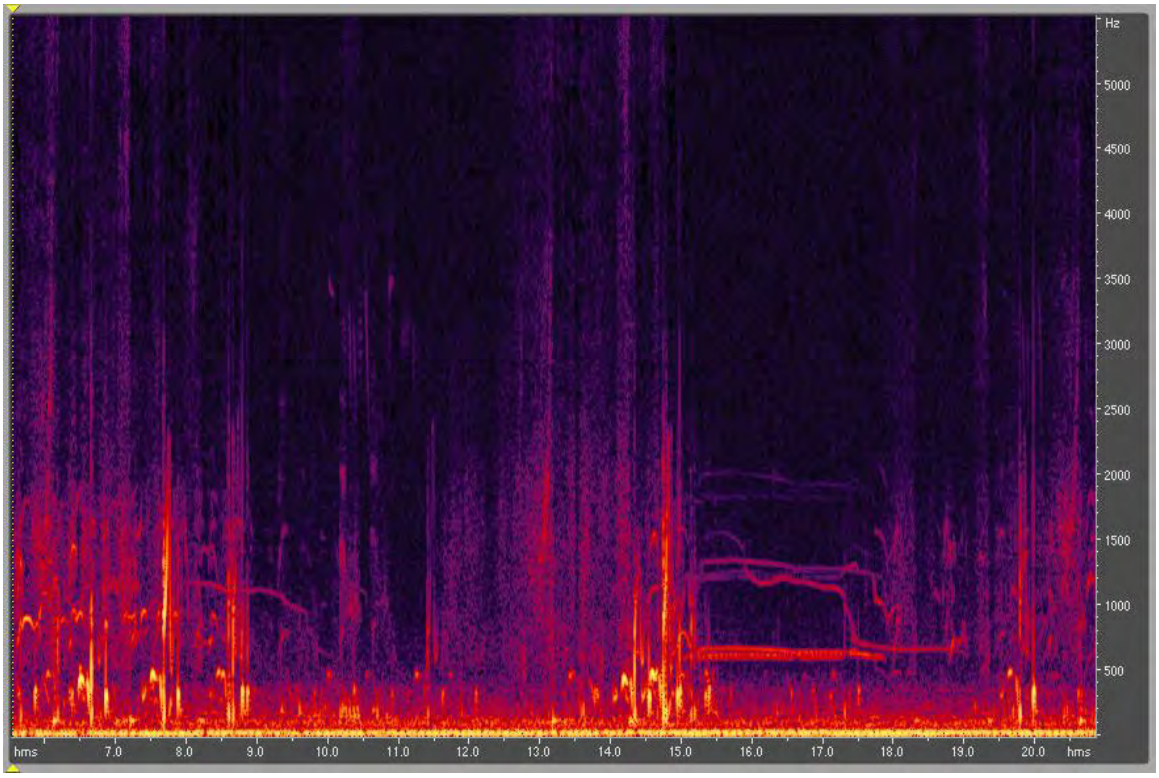



Figure 12. Spectrogram of sounds at PAPA017 (Oil Road Fork lek), with Greater Sage-grouse sounds (20-5,000 Hz), coyote sounds (500-2,000 Hz), and mechanical sounds (<500 Hz).

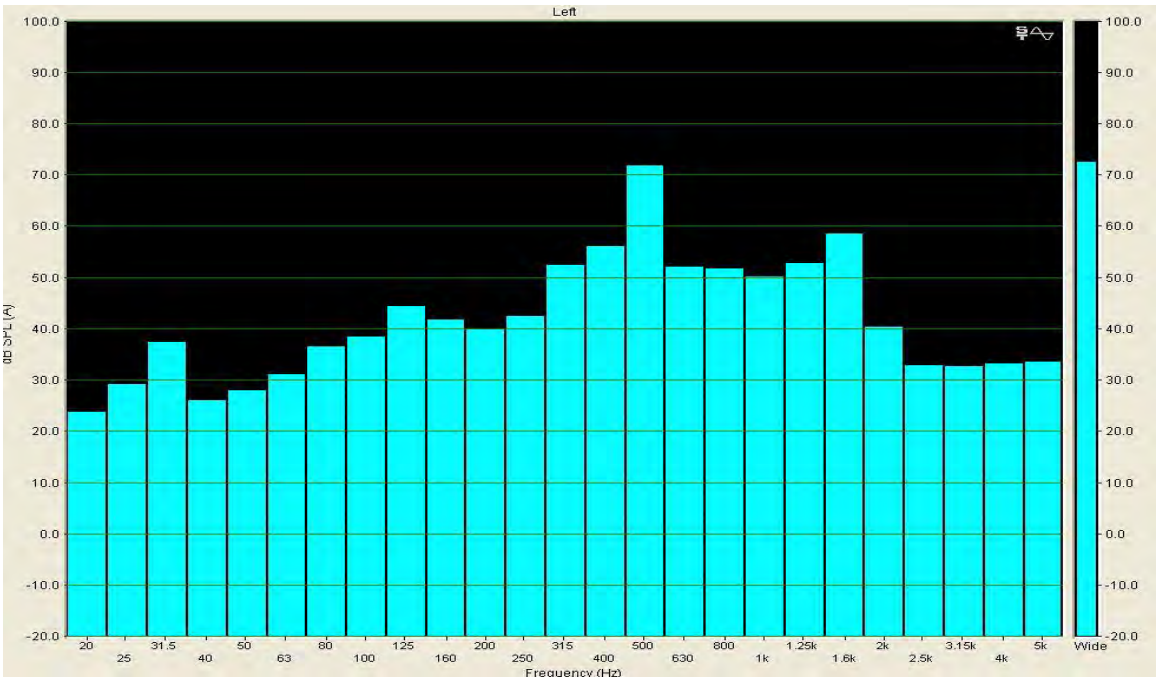



Figure 13. 1-second snapshot sounds at PAPA017 (Oil Road Fork lek), with mechanical sounds, Greater Sage-grouse sounds, and coyote sounds, but with less detail than narrow band analysis.

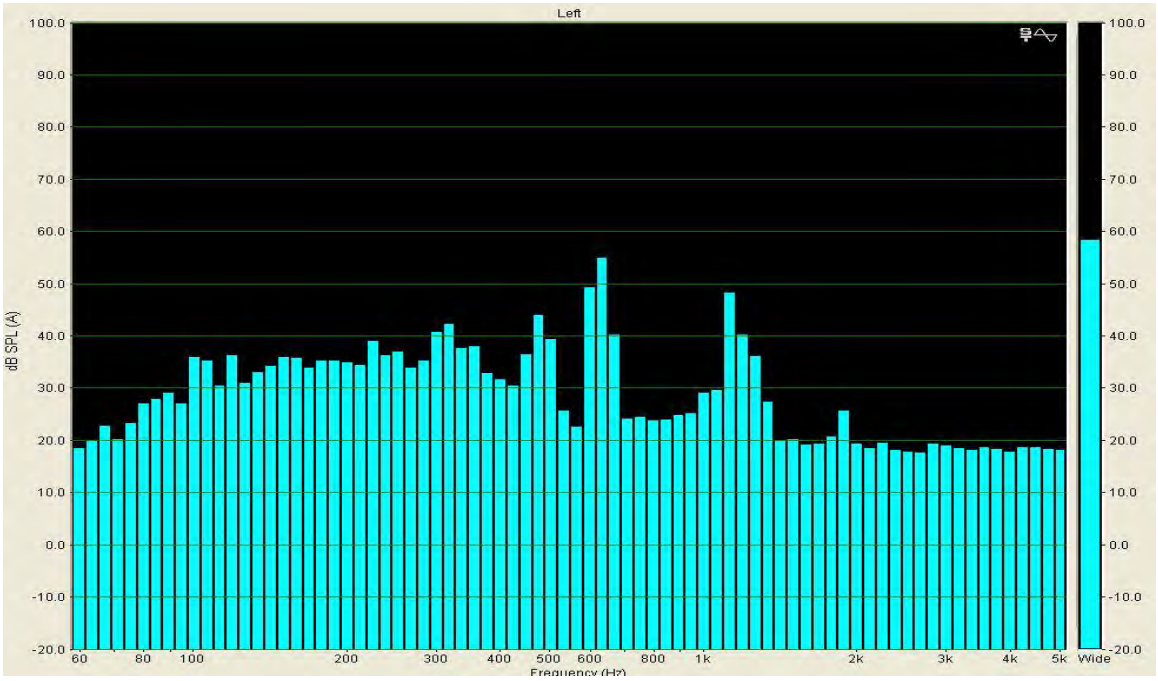



Figure 14. 1-second snapshot of sounds at PAPA017. This view shows a narrower band frequency analysis, with finer detail for each frequency. Mechanical sounds at about 70 Hz, Greater Sage-grouse sounds at 300-500 Hz, and coyote sounds at about 600 Hz and 1300 Hz.

## Appendix G. Equipment component list, serial number, and calibration date.

Table 95. Equipment component list, serial number, and calibration date.

| SLM LD831 Serial Num. | Calibration Date | PRM831 Serial Num. | Calibration Date | MIC 377B20 Serial Num. | Calibration Date |
|---|---|---|---|---|---|
| 2201 | 20130308 | 12174 | 20130122 | 135422 | 20130122 |
| 2258 | 20130109 | 19105 | 20120820 | 131849 | 20120820 |
| 2544 | 20130321 | 23771 | 20130212 | 118070 | 20130212 |
| 2573 | 20120720 | 19107 | 20130122 | 135552 | 20130122 |
| 2661 | 20121128 | 19134 | 20120122 | 135427 | 20130122 |
| 3140 | 20130118 | 23868 | 20110922 | 111498 | 20110922 |
| 1304 | 20110922 | 0474 | 20110922 | 112333 | 20110922 |
| 1308 | 20110922 | 0476 | 20110922 | 111473 | 20110922 |
| 1311 | 20110922 | 0473 | 20110922 | 111471 | 20110922 |

| Calibrators | SN | Calibration Date |
|---|---|---|
| B&K 4231 | 2094637 | 20100211 |
| B&K 4231 | 2094432 | 20100720 |

# Sound Levels at Greater Sage-grouse Leks in the Pinedale Anticline Project Area, WY, April 2013-2014

## Dec. 31, 2014

**Prepared by:**
Skip Ambrose[a]
Chris Florian[a]
John MacDonald, PE[b]

[a]Sandhill Company
HC 64 Box 2205
393 Castle Creek Lane
Castle Valley, UT 84532
Email: skipambrose@frontiernet.net
Office: 435-259-0401
Cell: 435-220-0129

[b]3142 Ash Park Loop
Winter Park, FL 32792

**Sound Levels at Greater Sage-grouse Leks, Pinedale Anticline Project Area, Wyoming, April 2013**


**Executive Summary**

Greater sage-grouse (*Centrocercus urophasianus*) use elaborate audio and visual display behaviors to attract and select mates, and depend on audio communication between females and chicks during brood rearing. A potential threat to greater sage-grouse is anthropogenic noise associated with human activity, including noise from oil and gas development and production. Several greater sage-grouse leks occur in and around the Pinedale Anticline Project Area (PAPA), a large natural gas development area south of Pinedale, WY.

The Bureau of Land Management's Record of Decision specified sound level thresholds above baseline levels that should not be exceeded by industry. Specific changes requiring mitigation are described as follows: "Decibel levels at the lek more than 10 dBA above baseline measured from the edge of the lek." The ROD used 39 dBA as a baseline ambient based on an EPA study that measured sound levels in a rural farming area in California in 1971.

The objective of this project was to monitor sound levels at 19 greater sage-grouse leks in the PAPA area south of Pinedale, WY.

*Results*

Acoustic data were collected at 19 greater sage-grouse leks in the PAPA in April 2013 and again in 2014. A total of 2087 hours of acoustic data were collected (999 hours 2013 and 1088 in 2014), for an average of 52.5 hours at each lek in 2013 and 57.3 hours at each lek in 2014.

$L_{50}$ dBA at leks in the PAPA ranged from 24.0 dBA to 36.9 dBA for all hours (0000-2400) and from 16.0 dBA to 38.5 dBA for hours important to lek behavior (1800-0800). There was little difference in sound levels at specific leks in 2013 and 2014 except in situations when the type of gas field activity at the closest pad changed significantly. Sound levels at leks were highly correlated with the distance to the nearest pad with gas field activity.

Of the 2087 hours measured at the PAPA leks in 2013 and 2014, no hours exceeded 49 dBA (39 + 10 = 49 dBA). However, results of recent acoustic studies in Wyoming demonstrate that 39 dBA is not an accurate baseline ambient sound level in undeveloped sage habitats of Wyoming.

**Table of Contents**

**Executive Summary** ..... 2

**Table of Contents** ..... 3

**List of Tables** ..... 4

**List of Figures** ..... 4

**Introduction** ..... 5

**Objective** ..... 5

**Study Area** ..... 5

**Methods** ..... 5

*Definitions* ..... *5*

*Measurement Protocol* ..... *7*

*Instrumentation* ..... *8*

*Data Analysis* ..... *10*

*Measurement Locations* ..... *11*

*Measurement Schedule* ..... *11*

**Results** ..... 12

*Data Collection* ..... *12*

*Sound Levels* ..... *12*

**Discussion** ..... 15

*Sound Levels at PAPA Leks, 2013 and 2014* ..... *15*

*Sound Levels and Distance to Pad* ..... *15*

*Hours Exceeding Baseline Ambient + 10 dBA* ..... *17*

**Acknowledgements** ..... 17

**Literature Cited** ..... 18

**Appendix A. Definitions of Common Acoustic Terms** ..... 20

**Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013** ..... 22

**Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014** ..... 34

**Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013** ..... 46

**Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014** ..... 62

**Appendix F. Credentials of Authors** ..... 78

## List of Tables

Table 1. Measurement site number, lek name, date-time start, date-time end, and number of hours, PAPA, April 2013 and 2014. ..... 12
Table 2. $L_{50}$ dBA at 19 PAPA leks, April 2013 and 2014, for three time periods (0000-2400, 0800-1800, and 1800-0800). ..... 13

## List of Figures

Figure 1. PAPA greater sage-grouse noise monitoring project area and lek complexes. ... 6
Figure 2. Typical equipment deployment near lek, showing case (sound level meter, recorder, and battery) and microphone with foam windscreen and bird spike at 0.3 m above ground. ..... 9
Figure 3. Typical equipment deployment near lek..... 10
Figure 4. $L_{min}$, $L_{max}$, and $L_{50}$, PAPA001 (Big Fred Lek, close to pad), April 2013. ..... 14
Figure 5. $L_{min}$, $L_{max}$, and $L_{50}$, PAPA015 (Cat Lek, far from pad), April 2013. ..... 14
Figure 6. $L_{50}$ dBA at leks relative to distance to pad with some type of gas field activity, PAPA, 2013. ..... 16
Figure 7. $L_{50}$ dBA at leks relative to distance to pad with some type of gas field activity, PAPA, 2014. ..... 16

## Introduction

Greater sage-grouse (*Centrocercus urophasianus*) use elaborate audio and visual display behaviors to attract and select mates, and depend on audio communication between females and chicks during brood rearing. A potential threat to greater sage-grouse is anthropogenic noise associated with human activity, including noise from oil and gas development and production (Holloran 2005, BLM 2008, Patricelli et al. 2013).

The Record of Decision (ROD) (BLM 2008) specified noise thresholds above baseline levels that should not be exceeded by industry. Specific changes requiring mitigation are described as follows: "Decibel levels at the lek more than 10 dBA above baseline measured from the edge of the lek" (BLM 2008)." The ROD also specifies concurrent declines in grouse numbers, but that aspect was not part of this project. The ROD used 39 dBA as a baseline ambient based on an EPA 1971 study that measured sound levels in a rural farming area in California.

## Objective

The objective of this project was to measure and document sound levels at 19 leks in the Pinedale Anticline Project Area (PAPA).

## Study Area

The study area was south of Pinedale, WY, in the Pinedale Anticline Project Area (Figure 1). The 19 leks studied were in the Mesa, Duke's Triangle, and Yellowpoint complexes.

## Methods

*Definitions*

The following are definitions of the primary acoustic terms used in this report. Additional definitions are provided in Appendix D.

*A-Weighting (dBA)*: A-weighting is used to account for differences in human hearing sensitivity as a function of frequency. A-weighting de-emphasizes the high (6.3 kHz and above) and low (below 1 kHz) frequencies, and emphasizes the frequencies between 1 kHz and 6.3 kHz, in an effort to simulate the relative response of human hearing.

*Decibel (dB)*: A logarithmic measure commonly used in the measurement of sound. The decibel provides the possibility of representing a large span of signal levels in a simple manner as opposed to using the basic pressure unit Pascal. The difference between the sound pressure of silence versus a loud sound is a factor of 1,000,000:1 or more, therefore it is less cumbersome to use a small range of equivalent values: 0 to 130 decibels.

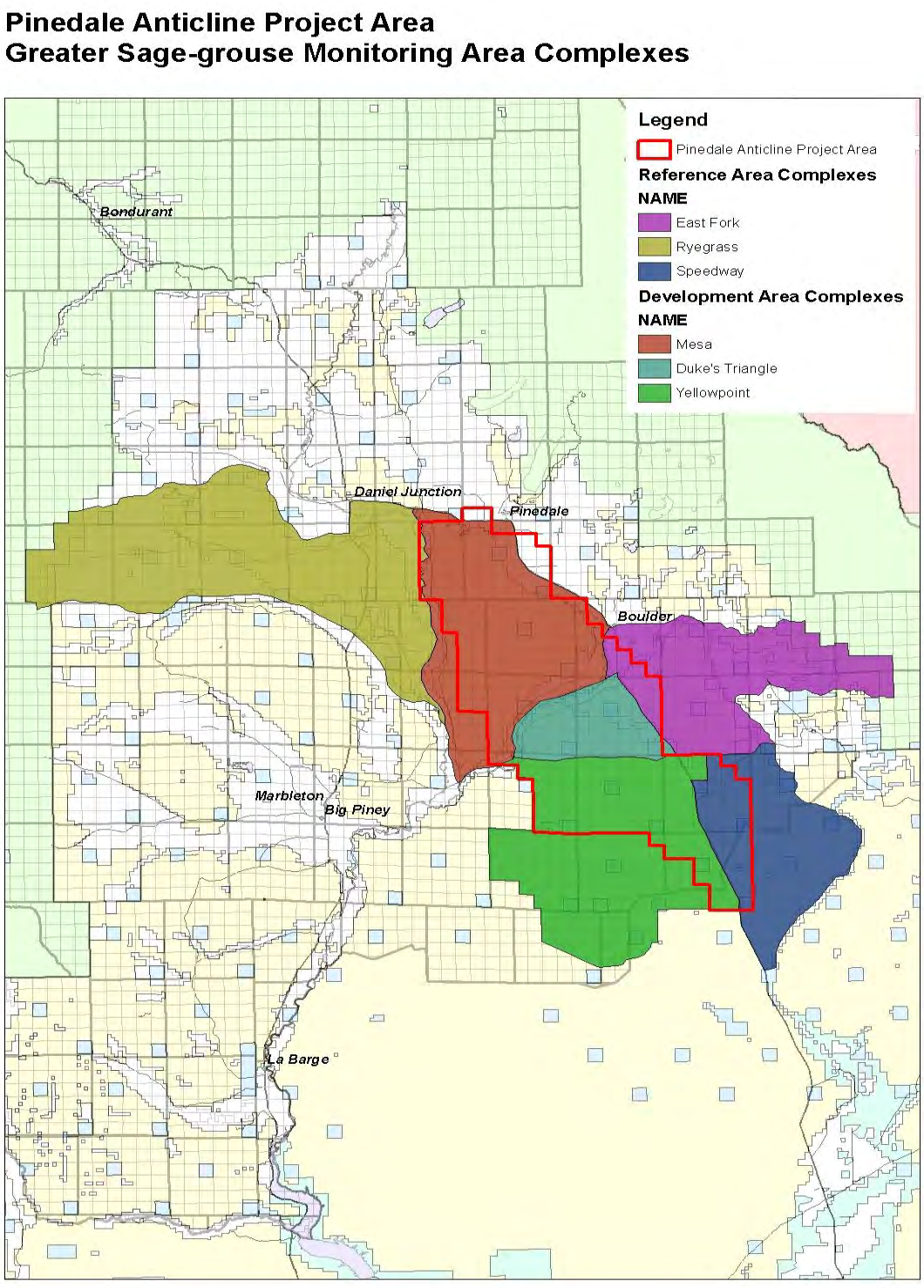



Figure 1. PAPA greater sage-grouse noise monitoring project area and lek complexes.

*$L_{eq}$ (*Equivalent Sound Level): The logarithmic average (i.e., on an energy basis) of sound pressure levels over a specific time period. "Energy averaged" sound levels are logarithmic values, and as such are generally much higher than arithmetic averages. $L_{eq}$ values are typically calculated for a specific time period (1-hour is commonly used). $L_{eq}$ values are computed from all of the 1-second $L_{eq}$ values for the specific time period. $L_{eq}$ must be used carefully in quantifying natural ambient sound levels because occasional loud sound levels may heavily influence (increase) the $L_{eq}$ value, even though sound levels for that period of time are typically lower.

*$L_x$ (Exceedance Percentile)*: This metric is the sound pressure level (L), in decibels, exceeded *x* percent of the time for the specified measurement period. $L_{50}$ is the sound pressure level exceeded 50 percent of the time ($L_{50}$ is the same as the median).

*Noise Floor*: The lower measurement limit of a sound level meter, also referred to as self-noise or electrical noise of all components of a sound level meter (meter, microphone, and preamplifier).

*Sound Level, Baseline Ambient*: The sound level in a given location including all sounds of nature but absent most human-caused sounds. $L_{90}$ is the sound pressure level exceeded 90 percent of the time, and is commonly used to establish the baseline ambient sound level.

*Sound Level, Existing Ambient*: The sound level of all sounds in a given area, including all natural sounds as well as all mechanical, electrical and other human-caused sounds. The existing ambient sound level is generally characterized by the $L_{50}$ exceedance level (i.e., the median).

*Measurement Protocol*

We followed "Procedures for Outdoor Measurement of Sound Pressure Level" (ANSI 1994) and acoustic measurement protocols developed for the Pinedale Anticline Project Office by Blickley and Patricelli (2012), "Noise monitoring recommendations for Greater Sage Grouse habitat in Wyoming." ANSI procedures recommend microphone heights of 1.2 m to 1.8 m but these were developed to assess noise impacts to humans. ANSI standards also state: "Other heights may be used if they prove to be more practicable or if they are specified in other pertinent standards" (ANSI 1994, Section 7.3.2.4). Several authors recommend that in wildlife acoustic studies, microphones be placed such that sound level measurements accurately reflect sound stimulus to which the target animal is exposed (Pater et al. 2009; Grubb et al. 1998, Delaney et al. 2009, Delaney et al. 2011; Blickley and Patricelli 2013). The approximate ear height of greater sage-grouse is 0.3 m (12"); therefore, microphones were placed 0.3 m above the ground. Standardizing microphone height at 0.3 m for acoustic studies relative to greater sage-grouse is consistent with flexibility and guidance provided by ANSI (1994, Section 7.3.2.4).

Wind can significantly influence sound level measurements in several ways. The sounds of wind through vegetation and rustling leaves are true sounds of nature and should be included in all analysis. The sound of wind against the foam windscreen is not a legitimate environmental sound, nor is the pressure change of wind across the diaphragm of the microphone. These wind-induced equipment sounds can significantly, and falsely, elevate sound levels. ANSI (S12.18-1994) standards suggest two methods to address wind influence on sound level data. Method 1 "General Method for Routine Measurements" requires omitting from analysis 1-second dB data when wind speed exceeds 5 m/s (11 mph). Method 2 "Precision Method for Accurate Measurements" requires omitting from analysis 1-second dB data when wind speed exceeds 3 m/s (6.7 mph). In separate Wyoming studies in 2013 and 2014, we collected wind speed data and sound level data at both 0.3 m and 1.5 m above ground. We found that wind speed very rarely exceeded 5 m/s or 3 m/s at our microphone height of 0.3 m. Wind commonly exceeded 5 m/s at 1.5 m at several locations (Ambrose, unpublished data). We calculated metrics with all seconds as well as with seconds that only included acoustic data during wind speed conditions less than 5 m/s. There was no difference in any metric due to the extreme rarity of elevated wind speed at 0.3 m; therefore we included all data in the analysis regardless of wind speed. Sound levels were often elevated due to wind sounds through vegetation, but these were actual environmental sounds and part of the acoustic environment of greater sage-grouse. We did not place anemometers at 1.5 m in the vicinity of the lek due to concern for potential negative impact on grouse presence and behavior at leks.

*Instrumentation*

We used two different sound level meters, a Larson-Davis 831 (4 each) and a Cesva SC310 (2 each). The Larson-Davis 831 meters used PCB 377B20 microphones, Larson-Davis PRM831 preamplifiers, and Larson-Davis EPS2106 Environmental Shrouds (foam windscreen and bird spike). The Cesva SC310 meters used Cesva PA13 preamplifiers and microphones. All acoustic equipment used for data collection (sound level meters, microphones, and preamplifiers) met or exceeded ANSI S1.4-1983 Type 1 standards. One-third octave band analyzers and dBA analyzers met ANSI S1.11-2004 and ANSI S1.42-2001, respectively. All acoustic equipment and field calibrators were calibrated to meet ANSI S1.40-2006 prior to deployment. All systems and calibrators were factory calibrated as recommended by the manufacturer, and all systems were field calibrated at the beginning and end of each measurement period at each location using a field calibrator that met ANSI S1.40-1984 standards. All system components (SLM, digital recorder, and anemometer) were synchronized with GPS time, and differences at the end of the measurement period noted. We used a Bruel and Kjaer (B&K) Acoustic Calibrator Type 4231 for field calibration.

We also collected continuous digital recordings at all measurement locations. We used Roland R05 digital recorders, and used the microphone output from the sound level meters for input to the R05 recorder. These recordings were used to review unusual sound events and to determine sound sources and the percent time that various sound sources were audible.

Sound level meters were set to collect 1-second dBA, dBF, and dBC, as well as unweighted one-third octave band data, 12.5-20,000 Hz. We expected sound levels at some locations to be very low (<15 dBA), so sound level meters were set to "low-range" with a gain of +20 dB. These settings ensured meters would collect data at the lowest measurement limit for these systems.

Figures 2 and 3 show typical deployment, with equipment case (sound level meter, recorder, and battery) and microphone with foam wind screen and bird spike.



Figure 2. Typical equipment deployment near lek, showing case (sound level meter, recorder, and battery) and microphone with foam windscreen and bird spike at 0.3 m above ground.



Figure 3. Typical equipment deployment near lek.

*Data Analysis*

In acoustic studies, it is common to report hourly $L_{min}$, $L_{max}$, $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$ metrics. Two different methods have generally been used to compute hourly metrics. The first is referred to as the "unpooled" approach, and the second as the "pooled" approach. Both approaches report hourly statistics, but the computational methods differ. The "unpooled" approach computes metrics for each individual hour, and summary metrics for a given hour are the medians of all the hourly metrics for that hour. The "pooled" approach combines all 1-second data for a given hour (such as all 0800 hours) into a single data set, and averages, medians, variances, etc., are computed from the pooled data. Prior studies have shown that results for pooled analyses are generally more conservative (i.e., lower) than results for unpooled analysis (Plotkin 2002). However, many management decisions are based on specific periods of the day, and analyzing data by hour helps to ensure hour-to-hour and day-to-day variation is addressed. In the case of greater sage-grouse, for example, "lekking" hours often receive special consideration.

We used the unpooled approach and analyzed sound level data as follows. For every hour (3600 seconds of data), $L_{min}$, $L_{max}$, $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$ were calculated. $L_{min}$ and $L_{max}$ were the minimum and maximum levels for that hour. $L_{eq}$ was the energy average (a logarithmic average) of that hour. $L_{10}$, $L_{50}$, and $L_{90}$ were levels exceeded 10%, 50%, and 90% of the time during that hour. All of our data sets were for multi-day periods, and summary hourly metrics for each site were calculated as follows. $L_{min}$ and $L_{max}$ were the minimum and maximum levels of all 0800 hours, all 0900 hours, all 1000 hours, etc., during the measurement period. Summary hourly and summary site metrics ($L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$) for each hour of day (0800, 0900, 1000, etc.), were calculated using the median $L_{eq}$, $L_{10}$, $L_{50}$, and $L_{90}$ of all 0800 hours, all 0900 hours, all 1000 hours, etc. The

computation of dBA metrics included all data points regardless of wind speed due to the extreme rarity of wind speeds >5 m/s at 0.3 m (<0.02% of all seconds).

For each site, summary metrics for three time periods were calculated, all hours (0000-2400), daytime hours (0800-1800), and nighttime hours (1800-0800). The time period 1800-0800 is specified in the Wyoming Governor's Executive Order 2011-5 relative to greater sage-grouse and noise.

We compared sound levels at leks relative to distance to the closest pad in the PAPA. We considered only those pads with some type of current gas field activity. Such activities included drilling, assembly/disassembly of drill rig, compressor station, central gathering facility, well head and pump facilities, and injection wells (both alone and in association with well pump facilities. Some pads had off-site electricity, while others relied on on-site generators for power. Sound levels for each gas field activity varied. In addition to different types of activities at pads (and resulting different sound levels), attenuation factors varied at each lek (such factors include terrain, land cover, wind speed and direction, and meteorological conditions). Although activity type, distance, and attenuation factors varied at each lek and pad, sound level data collected at each lek represented actual acoustic conditions experienced by greater sage-grouse at that lek.

*Measurement Locations*

We collected acoustic data at 19 greater sage-grouse leks in the PAPA in April 2013 and 2014 (Table 1). All of the locations were in the Mesa, Duke's Triangle, and Yellowpoint complexes. For those leks where grouse had not been observed in recent years, we placed the sound level meters within or at the perimeter of the lek as defined by WGFD. For those leks where greater sage-grouse had been observed in recent years, we placed the sound level meters >250 m from the edge of the lek to ensure that grouse display sounds did not have a significant influence on dB data. In situations where the equipment was some distance from the lek, we placed the equipment such that the distance between the acoustic equipment and the primary gas field sound source was the same as the distance from the center of the lek and the primary sound source. Exact measurement locations are not provided in this report due to security concerns regarding lek locations. Map datum NAD83 was used for this project.

*Measurement Schedule*

All measurements were made in April 2013 and April 2014, the primary lekking period for greater sage-grouse in the PAPA area. Our goal was to collect a minimum of 48 hours at each lek in each year in order to account for variability in sound levels due to natural causes (meteorological conditions, birds singing near the equipment, etc.). Very short measurement periods of only a few hours could significantly over- or under-estimate actual long-term sound levels.

## Results

*Data Collection*

Acoustic data were collected at 19 greater sage-grouse leks in the PAPA in April 2013 and 2014. A total of 2087 hours of acoustic data were collected (999 hours 2013 and 1088 in 2014) (Table 1). Mean number of hours at each lek was 53 hours in 2013 and 57 hours in 2014.

*Sound Levels*

$L_{50}$ dBA values at leks in the PAPA ranged from 24.0 dBA to 36.9 dBA for all hours (0000-2400), and from 16.0 dBA to 38.5 dBA for nighttime hours (1800-0800) in 2013 and 2014. In general, sound levels at leks varied according to the distance and type of gas field activity. We provide examples of acoustic metrics ($L_{min}$, $L_{max}$, and $L_{50}$) at two leks that were different distances from pads in Figures 4 and 5. On lek (Big Fred, PAPA001) was 720 m (2360 ft) from a pad (with drill rig), and the other lek (Cat, PAPA015) was 3080 m (10,110 ft) from a pad (with well heads and pumps).

$L_{50}$ dBA site summary metrics for three time periods (0000-2400, 0800-1800, and 1800-0800) for PAPA leks, April 2013 and 2014, are shown in Table 2. Hourly and summary dBA metrics and one-third octave band metrics for each lek for 2013 and 2014 year are presented in Appendices A, B, C, and D. At three locations, PAPA001, PAPA002, and PAPA017, activities at the nearest pads changed significantly from 2013 to 2014. As a results, sound levels at these locations changed significantly from 2013 to 2014.

Table 1. Measurement site number, lek name, date-time start, date-time end, and number of hours, PAPA, April 2013 and 2014.

| Site Num. | Lek Name | Date_Time Start | Date_Time End | Hrs | | Date_Time Start | Date_Time End | Hrs |
|---|---|---|---|---|---|---|---|---|
| PAPA001 | Big Fred | 20130405_1450 | 20130407_1520 | 47 | | 20140412_1200 | 20140414_0820 | 43 |
| PAPA002 | Little Fred | 20130405_1150 | 20130407_1235 | 47 | | 20140412_1040 | 20140414_0935 | 45 |
| PAPA003 | Lower Sand Springs | 20130405_1305 | 20130407_1645 | 50 | | 20140416_1200 | 20140418_1355 | 48 |
| PAPA004 | Two Buttes | 20130418_0910 | 20120421_1345 | 75 | | 20140415_1010 | 20140417_0905 | 46 |
| PAPA005 | Mesa Spring | 20130418_0950 | 20130421_1410 | 75 | | 20140417_0955 | 20140420_0715 | 68 |
| PAPA006 | Lovatt Draw Res. | 20130418_1025 | 20130421_1433 | 59 | | 20140414_1150 | 20140416_0755 | 43 |
| PAPA007 | Shelter Cabin Res. | 20130410_0855 | 20130412_1145 | 49 | | 20140414_1530 | 20140416_1110 | 43 |
| PAPA008 | The Rocks | 20130410_1015 | 20130412_1330 | 50 | | 20140424_1625 | 20140430_1520 | 98 |
| PAPA009 | South Rocks | 20130410_1115 | 20130412_1404 | 50 | | 20140420_1040 | 20140424_1525 | 61 |
| PAPA010 | Stud Horse Butte | 20130410_1200 | 20130412_1434 | 49 | | 20140420_1108 | 20140424_1540 | 99 |
| PAPA011 | Little Saddle | 20130412_0910 | 20130414_0910 | 47 | | 20140410_1305 | 20140412_0920 | 18 |
| PAPA012 | Alkali Draw | 20130412_1100 | 20130414_1020 | 46 | | 20140411_1605 | 20140414_1350 | 68 |
| PAPA013 | Sand Draw | 20130412_1245 | 20130414_1135 | 46 | | 20140411_1715 | 20140414_1445 | 68 |
| PAPA014 | Lovatt West | 20130418_1105 | 20130421_1456 | 75 | | 20140414_1230 | 20140416_0820 | 43 |
| PAPA015 | Cat | 20130421_1100 | 20130423_1300 | 49 | | 20140410_1145 | 20140412_0820 | 44 |
| PAPA016 | Tyler Draw North | 20130415_1000 | 20130417_0920 | 46 | | 20140424_1815 | 20140501_0914 | 108 |
| PAPA017 | Oil Fork Road | 20130415_1100 | 20130417_1005 | 46 | | 20140416_0905 | 20140418_1605 | 54 |
| PAPA018 | Mesa Road 3 | 20130415_1145 | 20130417_1115 | 47 | | 20140408_1010 | 20140410_0945 | 46 |
| PAPA019 | Bloom Res. Sat. | 20130415_1230 | 20130417_1134 | 46 | | 20140408_1055 | 20140410_1010 | 46 |

Table 2. $L_{50}$ dBA at 19 PAPA leks, April 2013 and 2014, for three time periods (0000-2400, 0800-1800, and 1800-0800).

| L50 | | 0000-2400 | | 0800-1800 | | 1800-0800 | |
|---|---|---|---|---|---|---|---|
| Site Num. | Lek Name | 2013 | 2014 | 2013 | 2014 | 2013 | 2014 |
| PAPA001* | Big Fred | 36.9 | 27.1 | 32.9 | 28.0 | 39.1 | 26.6 |
| PAPA002* | Little Fred | 29.2 | 23.8 | 30.4 | 23.6 | 28.6 | 24.4 |
| PAPA003 | Lower Sand Springs | 29.0 | 28.8 | 27.9 | 27.5 | 29.3 | 29.9 |
| PAPA004 | Two Buttes | 26.4 | 25.4 | 28.1 | 26.3 | 26.1 | 25.2 |
| PAPA005 | Mesa Spring | 29.9 | 27.0 | 30.6 | 23.9 | 29.9 | 28.3 |
| PAPA006 | Lovatt Draw Res. | 32.1 | 31.3 | 31.1 | 31.9 | 32.8 | 31.4 |
| PAPA007 | Shelter Cabin Res. | 26.6 | 26.9 | 29.2 | 27.9 | 24.1 | 26.4 |
| PAPA008 | The Rocks | 26.3 | 26.5 | 29.5 | 29.6 | 24.3 | 23.6 |
| PAPA009 | South Rocks | 26.2 | 24.7 | 29.0 | 24.1 | 25.2 | 25.1 |
| PAPA010 | Stud Horse Butte | 27.3 | 29.7 | 29.7 | 29.7 | 26.7 | 29.4 |
| PAPA011 | Little Saddle | 22.4 | 18.4 | 26.6 | 21.8 | 21.5 | 17.7 |
| PAPA012 | Alkali Draw | 22.6 | 19.0 | 28.3 | 18.4 | 21.5 | 18.4 |
| PAPA013 | Sand Draw | 27.3 | 25.1 | 33.3 | 21.6 | 25.4 | 25.8 |
| PAPA014 | Lovatt West | 29.6 | 30.7 | 28.7 | 32.4 | 29.9 | 31.0 |
| PAPA015 | Cat | 19.0 | 19.3 | 24.3 | 22.1 | 16.5 | 17.4 |
| PAPA016 | Tyler Draw North | 21.5 | 24.5 | 23.7 | 29.8 | 20.6 | 20.3 |
| PAPA017* | Oil Fork Road | 24.8 | 28.8 | 24.4 | 26.2 | 25.1 | 31.5 |
| PAPA018 | Mesa Road 3 | 24.1 | 20.1 | 23.3 | 20.5 | 24.9 | 17.5 |
| PAPA019 | Bloom Res. Sat. | 22.0 | 19.1 | 21.4 | 20.8 | 24.3 | 16.4 |

*Gas field activities at pads nearest these leks changed significantly from 2013 to 2014, thus sound levels changed also.

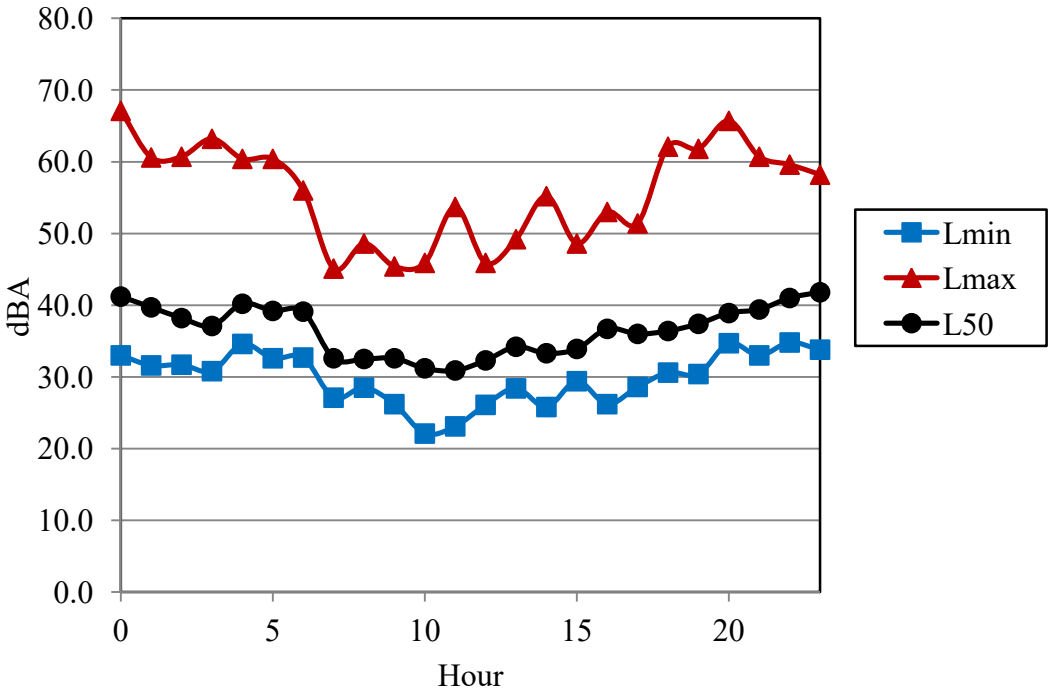



Figure 4. $L_{min}$, $L_{max}$, and $L_{50}$, PAPA001 (Big Fred Lek, close to pad), April 2013.

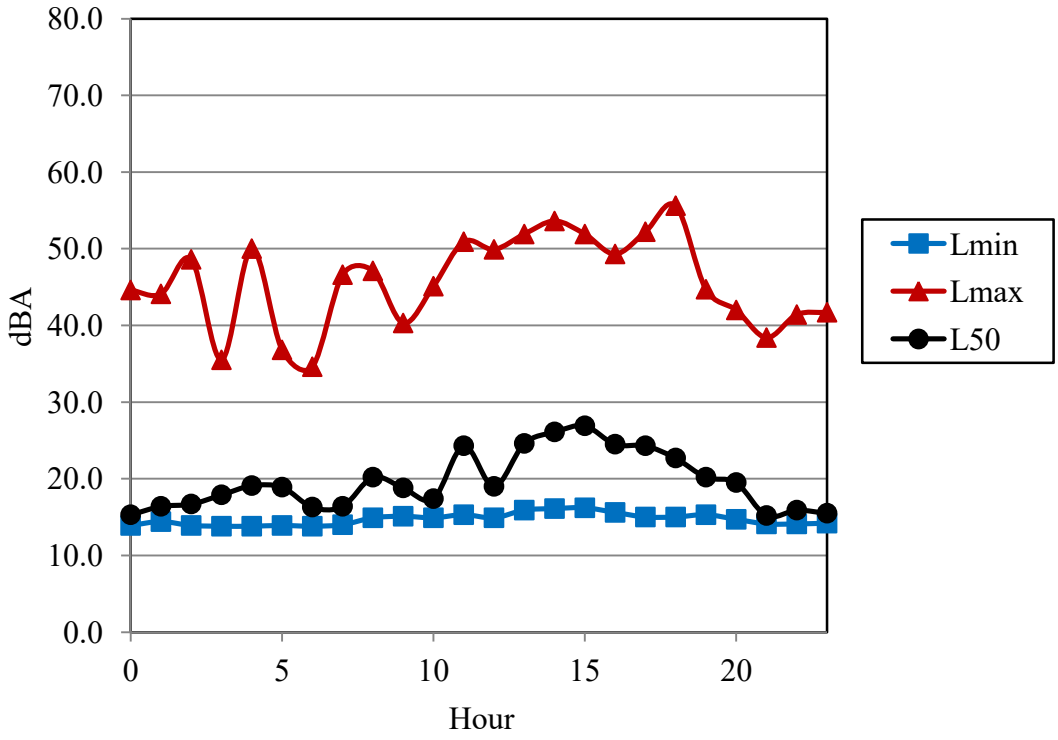



Figure 5. $L_{min}$, $L_{max}$, and $L_{50}$, PAPA015 (Cat Lek, far from pad), April 2013.

## Discussion

*Sound Levels at PAPA Leks, 2013 and 2014*

Sound levels at each lek in the PAPA in 2013 were generally similar to sound levels at that same lek in 2014, with the exception of three locations where nearby gas field operations changed significantly. Excluding these three locations, the mean difference in $L_{50}$ dBA from 2013 to 2014 for all hours (0000-2400) was 1.0 dBA (higher in 2013; SD=2.17 dBA). The mean difference in $L_{50}$ dBA for nighttime hours (1800-0800) was 1.2 dBA (higher in 2013, SD 3.05 dBA).

At some leks, sound levels differed in 2013 and 2014 but gas field activity and distance had not changed. In these cases, we suspect the differences in sound levels were due to different meteorological conditions during the measurement period, primarily wind. Wind can elevate sound levels at leks in three ways: (1) wind on the foam wind screen and wind pressure on the microphone diaphragm; (2) wind through vegetation; and (3) wind direction (sound levels at leks downwind from gas field activities will be greater than those upwind). Wind speed at 0.3 m (microphone height) rarely exceeds 1-2 m, thus wind on the foam windscreen or microphone diaphragm is generally not a concern. The prevailing wind direction in the PAPA area in April is from the northwest (NOAA 2014), thus we would expect similar directional influences in most years. The primary influence of wind on dB data (when microphone is 0.3 m) is the sound of wind through the vegetation. In order to better assess changes in sound levels at leks (and to account for different meteorological conditions) and to minimize negative influence on grouse presence and behavior (no equipment >0.3 m), longer measurement periods should be considered.

*Sound Levels and Distance to Pad*

$L_{50}$ dBA and distance to pad were highly correlated (2013: $R = -0.71$, $P = 0.001$; 2014: $R = -0.82$, $P < 0.000$) (Figures 6 and 7). Although sound levels at each pad varied due to the type of activity at that pad, and attenuation rates at each lek varied due to terrain and other variables, the closer the lek was to a pad with some type of activity, the higher the $L_{50}$ dBA.

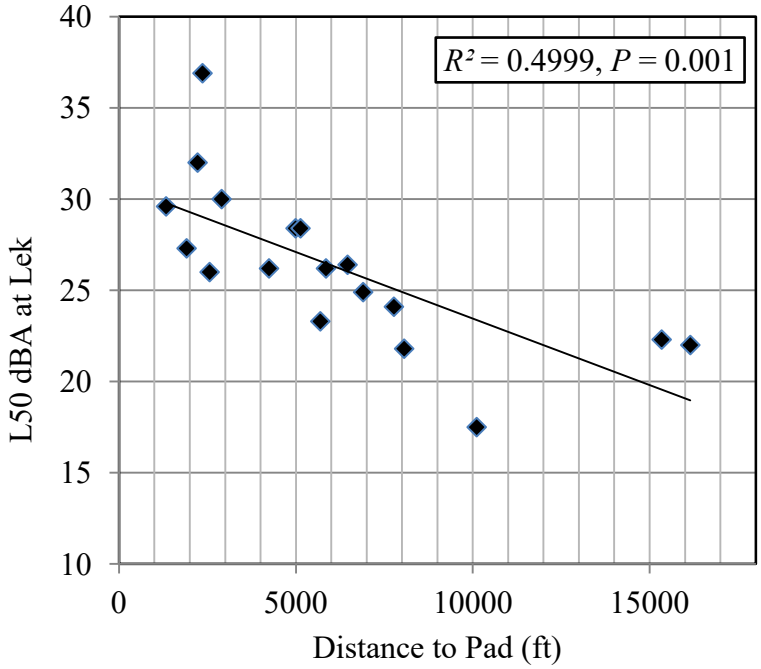



Figure 6. $L_{50}$ dBA at leks relative to distance to pad with some type of gas field activity, PAPA, 2013.

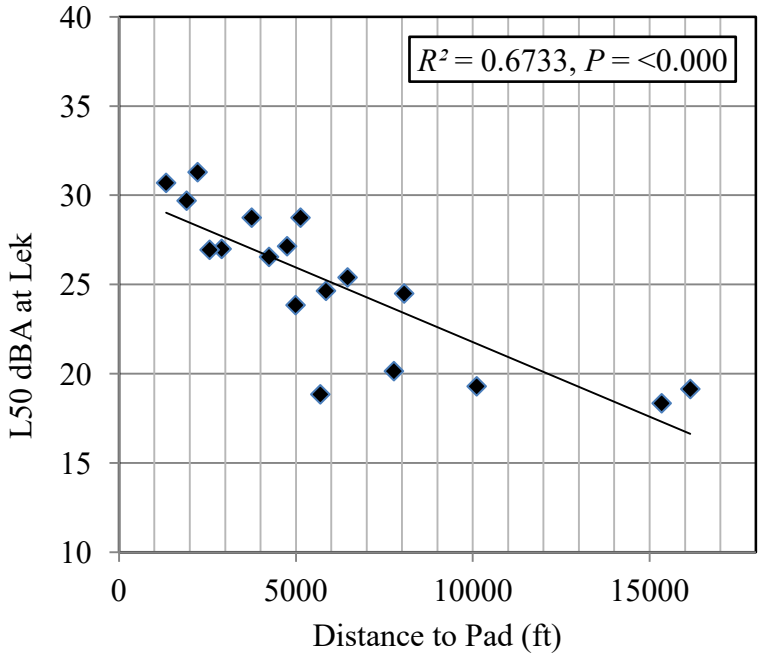



Figure 7. $L_{50}$ dBA at leks relative to distance to pad with some type of gas field activity, PAPA, 2014.

*Hours Exceeding Baseline Ambient + 10 dBA*

The Record of Decision (ROD) (BLM 2008) specified noise thresholds above baseline levels that should not be exceeded by industry. Specific changes requiring mitigation are described as follows: "Decibel levels at the lek more than 10 dBA above baseline measured from the edge of the lek" (BLM 2008)." The ROD also specifies concurrent declines in grouse numbers, but that aspect was not part of this project. The ROD used 39 dBA as a baseline ambient based on an EPA 1971 study that measured sound levels in a farming area in California (EPA 1971). Of the 2087 hours measured at the PAPA leks in 2013 and 2014, no hours exceeded 49 dBA (39 + 10 = 49 dBA). However, results of recent acoustic studies in Wyoming demonstrate that 39 dBA is not an accurate baseline ambient sound level in undeveloped sage habitats of Wyoming (KC Harvey 2005; Patricelli et al. 2013; Ambrose et al. 2014).

**Acknowledgements**

Several individuals assisted us during this study, including Therese Hartman (WGFD), Dean Clause (WGFD), Theresa Gulbrandson (BLM), and Josh Hemenway (BLM). We appreciate their help.

**Literature Cited**

Ambrose, S., and C. Florian. 2014. Sound Levels at Greater Sage-grouse Leks, Pinedale Anticline Project Area, Wyoming, April 2013. Unpublished report to Wyoming Department of Game and Fish, Cheyenne, WY.

Ambrose, S., C. Florian, and J. MacDonald. 2014. Ambient sound levels in sage habitats in Wyoming, April 2014. Unpublished report to Wyoming Department of Game and Fish, Cheyenne, WY.

American National Standard (ANSI). 1994. Procedures for Outdoor Measurement of Sound Pressure Level. American National Standards, Inc. New York, NY.

Blickley, J. L., and G. L. Patricelli. 2012. Potential acoustic masking of greater sage-grouse (*Centrocercus urophasianus*) display components by chronic industrial noise. Ornithological Monographs Volume (2012), No. 74, 23–35.

Blickley, J. L, and G. L. Patricelli. 2013. Noise monitoring recommendations for Greater Sage Grouse habitat in Wyoming. Prepared for the PAPA, Pinedale, WY.

Bureau of Land Management (BLM). 2008. Record of Decision, Final Supplemental Environmental Impact Statement for the Pinedale Anticline Oil and Gas Exploration and Development Project, Sublette County, Wyoming. US Department of the Interior, Bureau of Land Management, Cheyenne, Wyoming.

Delaney, D. K., T. G. Grubb, P. Beier, L. L. Pater, and M. H. Reiser. 1999. Effects of helicopter noise on Mexican spotted owls. Journal of Wildlife Management 63:60–76.

Delaney, D. K., L. L. Pater, L. D. Carlile, E. W. Spadgenske, T. A. Beaty, and R. H. Melton. 2011. Responses of red-cockaded woodpeckers to military training operations. Wildlife Monographs, No. 177, 1-38.

Environmental Protection Agency (EPA). 1971. Community Noise. U.S. Environmental Protection Agency, Office of Noise Abatement and Control, Washington, D.C. 20460.

Grubb, T. G., L. L. Pater, and D. K. Delaney. 1998. Logging truck noise near nesting northern goshawks. U.S. Forest Service Research Note RM-RMRSRN-3, Rocky Mountain Research Station, Ft. Collins, Colorado, USA.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Department of Zoology and Physiology, University of Wyoming, Laramie.

KC Harvey. 2009. Pinedale Anticline Project Area Sage Grouse Monitoring, Noise Monitoring Report. Unpublished report to Pinedale Area Project Office, Pinedale, WY.

National Weather Service (NWS). 2014. National Climate Data, National Oceanic and Atmospheric Administration. Silver Springs, MD.

Pater, L. L., T. G. Grubb, and D. K. Delaney. 2009. Recommendations for Improved Assessment of Noise Impacts on Wildlife. J. Wildlife Management 73(5):788-795.

Patricelli, G. L., J. L. Blickley, and S. L. Hooper. Recommended management strategies to limit anthropogenic noise impacts on greater sage-grouse in Wyoming. Human-Wildlife Interactions 7(2):23-249, Fall 2013.

Plotkin, K. J. 2002. Review of Technical Acoustical Issues Regarding Noise Measurements in National Parks. Wyle Report WR-01-20. Wyle Laboratories, Arlington, VA.

## Appendix A. Definitions of Common Acoustic Terms.

*Audibility*: Audibility is the ability of animals with normal hearing, including humans, to hear a given sound. Audibility is affected by the hearing ability of the animal, other simultaneous interfering sounds or stimuli, and by the frequency content and amplitude of the sound.

*A-Weighting (dBA)*: A-weighting is used to account for differences in human hearing sensitivity as a function of frequency. A-weighting de-emphasizes the high (6.3 kHz and above) and low (below 1 kHz) frequencies, and emphasizes the frequencies between 1 kHz and 6.3 kHz, in an effort to simulate the relative response of human hearing.

*Decibel (dB)*: A logarithmic measure commonly used in the measurement of sound. The decibel provides the possibility of representing a large span of signal levels in a simple manner as opposed to using the basic pressure unit Pascal. The difference between the sound pressure of silence versus a loud sound is a factor of 1,000,000:1 or more, therefore it is less cumbersome to use a small range of equivalent values: 0 to 130 decibels.

*Frequency*: The number of times per second that the sine wave of sound repeats itself. It can be expressed in cycles per second, or Hertz (Hz). Frequency equals Speed of Sound / Wavelength.

$L_{eq}$ *(*Equivalent Sound Level): The logarithmic average (i.e., on an energy basis) of sound pressure levels over a specific time period. "Energy averaged" sound levels are logarithmic values, and as such are generally much higher than arithmetic averages. $L_{eq}$ values are typically calculated for a specific time period (1-hour and 12-hour time periods are often used). $L_{eq}$ values are computed from all of the 1-second $L_{eq}$ values for the specific time period. $L_{eq}$ must be used carefully in quantifying natural ambient sound levels because occasional loud sound levels may heavily influence (increase) the $L_{eq}$ value, even though sound levels for that period of time are typically lower.

$L_{max}$: The maximum sound pressure level for a given period.

$L_{min}$: The minimum sound pressure level for a given period.

$L_x$ *(Exceedance Percentile)*: This metric is the sound pressure level (L), in decibels, exceeded *x* percent of the time for the specified measurement period. $L_{50}$ is the sound pressure level exceeded 50 percent of the time ($L_{50}$ is the same as the median).

*Noise Floor*: The lower measurement limit of a sound level meter, also referred to as self-noise or electrical noise of all components of a sound level meter (meter, microphone, and preamplifier).

*Sound Level*: Generally, *sound level* refers to the *weighted* sound pressure level obtained by frequency weighting, usually A- or C-weighted.

*Sound Level, Baseline Ambient*: The sound level in a given location including all sounds of nature but absent most human-caused sounds. $L_{90}$ is the sound pressure level exceeded 90 percent of the time, and is commonly used to establish the baseline ambient sound level.

*Sound Level, Existing Ambient*: The sound level of all sounds in a given area, including all natural sounds as well as all mechanical, electrical and other human-caused sounds. The existing ambient sound level is generally characterized by the $L_{50}$ exceedance level (i.e., the median).

*Sound Pressure*: Sound pressure is the instantaneous difference between the actual pressure produced by a sound wave and the average barometric pressure at a given point in space. Not all pressure fluctuations detected by a microphone are sound (e.g., wind over the microphone). Sound pressure is measured in Pascals (Pa), Newtons per square meter, which is the metric equivalent of pounds per square inch.

*Sound Pressure Level (SPL)*: The logarithmic form of sound pressure. Generally, sound pressure level refers to unweighted sound pressure levels of one-third octave bands.

.

*Time Weighting*: The response speed of a sound level meter. Fast and slow time response were developed primarily to slow needle movement in analog meters so investigators could read and record sound levels. This is not needed with modern digital sound level meters. Both fast and slow time response add a decay factor. Decay factors can induce some error, although over time there is little difference in fast, slow, or actual sound levels.

## Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013.

| Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA001 | 2013 | 0 | 33.0 | 67.1 | 42.6 | 44.0 | 41.2 | 36.6 |
| PAPA001 | 2013 | 1 | 31.6 | 60.6 | 42.2 | 44.0 | 39.7 | 37.2 |
| PAPA001 | 2013 | 2 | 31.7 | 60.7 | 41.0 | 43.6 | 38.2 | 35.8 |
| PAPA001 | 2013 | 3 | 30.8 | 63.2 | 38.9 | 39.3 | 37.1 | 34.8 |
| PAPA001 | 2013 | 4 | 34.6 | 60.4 | 41.8 | 44.4 | 40.2 | 37.1 |
| PAPA001 | 2013 | 5 | 32.6 | 60.4 | 41.1 | 44.3 | 39.2 | 37.3 |
| PAPA001 | 2013 | 6 | 32.7 | 56.0 | 40.2 | 42.0 | 39.1 | 36.2 |
| PAPA001 | 2013 | 7 | 27.1 | 45.1 | 33.8 | 36.5 | 32.6 | 29.4 |
| PAPA001 | 2013 | 8 | 28.5 | 48.6 | 33.4 | 34.9 | 32.5 | 31.0 |
| PAPA001 | 2013 | 9 | 26.2 | 45.4 | 33.2 | 34.6 | 32.6 | 30.8 |
| PAPA001 | 2013 | 10 | 22.1 | 45.9 | 32.3 | 34.2 | 31.2 | 28.6 |
| PAPA001 | 2013 | 11 | 23.1 | 53.7 | 34.1 | 35.4 | 30.9 | 27.9 |
| PAPA001 | 2013 | 12 | 26.1 | 45.9 | 33.4 | 35.5 | 32.3 | 29.3 |
| PAPA001 | 2013 | 13 | 28.4 | 49.2 | 35.4 | 37.6 | 34.2 | 31.7 |
| PAPA001 | 2013 | 14 | 25.8 | 55.2 | 36.0 | 37.8 | 33.3 | 29.3 |
| PAPA001 | 2013 | 15 | 29.4 | 48.6 | 34.8 | 36.1 | 33.9 | 32.0 |
| PAPA001 | 2013 | 16 | 26.2 | 53.0 | 38.1 | 40.9 | 36.7 | 33.8 |
| PAPA001 | 2013 | 17 | 28.6 | 51.4 | 36.8 | 38.8 | 36.0 | 33.7 |
| PAPA001 | 2013 | 18 | 30.6 | 62.1 | 37.5 | 39.2 | 36.4 | 34.4 |
| PAPA001 | 2013 | 19 | 30.4 | 61.8 | 39.5 | 40.9 | 37.4 | 34.7 |
| PAPA001 | 2013 | 20 | 34.7 | 65.7 | 41.0 | 41.9 | 38.9 | 37.1 |
| PAPA001 | 2013 | 21 | 33.0 | 60.7 | 40.6 | 41.8 | 39.4 | 37.3 |
| PAPA001 | 2013 | 22 | 34.8 | 59.6 | 42.0 | 43.6 | 41.0 | 39.3 |
| PAPA001 | 2013 | 23 | 33.8 | 58.2 | 43.1 | 45.3 | 41.8 | 38.7 |
| PAPA002 | 2013 | 0 | 20.6 | 47.7 | 29.2 | 31.4 | 27.6 | 25.1 |
| PAPA002 | 2013 | 1 | 22.4 | 49.3 | 29.4 | 31.0 | 26.9 | 24.9 |
| PAPA002 | 2013 | 2 | 23.9 | 52.1 | 32.0 | 34.5 | 30.5 | 26.0 |
| PAPA002 | 2013 | 3 | 24.3 | 55.9 | 31.0 | 31.0 | 28.8 | 27.2 |
| PAPA002 | 2013 | 4 | 25.6 | 48.4 | 31.4 | 33.2 | 29.8 | 27.4 |
| PAPA002 | 2013 | 5 | 25.9 | 50.3 | 33.9 | 35.6 | 32.6 | 29.6 |
| PAPA002 | 2013 | 6 | 26.0 | 46.3 | 32.4 | 34.1 | 31.1 | 29.1 |
| PAPA002 | 2013 | 7 | 24.8 | 49.4 | 33.8 | 36.0 | 32.3 | 28.9 |
| PAPA002 | 2013 | 8 | 24.6 | 55.7 | 34.7 | 36.8 | 32.4 | 29.2 |
| PAPA002 | 2013 | 9 | 24.3 | 57.0 | 32.9 | 35.1 | 31.5 | 28.7 |
| PAPA002 | 2013 | 10 | 21.2 | 46.6 | 30.2 | 32.9 | 27.8 | 25.0 |
| PAPA002 | 2013 | 11 | 19.5 | 52.9 | 28.4 | 28.4 | 25.1 | 23.4 |
| PAPA002 | 2013 | 12 | 20.1 | 39.6 | 25.7 | 27.4 | 23.5 | 21.7 |

Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013.

| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|
| PAPA002 | 2013 | 13 | 20.1 | 48.6 | 32.7 | 35.9 | 27.0 | 23.2 |
| PAPA002 | 2013 | 14 | 21.9 | 49.2 | 32.0 | 34.6 | 29.7 | 25.8 |
| PAPA002 | 2013 | 15 | 20.6 | 56.8 | 35.9 | 39.5 | 31.1 | 23.9 |
| PAPA002 | 2013 | 16 | 19.5 | 60.2 | 37.5 | 39.1 | 33.8 | 29.1 |
| PAPA002 | 2013 | 17 | 19.6 | 56.9 | 35.4 | 38.1 | 31.5 | 26.9 |
| PAPA002 | 2013 | 18 | 19.1 | 55.6 | 34.9 | 37.8 | 32.5 | 26.4 |
| PAPA002 | 2013 | 19 | 18.8 | 51.3 | 33.6 | 36.8 | 28.5 | 22.2 |
| PAPA002 | 2013 | 20 | 20.9 | 51.4 | 28.6 | 29.7 | 25.8 | 23.6 |
| PAPA002 | 2013 | 21 | 19.0 | 46.4 | 25.6 | 26.9 | 24.0 | 21.4 |
| PAPA002 | 2013 | 22 | 19.2 | 41.7 | 26.0 | 28.1 | 24.1 | 21.9 |
| PAPA002 | 2013 | 23 | 20.5 | 47.4 | 29.4 | 32.2 | 26.8 | 23.8 |
| PAPA003 | 2013 | 0 | 21.5 | 49.0 | 32.3 | 35.0 | 29.6 | 26.5 |
| PAPA003 | 2013 | 1 | 21.9 | 51.3 | 30.4 | 31.5 | 29.0 | 25.7 |
| PAPA003 | 2013 | 2 | 22.5 | 47.8 | 32.5 | 35.1 | 30.8 | 26.8 |
| PAPA003 | 2013 | 3 | 23.8 | 52.2 | 30.4 | 31.0 | 28.1 | 26.1 |
| PAPA003 | 2013 | 4 | 25.0 | 49.6 | 32.9 | 34.4 | 31.6 | 27.5 |
| PAPA003 | 2013 | 5 | 24.9 | 51.7 | 34.5 | 36.3 | 33.3 | 30.8 |
| PAPA003 | 2013 | 6 | 26.9 | 50.5 | 33.5 | 34.7 | 32.3 | 30.9 |
| PAPA003 | 2013 | 7 | 26.5 | 54.3 | 35.7 | 37.8 | 34.1 | 30.3 |
| PAPA003 | 2013 | 8 | 28.1 | 59.1 | 36.6 | 38.3 | 34.5 | 31.9 |
| PAPA003 | 2013 | 9 | 22.2 | 53.0 | 34.7 | 37.8 | 33.6 | 27.4 |
| PAPA003 | 2013 | 10 | 18.6 | 50.5 | 27.6 | 29.3 | 26.2 | 22.7 |
| PAPA003 | 2013 | 11 | 19.4 | 47.8 | 28.6 | 29.7 | 25.6 | 23.4 |
| PAPA003 | 2013 | 12 | 19.9 | 48.7 | 28.7 | 31.5 | 24.8 | 22.1 |
| PAPA003 | 2013 | 13 | 19.2 | 49.4 | 28.6 | 30.5 | 25.1 | 22.1 |
| PAPA003 | 2013 | 14 | 19.2 | 48.6 | 30.9 | 32.9 | 28.9 | 24.9 |
| PAPA003 | 2013 | 15 | 20.3 | 52.2 | 35.0 | 36.6 | 26.8 | 23.9 |
| PAPA003 | 2013 | 16 | 19.4 | 52.7 | 32.9 | 35.6 | 30.5 | 26.2 |
| PAPA003 | 2013 | 17 | 18.8 | 51.9 | 32.5 | 35.5 | 29.6 | 25.7 |
| PAPA003 | 2013 | 18 | 19.4 | 53.5 | 33.4 | 35.9 | 30.5 | 25.6 |
| PAPA003 | 2013 | 19 | 18.5 | 54.5 | 32.0 | 34.6 | 28.3 | 22.8 |
| PAPA003 | 2013 | 20 | 22.7 | 51.4 | 30.5 | 31.6 | 28.1 | 25.7 |
| PAPA003 | 2013 | 21 | 20.0 | 46.9 | 27.1 | 28.0 | 25.1 | 23.1 |
| PAPA003 | 2013 | 22 | 17.4 | 43.3 | 27.0 | 28.7 | 25.5 | 22.1 |
| PAPA003 | 2013 | 23 | 20.3 | 52.3 | 31.1 | 32.7 | 28.3 | 25.1 |
| PAPA004 | 2013 | 0 | 18.0 | 41.1 | 26.6 | 30.6 | 24.9 | 23.7 |
| PAPA004 | 2013 | 1 | 16.5 | 48.5 | 24.2 | 26.2 | 23.8 | 21.2 |
| PAPA004 | 2013 | 2 | 16.1 | 39.8 | 28.0 | 30.3 | 26.8 | 24.5 |
| PAPA004 | 2013 | 3 | 14.8 | 49.6 | 27.0 | 29.3 | 26.7 | 23.1 |

Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013.

| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|
| PAPA004 | 2013 | 4 | 15.0 | 43.6 | 26.6 | 29.4 | 25.5 | 22.2 |
| PAPA004 | 2013 | 5 | 18.3 | 57.1 | 27.1 | 30.0 | 26.0 | 23.0 |
| PAPA004 | 2013 | 6 | 17.0 | 43.1 | 27.8 | 29.7 | 27.2 | 23.5 |
| PAPA004 | 2013 | 7 | 20.0 | 44.0 | 27.6 | 29.9 | 26.1 | 23.0 |
| PAPA004 | 2013 | 8 | 16.8 | 52.4 | 29.9 | 28.5 | 22.6 | 19.8 |
| PAPA004 | 2013 | 9 | 17.3 | 43.6 | 24.5 | 26.8 | 22.7 | 19.6 |
| PAPA004 | 2013 | 10 | 17.2 | 52.1 | 23.9 | 24.5 | 21.2 | 19.6 |
| PAPA004 | 2013 | 11 | 16.3 | 51.2 | 26.6 | 29.7 | 23.5 | 20.4 |
| PAPA004 | 2013 | 12 | 19.8 | 49.2 | 30.4 | 33.8 | 27.2 | 23.0 |
| PAPA004 | 2013 | 13 | 19.2 | 51.3 | 32.3 | 35.9 | 29.0 | 23.1 |
| PAPA004 | 2013 | 14 | 19.7 | 54.9 | 35.0 | 38.0 | 31.4 | 25.4 |
| PAPA004 | 2013 | 15 | 19.0 | 52.7 | 36.8 | 40.6 | 33.5 | 27.7 |
| PAPA004 | 2013 | 16 | 19.1 | 52.8 | 36.0 | 39.5 | 32.7 | 26.3 |
| PAPA004 | 2013 | 17 | 18.5 | 58.7 | 37.9 | 41.2 | 34.5 | 28.4 |
| PAPA004 | 2013 | 18 | 16.6 | 52.8 | 37.4 | 41.0 | 33.5 | 27.7 |
| PAPA004 | 2013 | 19 | 16.4 | 55.4 | 31.7 | 35.1 | 28.8 | 25.2 |
| PAPA004 | 2013 | 20 | 16.4 | 61.5 | 28.9 | 30.5 | 28.1 | 26.1 |
| PAPA004 | 2013 | 21 | 15.3 | 43.7 | 28.3 | 31.3 | 24.7 | 22.3 |
| PAPA004 | 2013 | 22 | 14.6 | 50.7 | 27.3 | 29.6 | 24.2 | 21.1 |
| PAPA004 | 2013 | 23 | 15.1 | 44.4 | 26.4 | 28.7 | 24.7 | 21.9 |
| PAPA005 | 2013 | 0 | 22.2 | 53.6 | 32.4 | 34.4 | 31.8 | 30.0 |
| PAPA005 | 2013 | 1 | 21.7 | 50.5 | 28.3 | 30.9 | 27.6 | 24.1 |
| PAPA005 | 2013 | 2 | 21.4 | 45.3 | 30.9 | 34.4 | 29.3 | 26.7 |
| PAPA005 | 2013 | 3 | 19.7 | 47.1 | 30.1 | 32.5 | 29.2 | 26.8 |
| PAPA005 | 2013 | 4 | 18.3 | 46.4 | 30.7 | 33.2 | 29.8 | 27.5 |
| PAPA005 | 2013 | 5 | 22.9 | 45.7 | 30.5 | 32.4 | 29.3 | 27.2 |
| PAPA005 | 2013 | 6 | 21.8 | 45.5 | 31.9 | 32.8 | 29.3 | 25.0 |
| PAPA005 | 2013 | 7 | 21.1 | 44.0 | 29.9 | 32.8 | 28.3 | 24.3 |
| PAPA005 | 2013 | 8 | 20.4 | 50.9 | 31.7 | 33.9 | 29.2 | 26.5 |
| PAPA005 | 2013 | 9 | 20.1 | 45.7 | 30.2 | 33.6 | 27.7 | 23.7 |
| PAPA005 | 2013 | 10 | 20.5 | 51.9 | 28.6 | 30.8 | 27.5 | 24.7 |
| PAPA005 | 2013 | 11 | 17.2 | 51.6 | 28.3 | 30.1 | 26.2 | 23.8 |
| PAPA005 | 2013 | 12 | 20.1 | 62.2 | 34.9 | 35.7 | 29.9 | 26.7 |
| PAPA005 | 2013 | 13 | 21.4 | 56.8 | 35.4 | 38.6 | 31.4 | 27.0 |
| PAPA005 | 2013 | 14 | 22.8 | 63.6 | 37.4 | 41.0 | 34.5 | 28.4 |
| PAPA005 | 2013 | 15 | 22.3 | 66.6 | 40.0 | 42.5 | 35.6 | 28.9 |
| PAPA005 | 2013 | 16 | 23.6 | 57.1 | 39.5 | 42.8 | 36.9 | 31.6 |
| PAPA005 | 2013 | 17 | 21.6 | 60.2 | 41.9 | 45.4 | 39.4 | 33.7 |
| PAPA005 | 2013 | 18 | 21.2 | 54.5 | 41.0 | 44.5 | 37.9 | 32.9 |

Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013.

| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|
| PAPA005 | 2013 | 19 | 22.5 | 52.5 | 35.5 | 38.9 | 32.8 | 29.4 |
| PAPA005 | 2013 | 20 | 22.9 | 51.0 | 36.7 | 39.7 | 34.7 | 28.6 |
| PAPA005 | 2013 | 21 | 18.3 | 43.8 | 31.2 | 33.0 | 30.3 | 28.6 |
| PAPA005 | 2013 | 22 | 18.1 | 50.3 | 31.0 | 32.1 | 29.9 | 28.4 |
| PAPA005 | 2013 | 23 | 17.4 | 53.7 | 30.9 | 32.4 | 30.6 | 28.8 |
| PAPA006 | 2013 | 0 | 22.0 | 49.8 | 31.8 | 33.2 | 30.3 | 27.6 |
| PAPA006 | 2013 | 1 | 25.7 | 45.1 | 32.0 | 33.8 | 31.2 | 29.0 |
| PAPA006 | 2013 | 2 | 27.9 | 47.1 | 33.8 | 35.7 | 32.9 | 31.2 |
| PAPA006 | 2013 | 3 | 27.0 | 41.4 | 33.5 | 35.6 | 32.9 | 30.6 |
| PAPA006 | 2013 | 4 | 29.5 | 42.0 | 34.0 | 35.8 | 33.4 | 31.7 |
| PAPA006 | 2013 | 5 | 28.7 | 52.6 | 33.5 | 34.8 | 32.7 | 30.9 |
| PAPA006 | 2013 | 6 | 31.4 | 60.4 | 47.5 | 52.9 | 37.3 | 33.4 |
| PAPA006 | 2013 | 7 | 28.4 | 54.4 | 35.7 | 37.0 | 34.4 | 32.5 |
| PAPA006 | 2013 | 8 | 26.8 | 53.0 | 33.7 | 35.2 | 31.1 | 28.8 |
| PAPA006 | 2013 | 9 | 25.4 | 47.7 | 30.6 | 32.6 | 29.4 | 27.7 |
| PAPA006 | 2013 | 10 | 24.8 | 46.6 | 31.1 | 32.6 | 29.8 | 28.0 |
| PAPA006 | 2013 | 11 | 23.2 | 50.9 | 32.2 | 34.0 | 30.2 | 28.2 |
| PAPA006 | 2013 | 12 | 23.8 | 60.6 | 34.8 | 35.2 | 31.0 | 28.1 |
| PAPA006 | 2013 | 13 | 25.1 | 58.0 | 33.3 | 36.1 | 31.2 | 28.6 |
| PAPA006 | 2013 | 14 | 25.1 | 50.7 | 34.6 | 37.3 | 33.0 | 29.8 |
| PAPA006 | 2013 | 15 | 24.8 | 55.5 | 37.3 | 41.1 | 33.9 | 29.9 |
| PAPA006 | 2013 | 16 | 23.7 | 55.4 | 35.8 | 38.7 | 34.1 | 31.4 |
| PAPA006 | 2013 | 17 | 23.2 | 54.9 | 36.6 | 39.5 | 34.8 | 30.7 |
| PAPA006 | 2013 | 18 | 22.6 | 52.9 | 36.4 | 39.4 | 35.0 | 31.5 |
| PAPA006 | 2013 | 19 | 22.4 | 54.2 | 31.2 | 33.7 | 29.8 | 27.1 |
| PAPA006 | 2013 | 20 | 25.0 | 51.3 | 31.5 | 33.8 | 31.5 | 26.9 |
| PAPA006 | 2013 | 21 | 24.6 | 47.0 | 33.8 | 35.6 | 33.2 | 31.4 |
| PAPA006 | 2013 | 22 | 23.7 | 45.9 | 32.1 | 33.6 | 30.1 | 28.1 |
| PAPA006 | 2013 | 23 | 21.4 | 51.6 | 31.2 | 32.9 | 28.7 | 26.1 |
| PAPA007 | 2013 | 0 | 18.1 | 38.6 | 23.1 | 24.4 | 21.8 | 20.1 |
| PAPA007 | 2013 | 1 | 18.0 | 32.8 | 23.0 | 24.9 | 22.6 | 20.3 |
| PAPA007 | 2013 | 2 | 17.1 | 40.5 | 24.1 | 25.2 | 22.0 | 20.6 |
| PAPA007 | 2013 | 3 | 18.3 | 39.2 | 23.2 | 24.9 | 22.7 | 20.7 |
| PAPA007 | 2013 | 4 | 17.9 | 39.1 | 23.5 | 25.4 | 22.6 | 20.9 |
| PAPA007 | 2013 | 5 | 19.4 | 44.0 | 25.8 | 27.6 | 24.3 | 22.1 |
| PAPA007 | 2013 | 6 | 21.8 | 38.5 | 27.6 | 29.6 | 26.9 | 24.7 |
| PAPA007 | 2013 | 7 | 22.3 | 46.2 | 27.3 | 28.8 | 26.1 | 24.3 |
| PAPA007 | 2013 | 8 | 19.5 | 49.3 | 28.1 | 30.2 | 26.3 | 23.4 |
| PAPA007 | 2013 | 9 | 18.6 | 48.9 | 30.4 | 33.1 | 25.5 | 22.4 |

| Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA007 | 2013 | 10 | 19.7 | 52.0 | 32.4 | 35.8 | 29.7 | 24.5 |
| PAPA007 | 2013 | 11 | 22.1 | 52.8 | 33.1 | 34.8 | 29.9 | 26.0 |
| PAPA007 | 2013 | 12 | 21.7 | 73.2 | 39.4 | 34.0 | 29.4 | 25.8 |
| PAPA007 | 2013 | 13 | 21.4 | 50.8 | 30.6 | 33.6 | 28.5 | 24.6 |
| PAPA007 | 2013 | 14 | 20.9 | 47.7 | 30.9 | 33.8 | 28.5 | 24.7 |
| PAPA007 | 2013 | 15 | 21.4 | 50.8 | 31.6 | 34.6 | 29.0 | 25.5 |
| PAPA007 | 2013 | 16 | 19.6 | 50.0 | 34.6 | 38.4 | 30.7 | 25.3 |
| PAPA007 | 2013 | 17 | 20.4 | 49.1 | 34.8 | 38.3 | 31.6 | 26.3 |
| PAPA007 | 2013 | 18 | 23.1 | 54.3 | 37.5 | 41.1 | 34.8 | 29.8 |
| PAPA007 | 2013 | 19 | 19.5 | 50.0 | 34.2 | 37.6 | 31.5 | 26.7 |
| PAPA007 | 2013 | 20 | 20.8 | 49.6 | 31.1 | 34.0 | 28.8 | 25.6 |
| PAPA007 | 2013 | 21 | 20.0 | 44.1 | 27.2 | 29.6 | 25.8 | 23.6 |
| PAPA007 | 2013 | 22 | 20.2 | 45.0 | 26.3 | 28.7 | 24.0 | 22.1 |
| PAPA007 | 2013 | 23 | 20.4 | 36.7 | 24.0 | 25.9 | 23.2 | 21.9 |
| PAPA008 | 2013 | 0 | 19.7 | 36.5 | 23.7 | 25.0 | 22.5 | 21.1 |
| PAPA008 | 2013 | 1 | 20.4 | 34.5 | 24.3 | 25.9 | 23.6 | 21.9 |
| PAPA008 | 2013 | 2 | 19.5 | 46.0 | 25.2 | 26.6 | 23.9 | 22.4 |
| PAPA008 | 2013 | 3 | 19.5 | 36.2 | 24.5 | 25.8 | 24.0 | 22.4 |
| PAPA008 | 2013 | 4 | 18.8 | 34.7 | 23.7 | 25.7 | 22.8 | 21.1 |
| PAPA008 | 2013 | 5 | 20.2 | 36.7 | 24.5 | 26.2 | 23.8 | 22.0 |
| PAPA008 | 2013 | 6 | 21.3 | 51.5 | 26.9 | 28.4 | 25.2 | 23.3 |
| PAPA008 | 2013 | 7 | 21.2 | 43.8 | 27.3 | 29.3 | 26.1 | 24.1 |
| PAPA008 | 2013 | 8 | 19.2 | 53.6 | 29.2 | 30.2 | 25.6 | 23.5 |
| PAPA008 | 2013 | 9 | 18.9 | 50.9 | 29.9 | 31.7 | 26.5 | 23.5 |
| PAPA008 | 2013 | 10 | 20.9 | 47.1 | 32.9 | 36.0 | 30.8 | 26.2 |
| PAPA008 | 2013 | 11 | 19.2 | 49.5 | 28.9 | 32.3 | 26.5 | 25.1 |
| PAPA008 | 2013 | 12 | 18.0 | 64.5 | 35.9 | 31.3 | 26.5 | 25.0 |
| PAPA008 | 2013 | 13 | 22.4 | 49.8 | 31.6 | 34.4 | 29.9 | 25.8 |
| PAPA008 | 2013 | 14 | 20.5 | 52.6 | 31.7 | 34.2 | 30.0 | 26.4 |
| PAPA008 | 2013 | 15 | 21.5 | 47.6 | 31.3 | 34.2 | 29.1 | 25.5 |
| PAPA008 | 2013 | 16 | 22.3 | 49.0 | 33.4 | 36.9 | 30.7 | 26.4 |
| PAPA008 | 2013 | 17 | 22.9 | 47.6 | 35.0 | 38.2 | 32.7 | 27.8 |
| PAPA008 | 2013 | 18 | 21.2 | 49.6 | 36.0 | 39.5 | 33.8 | 27.9 |
| PAPA008 | 2013 | 19 | 22.4 | 51.7 | 35.2 | 38.5 | 33.1 | 28.1 |
| PAPA008 | 2013 | 20 | 21.5 | 49.9 | 32.6 | 35.8 | 30.3 | 26.3 |
| PAPA008 | 2013 | 21 | 20.9 | 42.9 | 25.9 | 28.2 | 24.8 | 22.8 |
| PAPA008 | 2013 | 22 | 21.2 | 38.6 | 26.2 | 28.6 | 24.7 | 23.1 |
| PAPA008 | 2013 | 23 | 20.3 | 35.2 | 24.2 | 25.8 | 23.5 | 22.3 |
| PAPA009 | 2013 | 0 | 18.6 | 34.8 | 24.2 | 26.6 | 23.1 | 21.0 |

Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013.

| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|
| PAPA009 | 2013 | 1 | 17.2 | 40.1 | 25.2 | 27.6 | 23.8 | 22.1 |
| PAPA009 | 2013 | 2 | 17.6 | 49.2 | 26.1 | 27.8 | 25.2 | 23.4 |
| PAPA009 | 2013 | 3 | 18.1 | 38.8 | 26.2 | 29.0 | 24.9 | 22.2 |
| PAPA009 | 2013 | 4 | 19.4 | 33.6 | 25.0 | 27.1 | 24.3 | 22.1 |
| PAPA009 | 2013 | 5 | 21.6 | 32.9 | 25.9 | 28.0 | 25.3 | 23.3 |
| PAPA009 | 2013 | 6 | 21.5 | 39.8 | 25.4 | 26.9 | 25.1 | 23.5 |
| PAPA009 | 2013 | 7 | 21.8 | 44.6 | 27.1 | 28.6 | 26.3 | 24.4 |
| PAPA009 | 2013 | 8 | 18.7 | 46.2 | 28.7 | 30.5 | 26.2 | 23.0 |
| PAPA009 | 2013 | 9 | 18.8 | 47.6 | 30.0 | 32.3 | 26.6 | 23.9 |
| PAPA009 | 2013 | 10 | 19.9 | 47.6 | 31.9 | 35.1 | 29.8 | 25.6 |
| PAPA009 | 2013 | 11 | 19.6 | 50.4 | 31.2 | 34.6 | 28.7 | 24.6 |
| PAPA009 | 2013 | 12 | 18.2 | 59.0 | 34.1 | 30.0 | 23.5 | 22.1 |
| PAPA009 | 2013 | 13 | 18.4 | 54.2 | 30.4 | 32.9 | 26.2 | 23.3 |
| PAPA009 | 2013 | 14 | 22.1 | 47.3 | 31.0 | 33.6 | 29.5 | 26.1 |
| PAPA009 | 2013 | 15 | 21.5 | 47.7 | 31.3 | 33.9 | 29.4 | 25.9 |
| PAPA009 | 2013 | 16 | 23.5 | 49.6 | 32.5 | 35.6 | 30.0 | 26.1 |
| PAPA009 | 2013 | 17 | 22.9 | 48.3 | 33.8 | 37.1 | 31.5 | 27.3 |
| PAPA009 | 2013 | 18 | 22.3 | 48.7 | 35.0 | 38.2 | 33.1 | 28.2 |
| PAPA009 | 2013 | 19 | 22.1 | 52.1 | 33.2 | 36.2 | 31.1 | 27.1 |
| PAPA009 | 2013 | 20 | 21.6 | 45.0 | 31.4 | 34.3 | 29.8 | 27.0 |
| PAPA009 | 2013 | 21 | 20.8 | 38.7 | 26.1 | 28.3 | 25.0 | 23.1 |
| PAPA009 | 2013 | 22 | 21.6 | 37.0 | 26.3 | 28.3 | 25.5 | 23.6 |
| PAPA009 | 2013 | 23 | 20.0 | 39.8 | 26.7 | 28.6 | 25.7 | 23.7 |
| PAPA010 | 2013 | 0 | 19.5 | 36.7 | 24.6 | 26.6 | 23.4 | 21.9 |
| PAPA010 | 2013 | 1 | 18.9 | 40.1 | 27.1 | 29.8 | 25.8 | 23.2 |
| PAPA010 | 2013 | 2 | 19.7 | 50.0 | 28.8 | 31.5 | 26.5 | 24.1 |
| PAPA010 | 2013 | 3 | 18.1 | 42.0 | 27.1 | 29.8 | 25.8 | 22.6 |
| PAPA010 | 2013 | 4 | 20.4 | 36.2 | 25.9 | 27.9 | 25.0 | 23.0 |
| PAPA010 | 2013 | 5 | 21.5 | 37.4 | 27.6 | 29.4 | 27.1 | 25.4 |
| PAPA010 | 2013 | 6 | 22.6 | 40.1 | 29.3 | 31.2 | 28.1 | 26.2 |
| PAPA010 | 2013 | 7 | 22.9 | 43.4 | 27.5 | 29.3 | 26.7 | 25.1 |
| PAPA010 | 2013 | 8 | 19.0 | 46.0 | 29.7 | 31.5 | 26.6 | 23.1 |
| PAPA010 | 2013 | 9 | 19.4 | 48.5 | 31.1 | 33.7 | 27.6 | 24.3 |
| PAPA010 | 2013 | 10 | 20.1 | 60.3 | 34.1 | 36.3 | 30.3 | 25.7 |
| PAPA010 | 2013 | 11 | 19.8 | 51.6 | 31.9 | 35.3 | 29.2 | 24.8 |
| PAPA010 | 2013 | 12 | 19.1 | 49.9 | 32.5 | 35.9 | 29.4 | 25.2 |
| PAPA010 | 2013 | 13 | 19.9 | 52.0 | 30.0 | 33.0 | 26.6 | 23.5 |
| PAPA010 | 2013 | 14 | 23.1 | 50.8 | 32.1 | 34.6 | 30.3 | 26.9 |
| PAPA010 | 2013 | 15 | 22.6 | 50.4 | 31.9 | 34.4 | 30.1 | 26.8 |

| Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA010 | 2013 | 16 | 22.4 | 50.6 | 33.5 | 36.8 | 31.0 | 27.2 |
| PAPA010 | 2013 | 17 | 22.8 | 51.7 | 34.5 | 37.8 | 31.9 | 27.7 |
| PAPA010 | 2013 | 18 | 24.5 | 50.0 | 36.2 | 39.4 | 34.1 | 29.5 |
| PAPA010 | 2013 | 19 | 22.5 | 53.8 | 33.0 | 35.9 | 29.9 | 26.3 |
| PAPA010 | 2013 | 20 | 22.7 | 48.9 | 31.2 | 34.0 | 29.2 | 26.5 |
| PAPA010 | 2013 | 21 | 22.1 | 42.4 | 28.3 | 31.0 | 26.7 | 24.6 |
| PAPA010 | 2013 | 22 | 22.7 | 36.6 | 27.6 | 29.5 | 26.9 | 25.1 |
| PAPA010 | 2013 | 23 | 20.8 | 39.4 | 26.9 | 28.6 | 25.8 | 24.2 |
| PAPA011 | 2013 | 0 | 15.3 | 39.0 | 20.2 | 21.8 | 19.4 | 17.8 |
| PAPA011 | 2013 | 1 | 16.0 | 38.6 | 21.5 | 23.5 | 20.4 | 18.0 |
| PAPA011 | 2013 | 2 | 16.0 | 36.9 | 21.1 | 23.2 | 19.8 | 18.1 |
| PAPA011 | 2013 | 3 | 16.0 | 41.8 | 22.4 | 24.4 | 21.2 | 19.3 |
| PAPA011 | 2013 | 4 | 15.8 | 42.7 | 23.6 | 25.7 | 22.1 | 20.1 |
| PAPA011 | 2013 | 5 | 16.0 | 40.0 | 26.5 | 30.5 | 23.4 | 19.5 |
| PAPA011 | 2013 | 6 | 17.2 | 44.1 | 28.4 | 32.3 | 25.0 | 19.9 |
| PAPA011 | 2013 | 7 | 16.8 | 39.5 | 24.6 | 27.6 | 21.7 | 19.2 |
| PAPA011 | 2013 | 8 | 17.7 | 48.9 | 27.2 | 29.3 | 22.3 | 20.0 |
| PAPA011 | 2013 | 9 | 17.1 | 49.5 | 28.1 | 28.1 | 21.0 | 18.7 |
| PAPA011 | 2013 | 10 | 17.8 | 57.4 | 30.2 | 32.2 | 26.8 | 22.7 |
| PAPA011 | 2013 | 11 | 16.6 | 51.6 | 29.0 | 31.9 | 25.9 | 21.9 |
| PAPA011 | 2013 | 12 | 16.5 | 50.6 | 32.1 | 34.2 | 27.2 | 22.6 |
| PAPA011 | 2013 | 13 | 16.8 | 54.7 | 35.3 | 38.8 | 32.7 | 26.9 |
| PAPA011 | 2013 | 14 | 16.5 | 49.2 | 30.0 | 33.5 | 27.3 | 23.2 |
| PAPA011 | 2013 | 15 | 16.6 | 51.0 | 32.0 | 35.3 | 29.1 | 23.9 |
| PAPA011 | 2013 | 16 | 16.1 | 48.8 | 30.3 | 33.5 | 26.5 | 20.7 |
| PAPA011 | 2013 | 17 | 16.0 | 51.3 | 26.2 | 28.0 | 21.6 | 18.1 |
| PAPA011 | 2013 | 18 | 15.5 | 54.2 | 27.1 | 28.3 | 22.5 | 19.1 |
| PAPA011 | 2013 | 19 | 15.1 | 47.2 | 23.9 | 25.2 | 19.8 | 17.4 |
| PAPA011 | 2013 | 20 | 14.9 | 50.5 | 26.2 | 27.3 | 21.4 | 17.9 |
| PAPA011 | 2013 | 21 | 15.3 | 50.9 | 25.4 | 28.0 | 23.2 | 20.1 |
| PAPA011 | 2013 | 22 | 15.2 | 46.2 | 23.4 | 25.6 | 21.3 | 18.7 |
| PAPA011 | 2013 | 23 | 15.1 | 44.0 | 24.3 | 26.9 | 22.7 | 18.1 |
| PAPA012 | 2013 | 0 | 16.0 | 36.0 | 21.6 | 23.5 | 20.7 | 19.0 |
| PAPA012 | 2013 | 1 | 18.4 | 44.2 | 23.4 | 24.9 | 21.6 | 19.9 |
| PAPA012 | 2013 | 2 | 16.7 | 39.7 | 22.4 | 24.4 | 21.2 | 19.7 |
| PAPA012 | 2013 | 3 | 16.7 | 40.5 | 22.6 | 24.3 | 21.2 | 19.7 |
| PAPA012 | 2013 | 4 | 16.1 | 42.0 | 23.2 | 25.1 | 21.3 | 19.4 |
| PAPA012 | 2013 | 5 | 17.3 | 44.0 | 24.1 | 27.2 | 21.8 | 20.0 |
| PAPA012 | 2013 | 6 | 19.2 | 41.0 | 27.5 | 30.0 | 26.1 | 22.7 |

Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013.

| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|
| PAPA012 | 2013 | 7 | 18.0 | 59.5 | 27.9 | 28.7 | 24.3 | 21.7 |
| PAPA012 | 2013 | 8 | 19.0 | 48.9 | 28.6 | 31.2 | 24.5 | 21.6 |
| PAPA012 | 2013 | 9 | 17.4 | 50.6 | 29.1 | 31.5 | 26.0 | 21.6 |
| PAPA012 | 2013 | 10 | 17.6 | 65.5 | 37.3 | 33.9 | 27.1 | 21.4 |
| PAPA012 | 2013 | 11 | 19.8 | 47.0 | 33.1 | 36.7 | 29.8 | 23.7 |
| PAPA012 | 2013 | 12 | 17.1 | 49.0 | 32.2 | 35.8 | 28.6 | 22.6 |
| PAPA012 | 2013 | 13 | 17.0 | 53.2 | 35.5 | 39.2 | 31.7 | 25.2 |
| PAPA012 | 2013 | 14 | 16.9 | 54.5 | 33.0 | 36.7 | 29.8 | 24.9 |
| PAPA012 | 2013 | 15 | 16.7 | 57.0 | 34.1 | 37.8 | 30.1 | 24.0 |
| PAPA012 | 2013 | 16 | 16.6 | 51.2 | 32.2 | 35.5 | 28.1 | 22.4 |
| PAPA012 | 2013 | 17 | 15.6 | 47.0 | 26.2 | 29.3 | 22.1 | 18.1 |
| PAPA012 | 2013 | 18 | 14.7 | 49.8 | 27.0 | 28.3 | 21.9 | 18.6 |
| PAPA012 | 2013 | 19 | 14.6 | 41.7 | 23.5 | 25.9 | 19.6 | 17.7 |
| PAPA012 | 2013 | 20 | 15.4 | 38.2 | 22.6 | 25.0 | 19.7 | 17.9 |
| PAPA012 | 2013 | 21 | 15.2 | 46.7 | 25.4 | 28.0 | 23.0 | 19.7 |
| PAPA012 | 2013 | 22 | 15.2 | 43.1 | 23.7 | 25.9 | 21.9 | 19.2 |
| PAPA012 | 2013 | 23 | 15.1 | 38.9 | 22.0 | 24.1 | 20.6 | 18.4 |
| PAPA013 | 2013 | 0 | 18.5 | 36.7 | 25.5 | 27.6 | 24.7 | 22.2 |
| PAPA013 | 2013 | 1 | 16.7 | 36.9 | 25.8 | 27.6 | 24.9 | 21.6 |
| PAPA013 | 2013 | 2 | 17.2 | 39.1 | 27.2 | 29.5 | 25.8 | 23.8 |
| PAPA013 | 2013 | 3 | 19.2 | 41.6 | 30.0 | 32.7 | 28.4 | 25.6 |
| PAPA013 | 2013 | 4 | 18.7 | 42.2 | 29.3 | 31.7 | 27.5 | 25.2 |
| PAPA013 | 2013 | 5 | 17.8 | 38.7 | 24.9 | 27.4 | 23.9 | 21.0 |
| PAPA013 | 2013 | 6 | 17.7 | 53.6 | 24.8 | 25.3 | 22.5 | 20.3 |
| PAPA013 | 2013 | 7 | 19.1 | 63.1 | 31.0 | 25.8 | 23.6 | 21.2 |
| PAPA013 | 2013 | 8 | 19.8 | 75.0 | 39.4 | 32.3 | 26.5 | 23.2 |
| PAPA013 | 2013 | 9 | 20.3 | 50.5 | 32.3 | 35.5 | 29.9 | 25.1 |
| PAPA013 | 2013 | 10 | 21.4 | 51.6 | 37.7 | 41.2 | 35.0 | 29.3 |
| PAPA013 | 2013 | 11 | 24.8 | 49.0 | 37.8 | 41.6 | 35.1 | 29.5 |
| PAPA013 | 2013 | 12 | 24.5 | 51.7 | 38.8 | 42.5 | 36.3 | 30.3 |
| PAPA013 | 2013 | 13 | 19.6 | 53.7 | 36.6 | 40.2 | 33.0 | 27.4 |
| PAPA013 | 2013 | 14 | 21.3 | 56.3 | 37.1 | 40.6 | 34.3 | 29.4 |
| PAPA013 | 2013 | 15 | 18.6 | 56.2 | 36.8 | 40.2 | 33.6 | 28.8 |
| PAPA013 | 2013 | 16 | 18.6 | 57.1 | 36.2 | 38.9 | 30.9 | 24.4 |
| PAPA013 | 2013 | 17 | 18.2 | 48.6 | 29.1 | 32.4 | 24.7 | 20.4 |
| PAPA013 | 2013 | 18 | 17.4 | 44.4 | 28.6 | 31.6 | 24.9 | 20.5 |
| PAPA013 | 2013 | 19 | 17.5 | 39.8 | 25.8 | 28.5 | 23.6 | 21.2 |
| PAPA013 | 2013 | 20 | 20.6 | 47.1 | 28.1 | 30.4 | 26.6 | 23.7 |
| PAPA013 | 2013 | 21 | 23.2 | 53.8 | 31.7 | 34.2 | 29.9 | 26.6 |

| Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA013 | 2013 | 22 | 22.6 | 47.4 | 30.9 | 33.4 | 29.3 | 26.3 |
| PAPA013 | 2013 | 23 | 19.4 | 45.5 | 28.8 | 31.9 | 27.1 | 23.1 |
| PAPA014 | 2013 | 0 | 19.8 | 36.4 | 29.7 | 30.7 | 29.5 | 28.5 |
| PAPA014 | 2013 | 1 | 24.9 | 38.9 | 31.4 | 33.0 | 30.2 | 27.3 |
| PAPA014 | 2013 | 2 | 23.7 | 41.6 | 30.7 | 32.0 | 30.5 | 28.9 |
| PAPA014 | 2013 | 3 | 25.9 | 42.4 | 29.0 | 30.0 | 28.9 | 27.7 |
| PAPA014 | 2013 | 4 | 25.6 | 43.1 | 30.8 | 33.3 | 29.7 | 27.3 |
| PAPA014 | 2013 | 5 | 27.0 | 46.7 | 33.0 | 35.3 | 32.6 | 29.7 |
| PAPA014 | 2013 | 6 | 27.6 | 43.6 | 31.1 | 32.5 | 30.9 | 29.6 |
| PAPA014 | 2013 | 7 | 23.1 | 43.7 | 31.3 | 33.9 | 30.2 | 28.4 |
| PAPA014 | 2013 | 8 | 21.0 | 52.4 | 31.1 | 32.4 | 28.0 | 24.1 |
| PAPA014 | 2013 | 9 | 19.8 | 48.7 | 26.4 | 28.7 | 24.8 | 22.6 |
| PAPA014 | 2013 | 10 | 19.0 | 58.0 | 28.6 | 28.4 | 25.4 | 23.1 |
| PAPA014 | 2013 | 11 | 19.6 | 47.0 | 30.4 | 33.3 | 26.9 | 23.3 |
| PAPA014 | 2013 | 12 | 19.8 | 56.8 | 32.0 | 34.6 | 28.2 | 23.9 |
| PAPA014 | 2013 | 13 | 19.9 | 58.3 | 33.2 | 36.2 | 29.3 | 24.9 |
| PAPA014 | 2013 | 14 | 19.8 | 49.3 | 33.3 | 36.8 | 30.6 | 25.4 |
| PAPA014 | 2013 | 15 | 20.9 | 55.0 | 37.2 | 40.8 | 31.9 | 25.0 |
| PAPA014 | 2013 | 16 | 21.1 | 59.5 | 36.8 | 40.2 | 34.7 | 28.9 |
| PAPA014 | 2013 | 17 | 20.5 | 55.0 | 37.0 | 40.1 | 34.8 | 29.8 |
| PAPA014 | 2013 | 18 | 19.9 | 50.9 | 35.4 | 38.9 | 33.2 | 27.8 |
| PAPA014 | 2013 | 19 | 20.0 | 52.6 | 30.2 | 33.6 | 28.4 | 24.5 |
| PAPA014 | 2013 | 20 | 21.6 | 51.5 | 29.9 | 30.6 | 28.9 | 24.5 |
| PAPA014 | 2013 | 21 | 22.6 | 44.2 | 29.1 | 30.8 | 29.2 | 27.1 |
| PAPA014 | 2013 | 22 | 23.7 | 44.7 | 32.4 | 36.5 | 30.0 | 27.0 |
| PAPA014 | 2013 | 23 | 21.2 | 38.7 | 29.8 | 31.8 | 29.1 | 27.2 |
| PAPA015 | 2013 | 0 | 13.9 | 44.6 | 19.3 | 17.2 | 15.3 | 14.6 |
| PAPA015 | 2013 | 1 | 14.4 | 44.1 | 21.8 | 22.3 | 16.4 | 15.3 |
| PAPA015 | 2013 | 2 | 13.9 | 48.6 | 21.5 | 23.8 | 16.7 | 14.9 |
| PAPA015 | 2013 | 3 | 13.8 | 35.5 | 19.1 | 21.3 | 17.9 | 15.1 |
| PAPA015 | 2013 | 4 | 13.8 | 50.0 | 26.3 | 22.6 | 19.1 | 17.8 |
| PAPA015 | 2013 | 5 | 13.9 | 36.8 | 20.2 | 22.2 | 18.9 | 17.2 |
| PAPA015 | 2013 | 6 | 13.8 | 34.6 | 17.5 | 19.1 | 16.3 | 15.2 |
| PAPA015 | 2013 | 7 | 14.0 | 46.6 | 20.5 | 20.7 | 16.4 | 14.7 |
| PAPA015 | 2013 | 8 | 14.9 | 47.1 | 23.4 | 25.7 | 20.2 | 17.0 |
| PAPA015 | 2013 | 9 | 15.1 | 40.3 | 22.0 | 24.8 | 18.8 | 16.3 |
| PAPA015 | 2013 | 10 | 14.9 | 45.1 | 23.5 | 26.9 | 17.4 | 15.7 |
| PAPA015 | 2013 | 11 | 15.3 | 50.9 | 29.0 | 32.7 | 24.3 | 19.5 |
| PAPA015 | 2013 | 12 | 14.9 | 49.9 | 29.4 | 24.8 | 19.0 | 17.2 |

Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013.

| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|
| PAPA015 | 2013 | 13 | 15.9 | 51.9 | 30.0 | 32.5 | 24.6 | 20.2 |
| PAPA015 | 2013 | 14 | 16.1 | 53.6 | 30.8 | 33.9 | 26.1 | 20.1 |
| PAPA015 | 2013 | 15 | 16.2 | 51.9 | 31.3 | 34.6 | 26.9 | 20.7 |
| PAPA015 | 2013 | 16 | 15.6 | 49.3 | 28.3 | 32.1 | 24.5 | 19.1 |
| PAPA015 | 2013 | 17 | 15.0 | 52.2 | 32.4 | 33.8 | 24.3 | 18.6 |
| PAPA015 | 2013 | 18 | 15.0 | 55.6 | 27.4 | 30.4 | 22.7 | 17.1 |
| PAPA015 | 2013 | 19 | 15.3 | 44.7 | 23.6 | 26.2 | 20.2 | 16.8 |
| PAPA015 | 2013 | 20 | 14.7 | 42.0 | 25.1 | 26.7 | 19.5 | 16.3 |
| PAPA015 | 2013 | 21 | 14.1 | 38.4 | 19.2 | 20.3 | 15.2 | 14.4 |
| PAPA015 | 2013 | 22 | 14.1 | 41.4 | 20.5 | 19.5 | 15.9 | 14.9 |
| PAPA015 | 2013 | 23 | 14.2 | 41.7 | 19.4 | 17.0 | 15.5 | 14.8 |
| PAPA016 | 2013 | 0 | 15.7 | 32.7 | 20.1 | 22.2 | 19.0 | 17.6 |
| PAPA016 | 2013 | 1 | 16.6 | 57.3 | 27.2 | 23.5 | 20.5 | 18.5 |
| PAPA016 | 2013 | 2 | 14.9 | 31.6 | 20.6 | 22.3 | 20.2 | 17.9 |
| PAPA016 | 2013 | 3 | 14.4 | 45.3 | 25.6 | 22.6 | 20.5 | 19.3 |
| PAPA016 | 2013 | 4 | 14.3 | 38.1 | 23.6 | 23.4 | 21.6 | 20.6 |
| PAPA016 | 2013 | 5 | 14.3 | 41.4 | 22.6 | 24.8 | 21.3 | 19.8 |
| PAPA016 | 2013 | 6 | 15.7 | 45.3 | 24.9 | 25.9 | 22.7 | 20.8 |
| PAPA016 | 2013 | 7 | 18.6 | 41.1 | 25.5 | 27.6 | 24.5 | 21.9 |
| PAPA016 | 2013 | 8 | 20.3 | 43.3 | 29.8 | 32.1 | 28.0 | 24.4 |
| PAPA016 | 2013 | 9 | 22.1 | 41.8 | 27.8 | 29.5 | 26.1 | 24.3 |
| PAPA016 | 2013 | 10 | 22.0 | 39.4 | 27.5 | 29.7 | 26.5 | 24.4 |
| PAPA016 | 2013 | 11 | 15.2 | 43.5 | 24.0 | 24.5 | 19.4 | 17.6 |
| PAPA016 | 2013 | 12 | 15.4 | 45.1 | 25.9 | 28.0 | 19.6 | 16.3 |
| PAPA016 | 2013 | 13 | 15.3 | 54.7 | 27.6 | 29.9 | 19.1 | 16.2 |
| PAPA016 | 2013 | 14 | 16.0 | 43.4 | 25.8 | 28.0 | 22.3 | 18.7 |
| PAPA016 | 2013 | 15 | 16.0 | 42.2 | 27.6 | 31.4 | 23.9 | 18.9 |
| PAPA016 | 2013 | 16 | 16.5 | 46.1 | 29.0 | 32.7 | 25.5 | 19.7 |
| PAPA016 | 2013 | 17 | 15.7 | 53.6 | 28.5 | 30.9 | 23.6 | 18.6 |
| PAPA016 | 2013 | 18 | 14.9 | 48.9 | 27.0 | 29.1 | 22.7 | 17.1 |
| PAPA016 | 2013 | 19 | 14.8 | 48.9 | 27.6 | 30.2 | 22.9 | 19.2 |
| PAPA016 | 2013 | 20 | 14.5 | 40.6 | 22.1 | 24.4 | 19.7 | 17.7 |
| PAPA016 | 2013 | 21 | 14.3 | 42.3 | 23.5 | 26.0 | 20.6 | 19.1 |
| PAPA016 | 2013 | 22 | 14.7 | 38.5 | 21.8 | 24.7 | 19.5 | 17.1 |
| PAPA016 | 2013 | 23 | 14.7 | 40.4 | 23.3 | 26.2 | 20.3 | 17.4 |
| PAPA017 | 2013 | 0 | 20.3 | 37.0 | 25.4 | 27.4 | 24.7 | 22.6 |
| PAPA017 | 2013 | 1 | 19.3 | 53.6 | 27.1 | 27.7 | 25.3 | 22.9 |
| PAPA017 | 2013 | 2 | 18.1 | 37.5 | 24.1 | 26.0 | 23.6 | 21.3 |
| PAPA017 | 2013 | 3 | 17.4 | 42.6 | 26.9 | 28.9 | 23.6 | 22.0 |

Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013.

| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
|---|---|---|---|---|---|---|---|---|
| PAPA017 | 2013 | 4 | 15.2 | 46.5 | 27.1 | 28.5 | 24.6 | 22.9 |
| PAPA017 | 2013 | 5 | 15.2 | 54.3 | 28.8 | 31.1 | 27.3 | 23.8 |
| PAPA017 | 2013 | 6 | 17.5 | 50.1 | 32.3 | 33.1 | 29.7 | 26.9 |
| PAPA017 | 2013 | 7 | 18.5 | 40.8 | 25.3 | 27.5 | 24.5 | 21.9 |
| PAPA017 | 2013 | 8 | 18.6 | 47.0 | 27.7 | 29.6 | 25.4 | 22.3 |
| PAPA017 | 2013 | 9 | 17.8 | 40.8 | 27.9 | 30.7 | 26.5 | 22.8 |
| PAPA017 | 2013 | 10 | 19.7 | 52.4 | 28.1 | 31.3 | 24.4 | 21.9 |
| PAPA017 | 2013 | 11 | 19.2 | 27.5 | 21.7 | 23.1 | 21.3 | 20.3 |
| PAPA017 | 2013 | 12 | 18.0 | 43.7 | 26.8 | 29.3 | 23.7 | 20.5 |
| PAPA017 | 2013 | 13 | 19.0 | 58.2 | 28.7 | 29.5 | 23.7 | 21.3 |
| PAPA017 | 2013 | 14 | 19.4 | 44.1 | 26.6 | 28.2 | 24.4 | 22.3 |
| PAPA017 | 2013 | 15 | 19.4 | 42.1 | 27.1 | 30.0 | 24.3 | 21.9 |
| PAPA017 | 2013 | 16 | 19.5 | 45.4 | 27.6 | 30.5 | 25.4 | 22.6 |
| PAPA017 | 2013 | 17 | 19.3 | 56.7 | 29.0 | 30.3 | 25.4 | 22.9 |
| PAPA017 | 2013 | 18 | 18.1 | 47.7 | 28.0 | 30.6 | 26.3 | 23.5 |
| PAPA017 | 2013 | 19 | 18.7 | 49.4 | 29.4 | 31.9 | 27.3 | 24.5 |
| PAPA017 | 2013 | 20 | 18.9 | 50.4 | 27.3 | 28.9 | 26.6 | 24.4 |
| PAPA017 | 2013 | 21 | 17.6 | 47.7 | 27.7 | 29.4 | 27.0 | 23.9 |
| PAPA017 | 2013 | 22 | 16.4 | 36.2 | 25.2 | 27.2 | 24.7 | 22.6 |
| PAPA017 | 2013 | 23 | 18.3 | 36.0 | 25.7 | 27.9 | 24.9 | 22.1 |
| PAPA018 | 2013 | 0 | 16.2 | 35.7 | 26.4 | 30.1 | 24.2 | 20.2 |
| PAPA018 | 2013 | 1 | 21.6 | 47.6 | 28.2 | 30.2 | 27.0 | 25.0 |
| PAPA018 | 2013 | 2 | 22.4 | 36.7 | 28.8 | 31.0 | 28.2 | 25.5 |
| PAPA018 | 2013 | 3 | 19.0 | 40.6 | 28.1 | 29.4 | 27.2 | 25.3 |
| PAPA018 | 2013 | 4 | 14.9 | 48.5 | 28.8 | 30.5 | 25.4 | 23.3 |
| PAPA018 | 2013 | 5 | 14.4 | 50.7 | 26.9 | 30.5 | 24.5 | 23.0 |
| PAPA018 | 2013 | 6 | 19.6 | 49.2 | 31.7 | 34.7 | 29.9 | 26.3 |
| PAPA018 | 2013 | 7 | 19.2 | 45.3 | 30.2 | 33.3 | 28.2 | 23.2 |
| PAPA018 | 2013 | 8 | 16.7 | 46.5 | 25.7 | 27.6 | 22.5 | 20.1 |
| PAPA018 | 2013 | 9 | 17.4 | 50.1 | 26.8 | 29.7 | 24.3 | 19.7 |
| PAPA018 | 2013 | 10 | 17.4 | 42.2 | 26.4 | 29.7 | 23.3 | 19.8 |
| PAPA018 | 2013 | 11 | 18.0 | 34.6 | 21.7 | 23.4 | 20.8 | 19.6 |
| PAPA018 | 2013 | 12 | 16.4 | 44.4 | 27.8 | 31.2 | 23.6 | 19.3 |
| PAPA018 | 2013 | 13 | 16.5 | 59.1 | 29.2 | 29.3 | 23.1 | 19.3 |
| PAPA018 | 2013 | 14 | 17.1 | 45.2 | 26.6 | 29.7 | 23.4 | 19.7 |
| PAPA018 | 2013 | 15 | 17.3 | 56.7 | 30.6 | 31.4 | 23.5 | 19.8 |
| PAPA018 | 2013 | 16 | 16.9 | 42.6 | 26.2 | 29.5 | 23.1 | 19.5 |
| PAPA018 | 2013 | 17 | 16.8 | 49.8 | 28.2 | 31.9 | 24.1 | 19.6 |
| PAPA018 | 2013 | 18 | 15.3 | 49.3 | 29.9 | 33.4 | 25.8 | 22.2 |

| Appendix B. Hourly dBA Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA018 | 2013 | 19 | 15.1 | 47.7 | 27.2 | 30.1 | 24.1 | 20.1 |
| PAPA018 | 2013 | 20 | 15.6 | 37.0 | 23.3 | 25.9 | 21.1 | 18.4 |
| PAPA018 | 2013 | 21 | 14.5 | 61.4 | 27.9 | 25.2 | 21.8 | 18.0 |
| PAPA018 | 2013 | 22 | 15.2 | 35.9 | 22.5 | 24.7 | 21.5 | 20.0 |
| PAPA018 | 2013 | 23 | 14.8 | 40.0 | 25.0 | 27.7 | 24.4 | 19.2 |
| PAPA019 | 2013 | 0 | 15.1 | 37.4 | 23.0 | 25.6 | 21.5 | 17.9 |
| PAPA019 | 2013 | 1 | 18.7 | 42.5 | 27.5 | 29.9 | 25.9 | 23.1 |
| PAPA019 | 2013 | 2 | 20.6 | 38.2 | 24.7 | 26.1 | 24.2 | 23.0 |
| PAPA019 | 2013 | 3 | 23.0 | 43.1 | 29.5 | 32.3 | 27.8 | 25.5 |
| PAPA019 | 2013 | 4 | 19.2 | 44.4 | 28.8 | 30.1 | 27.9 | 25.6 |
| PAPA019 | 2013 | 5 | 16.2 | 60.1 | 26.9 | 26.0 | 23.4 | 21.8 |
| PAPA019 | 2013 | 6 | 20.6 | 37.7 | 25.8 | 27.4 | 25.3 | 23.8 |
| PAPA019 | 2013 | 7 | 18.5 | 39.3 | 25.2 | 27.5 | 24.4 | 21.3 |
| PAPA019 | 2013 | 8 | 15.6 | 43.7 | 23.7 | 24.5 | 20.3 | 18.4 |
| PAPA019 | 2013 | 9 | 16.5 | 38.5 | 23.4 | 26.4 | 21.5 | 18.0 |
| PAPA019 | 2013 | 10 | 16.1 | 41.0 | 24.7 | 27.6 | 21.4 | 18.2 |
| PAPA019 | 2013 | 11 | 15.9 | 36.1 | 18.9 | 20.5 | 17.9 | 16.8 |
| PAPA019 | 2013 | 12 | 15.5 | 42.0 | 22.2 | 24.7 | 19.2 | 16.6 |
| PAPA019 | 2013 | 13 | 15.7 | 55.9 | 28.1 | 27.6 | 21.2 | 17.5 |
| PAPA019 | 2013 | 14 | 16.2 | 43.1 | 24.9 | 27.7 | 21.4 | 17.6 |
| PAPA019 | 2013 | 15 | 15.5 | 52.2 | 29.8 | 32.3 | 22.5 | 17.9 |
| PAPA019 | 2013 | 16 | 15.6 | 47.1 | 26.6 | 30.2 | 23.1 | 18.6 |
| PAPA019 | 2013 | 17 | 16.6 | 51.8 | 30.6 | 34.3 | 26.2 | 20.5 |
| PAPA019 | 2013 | 18 | 15.7 | 53.1 | 28.5 | 32.0 | 26.1 | 22.2 |
| PAPA019 | 2013 | 19 | 15.9 | 48.4 | 26.9 | 30.1 | 24.3 | 19.3 |
| PAPA019 | 2013 | 20 | 14.9 | 53.8 | 24.0 | 26.2 | 19.7 | 17.5 |
| PAPA019 | 2013 | 21 | 16.0 | 61.2 | 29.7 | 26.2 | 21.0 | 17.9 |
| PAPA019 | 2013 | 22 | 14.7 | 35.4 | 19.0 | 21.0 | 17.4 | 15.5 |
| PAPA019 | 2013 | 23 | 14.9 | 29.3 | 20.0 | 22.2 | 19.4 | 16.7 |

## Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014.

| Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA001 | 2014 | 0 | 22.0 | 51.8 | 29.4 | 28.2 | 25.6 | 24.2 |
| PAPA001 | 2014 | 1 | 22.9 | 37.9 | 26.7 | 28.0 | 26.2 | 24.9 |
| PAPA001 | 2014 | 2 | 23.0 | 47.3 | 27.9 | 28.8 | 26.5 | 25.0 |
| PAPA001 | 2014 | 3 | 23.0 | 44.6 | 27.7 | 29.1 | 26.6 | 24.8 |
| PAPA001 | 2014 | 4 | 21.1 | 49.4 | 28.0 | 30.1 | 26.8 | 24.8 |
| PAPA001 | 2014 | 5 | 21.0 | 38.0 | 26.8 | 28.6 | 26.3 | 24.6 |
| PAPA001 | 2014 | 6 | 20.9 | 41.0 | 26.2 | 28.0 | 25.6 | 23.7 |
| PAPA001 | 2014 | 7 | 20.6 | 42.7 | 26.4 | 28.2 | 25.6 | 23.6 |
| PAPA001 | 2014 | 8 | 25.4 | 43.2 | 33.0 | 35.5 | 32.1 | 28.7 |
| PAPA001 | 2014 | 9 | 24.0 | 40.8 | 31.7 | 34.3 | 31.0 | 27.7 |
| PAPA001 | 2014 | 10 | 22.7 | 44.1 | 33.1 | 36.2 | 31.0 | 27.0 |
| PAPA001 | 2014 | 11 | 21.9 | 40.4 | 29.6 | 32.1 | 28.7 | 25.2 |
| PAPA001 | 2014 | 12 | 21.6 | 55.6 | 30.7 | 31.9 | 27.7 | 24.8 |
| PAPA001 | 2014 | 13 | 22.3 | 53.2 | 28.5 | 31.0 | 26.7 | 24.5 |
| PAPA001 | 2014 | 14 | 22.0 | 54.7 | 30.7 | 31.7 | 28.0 | 24.8 |
| PAPA001 | 2014 | 15 | 20.6 | 52.3 | 32.7 | 35.0 | 30.6 | 26.9 |
| PAPA001 | 2014 | 16 | 20.7 | 46.7 | 30.9 | 33.3 | 30.1 | 27.2 |
| PAPA001 | 2014 | 17 | 20.7 | 42.6 | 29.1 | 31.5 | 28.3 | 25.8 |
| PAPA001 | 2014 | 18 | 20.7 | 45.2 | 28.1 | 30.0 | 27.0 | 24.7 |
| PAPA001 | 2014 | 19 | 21.4 | 54.2 | 30.6 | 30.2 | 27.1 | 25.1 |
| PAPA001 | 2014 | 20 | 20.7 | 47.8 | 29.3 | 30.1 | 27.2 | 25.2 |
| PAPA001 | 2014 | 21 | 20.5 | 46.7 | 30.5 | 31.2 | 28.0 | 26.2 |
| PAPA001 | 2014 | 22 | 21.2 | 52.4 | 31.1 | 30.7 | 28.0 | 25.5 |
| PAPA001 | 2014 | 23 | 22.2 | 47.8 | 27.6 | 28.6 | 26.3 | 24.7 |
| PAPA002 | 2014 | 0 | 22.3 | 58.8 | 31.5 | 29.1 | 26.9 | 25.2 |
| PAPA002 | 2014 | 1 | 21.9 | 45.0 | 28.0 | 29.6 | 27.0 | 24.9 |
| PAPA002 | 2014 | 2 | 21.7 | 44.8 | 26.8 | 27.0 | 24.9 | 23.6 |
| PAPA002 | 2014 | 3 | 21.8 | 50.7 | 28.9 | 30.4 | 25.6 | 24.0 |
| PAPA002 | 2014 | 4 | 21.0 | 51.1 | 28.4 | 30.5 | 26.8 | 24.8 |
| PAPA002 | 2014 | 5 | 20.7 | 45.8 | 26.1 | 27.6 | 25.3 | 24.1 |
| PAPA002 | 2014 | 6 | 20.7 | 40.8 | 24.5 | 26.0 | 23.8 | 22.1 |
| PAPA002 | 2014 | 7 | 20.8 | 45.0 | 23.0 | 23.6 | 22.4 | 21.7 |
| PAPA002 | 2014 | 8 | 21.0 | 40.8 | 24.0 | 25.2 | 22.7 | 21.8 |
| PAPA002 | 2014 | 9 | 20.3 | 40.1 | 25.8 | 27.5 | 23.9 | 21.7 |
| PAPA002 | 2014 | 10 | 20.1 | 45.6 | 29.4 | 31.4 | 23.4 | 21.0 |
| PAPA002 | 2014 | 11 | 20.5 | 62.6 | 32.8 | 29.9 | 23.6 | 21.2 |
| PAPA002 | 2014 | 12 | 20.7 | 53.2 | 31.4 | 32.4 | 23.4 | 22.1 |
| PAPA002 | 2014 | 13 | 20.6 | 46.2 | 29.0 | 31.1 | 24.2 | 22.5 |

| Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA002 | 2014 | 14 | 20.4 | 56.7 | 30.0 | 28.7 | 23.5 | 22.1 |
| PAPA002 | 2014 | 15 | 20.3 | 53.8 | 32.6 | 34.6 | 28.5 | 23.9 |
| PAPA002 | 2014 | 16 | 20.6 | 52.2 | 30.3 | 33.2 | 27.8 | 24.0 |
| PAPA002 | 2014 | 17 | 20.5 | 46.6 | 25.4 | 27.4 | 23.1 | 21.7 |
| PAPA002 | 2014 | 18 | 20.4 | 41.8 | 25.5 | 28.1 | 22.7 | 21.2 |
| PAPA002 | 2014 | 19 | 20.6 | 51.0 | 28.2 | 28.6 | 23.6 | 22.1 |
| PAPA002 | 2014 | 20 | 19.9 | 46.1 | 26.4 | 26.3 | 23.2 | 22.0 |
| PAPA002 | 2014 | 21 | 19.9 | 48.4 | 27.0 | 29.1 | 23.6 | 21.6 |
| PAPA002 | 2014 | 22 | 20.8 | 47.5 | 26.0 | 26.9 | 23.9 | 22.5 |
| PAPA002 | 2014 | 23 | 21.6 | 47.8 | 28.1 | 29.4 | 26.6 | 24.5 |
| PAPA003 | 2014 | 0 | 25.9 | 49.5 | 31.7 | 33.2 | 30.8 | 29.0 |
| PAPA003 | 2014 | 1 | 22.2 | 48.7 | 31.0 | 34.2 | 28.7 | 26.0 |
| PAPA003 | 2014 | 2 | 20.4 | 51.3 | 30.0 | 32.3 | 28.8 | 26.5 |
| PAPA003 | 2014 | 3 | 22.2 | 43.1 | 29.9 | 31.8 | 28.3 | 26.6 |
| PAPA003 | 2014 | 4 | 21.8 | 44.5 | 31.7 | 33.3 | 30.9 | 29.0 |
| PAPA003 | 2014 | 5 | 22.8 | 47.0 | 32.2 | 34.5 | 31.4 | 29.0 |
| PAPA003 | 2014 | 6 | 26.5 | 42.6 | 33.7 | 35.8 | 33.1 | 30.6 |
| PAPA003 | 2014 | 7 | 29.1 | 43.9 | 33.2 | 34.7 | 32.9 | 31.2 |
| PAPA003 | 2014 | 8 | 25.5 | 45.9 | 31.3 | 33.3 | 30.6 | 28.2 |
| PAPA003 | 2014 | 9 | 20.2 | 43.3 | 29.2 | 31.2 | 27.9 | 25.1 |
| PAPA003 | 2014 | 10 | 20.1 | 47.2 | 28.1 | 30.1 | 25.8 | 23.9 |
| PAPA003 | 2014 | 11 | 21.8 | 58.1 | 33.9 | 36.8 | 30.7 | 26.2 |
| PAPA003 | 2014 | 12 | 20.4 | 62.1 | 35.8 | 37.3 | 31.9 | 28.0 |
| PAPA003 | 2014 | 13 | 21.6 | 59.8 | 32.0 | 33.3 | 27.5 | 24.6 |
| PAPA003 | 2014 | 14 | 20.7 | 53.6 | 31.7 | 32.4 | 26.9 | 23.7 |
| PAPA003 | 2014 | 15 | 20.0 | 53.0 | 30.8 | 31.3 | 25.8 | 23.5 |
| PAPA003 | 2014 | 16 | 20.6 | 49.7 | 29.8 | 31.3 | 26.1 | 23.2 |
| PAPA003 | 2014 | 17 | 20.9 | 46.9 | 28.9 | 31.1 | 26.4 | 23.8 |
| PAPA003 | 2014 | 18 | 19.0 | 56.3 | 28.3 | 28.9 | 24.7 | 22.1 |
| PAPA003 | 2014 | 19 | 19.2 | 47.3 | 27.4 | 29.0 | 25.2 | 22.1 |
| PAPA003 | 2014 | 20 | 22.9 | 48.3 | 29.4 | 30.7 | 28.4 | 26.5 |
| PAPA003 | 2014 | 21 | 20.6 | 46.1 | 30.2 | 31.7 | 29.2 | 25.7 |
| PAPA003 | 2014 | 22 | 19.7 | 50.8 | 31.9 | 34.5 | 30.6 | 26.3 |
| PAPA003 | 2014 | 23 | 26.5 | 48.2 | 32.5 | 34.3 | 32.0 | 29.9 |
| PAPA004 | 2014 | 0 | 16.5 | 37.6 | 23.4 | 26.1 | 22.2 | 18.6 |
| PAPA004 | 2014 | 1 | 17.1 | 39.8 | 22.9 | 25.4 | 21.1 | 18.8 |
| PAPA004 | 2014 | 2 | 18.8 | 35.8 | 24.5 | 26.7 | 23.9 | 20.6 |
| PAPA004 | 2014 | 3 | 18.9 | 39.2 | 25.4 | 28.1 | 23.8 | 21.4 |
| PAPA004 | 2014 | 4 | 17.3 | 43.6 | 27.4 | 29.6 | 25.6 | 22.3 |
| PAPA004 | 2014 | 5 | 15.6 | 37.0 | 26.1 | 28.3 | 25.3 | 22.9 |

| Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA004 | 2014 | 6 | 16.9 | 55.9 | 27.7 | 28.5 | 25.5 | 23.4 |
| PAPA004 | 2014 | 7 | 17.1 | 43.9 | 27.7 | 29.0 | 25.2 | 23.4 |
| PAPA004 | 2014 | 8 | 19.6 | 70.5 | 37.5 | 32.4 | 27.4 | 25.0 |
| PAPA004 | 2014 | 9 | 17.7 | 64.9 | 40.0 | 29.6 | 21.2 | 18.9 |
| PAPA004 | 2014 | 10 | 16.6 | 51.4 | 28.9 | 31.0 | 22.4 | 18.4 |
| PAPA004 | 2014 | 11 | 17.1 | 62.1 | 33.9 | 28.4 | 23.6 | 20.4 |
| PAPA004 | 2014 | 12 | 17.8 | 45.4 | 27.7 | 30.5 | 23.9 | 20.2 |
| PAPA004 | 2014 | 13 | 19.7 | 56.0 | 34.4 | 32.0 | 27.1 | 23.4 |
| PAPA004 | 2014 | 14 | 19.7 | 53.8 | 35.0 | 38.7 | 31.4 | 24.2 |
| PAPA004 | 2014 | 15 | 19.1 | 56.9 | 36.1 | 39.7 | 32.9 | 27.3 |
| PAPA004 | 2014 | 16 | 18.7 | 57.4 | 36.4 | 40.2 | 32.0 | 25.1 |
| PAPA004 | 2014 | 17 | 18.7 | 55.9 | 34.9 | 38.5 | 31.6 | 26.0 |
| PAPA004 | 2014 | 18 | 17.4 | 47.5 | 31.1 | 34.5 | 27.6 | 22.8 |
| PAPA004 | 2014 | 19 | 16.6 | 54.5 | 31.9 | 34.3 | 26.3 | 22.7 |
| PAPA004 | 2014 | 20 | 16.4 | 59.3 | 32.8 | 35.1 | 28.3 | 24.7 |
| PAPA004 | 2014 | 21 | 17.5 | 52.8 | 30.2 | 32.1 | 26.2 | 20.6 |
| PAPA004 | 2014 | 22 | 15.1 | 37.9 | 24.0 | 25.6 | 21.4 | 18.9 |
| PAPA004 | 2014 | 23 | 15.6 | 40.9 | 21.7 | 23.3 | 20.2 | 18.6 |
| PAPA005 | 2014 | 0 | 21.3 | 36.2 | 28.3 | 30.6 | 27.8 | 25.2 |
| PAPA005 | 2014 | 1 | 20.1 | 39.1 | 29.1 | 30.9 | 28.6 | 27.2 |
| PAPA005 | 2014 | 2 | 18.9 | 40.6 | 31.3 | 33.4 | 30.7 | 28.9 |
| PAPA005 | 2014 | 3 | 19.9 | 40.3 | 32.6 | 34.1 | 32.4 | 29.2 |
| PAPA005 | 2014 | 4 | 18.9 | 43.9 | 32.3 | 34.7 | 31.1 | 29.4 |
| PAPA005 | 2014 | 5 | 19.9 | 49.2 | 34.8 | 35.8 | 32.2 | 30.1 |
| PAPA005 | 2014 | 6 | 21.3 | 48.2 | 32.5 | 34.1 | 31.6 | 30.0 |
| PAPA005 | 2014 | 7 | 23.7 | 43.8 | 33.5 | 35.0 | 33.0 | 30.9 |
| PAPA005 | 2014 | 8 | 21.3 | 55.4 | 35.4 | 37.1 | 33.3 | 28.4 |
| PAPA005 | 2014 | 9 | 19.1 | 53.6 | 31.2 | 32.4 | 29.7 | 27.5 |
| PAPA005 | 2014 | 10 | 18.4 | 66.5 | 36.2 | 30.7 | 26.1 | 23.5 |
| PAPA005 | 2014 | 11 | 19.5 | 57.6 | 24.1 | 25.8 | 22.6 | 21.4 |
| PAPA005 | 2014 | 12 | 19.8 | 57.0 | 34.8 | 30.9 | 23.5 | 22.2 |
| PAPA005 | 2014 | 13 | 20.1 | 56.4 | 31.3 | 29.2 | 23.9 | 22.1 |
| PAPA005 | 2014 | 14 | 19.7 | 62.8 | 33.1 | 30.1 | 23.6 | 22.0 |
| PAPA005 | 2014 | 15 | 19.7 | 57.0 | 30.7 | 33.4 | 27.2 | 22.8 |
| PAPA005 | 2014 | 16 | 18.4 | 61.7 | 35.5 | 33.8 | 26.8 | 23.1 |
| PAPA005 | 2014 | 17 | 18.3 | 47.4 | 29.0 | 29.4 | 24.5 | 21.4 |
| PAPA005 | 2014 | 18 | 18.1 | 53.1 | 30.3 | 27.2 | 22.8 | 20.9 |
| PAPA005 | 2014 | 19 | 17.7 | 55.2 | 31.4 | 24.3 | 21.3 | 19.7 |
| PAPA005 | 2014 | 20 | 18.0 | 56.3 | 34.1 | 36.6 | 22.1 | 20.3 |
| PAPA005 | 2014 | 21 | 17.7 | 42.4 | 25.1 | 25.8 | 21.7 | 20.2 |

| Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA005 | 2014 | 22 | 18.9 | 38.3 | 25.7 | 28.0 | 24.8 | 22.3 |
| PAPA005 | 2014 | 23 | 20.6 | 38.2 | 29.7 | 33.0 | 27.9 | 25.4 |
| PAPA006 | 2014 | 0 | 27.2 | 48.5 | 31.9 | 33.6 | 31.3 | 29.7 |
| PAPA006 | 2014 | 1 | 26.1 | 48.1 | 32.3 | 34.2 | 31.5 | 29.8 |
| PAPA006 | 2014 | 2 | 27.0 | 47.0 | 31.7 | 33.1 | 31.0 | 29.6 |
| PAPA006 | 2014 | 3 | 26.6 | 43.7 | 30.9 | 32.0 | 30.7 | 29.5 |
| PAPA006 | 2014 | 4 | 27.8 | 40.9 | 31.4 | 32.7 | 31.1 | 29.9 |
| PAPA006 | 2014 | 5 | 28.9 | 48.0 | 33.2 | 34.9 | 32.3 | 30.5 |
| PAPA006 | 2014 | 6 | 28.4 | 41.8 | 33.3 | 34.7 | 32.9 | 31.5 |
| PAPA006 | 2014 | 7 | 27.3 | 41.5 | 31.7 | 33.5 | 31.3 | 29.2 |
| PAPA006 | 2014 | 8 | 25.3 | 50.7 | 32.3 | 33.4 | 30.1 | 27.0 |
| PAPA006 | 2014 | 9 | 23.5 | 47.1 | 30.8 | 32.3 | 29.0 | 25.5 |
| PAPA006 | 2014 | 10 | 23.5 | 67.3 | 46.6 | 29.4 | 25.7 | 24.6 |
| PAPA006 | 2014 | 11 | 23.2 | 37.8 | 26.5 | 28.0 | 25.5 | 24.4 |
| PAPA006 | 2014 | 12 | 23.7 | 68.2 | 37.2 | 28.2 | 25.4 | 24.5 |
| PAPA006 | 2014 | 13 | 23.1 | 68.3 | 35.0 | 30.5 | 25.5 | 24.3 |
| PAPA006 | 2014 | 14 | 24.1 | 60.3 | 36.1 | 38.1 | 33.3 | 29.9 |
| PAPA006 | 2014 | 15 | 23.6 | 64.3 | 36.7 | 39.0 | 34.2 | 30.2 |
| PAPA006 | 2014 | 16 | 23.2 | 63.7 | 37.7 | 39.9 | 33.8 | 29.7 |
| PAPA006 | 2014 | 17 | 23.3 | 57.4 | 34.9 | 37.7 | 32.7 | 28.8 |
| PAPA006 | 2014 | 18 | 24.8 | 56.6 | 34.6 | 37.0 | 31.1 | 28.3 |
| PAPA006 | 2014 | 19 | 25.4 | 59.8 | 36.6 | 39.3 | 33.5 | 29.5 |
| PAPA006 | 2014 | 20 | 27.8 | 59.6 | 37.7 | 40.3 | 35.0 | 30.9 |
| PAPA006 | 2014 | 21 | 26.9 | 55.0 | 35.3 | 37.8 | 33.4 | 30.3 |
| PAPA006 | 2014 | 22 | 28.0 | 47.6 | 32.9 | 34.2 | 31.9 | 30.2 |
| PAPA006 | 2014 | 23 | 28.1 | 42.8 | 31.5 | 32.8 | 31.0 | 29.9 |
| PAPA007 | 2014 | 0 | 18.2 | 39.5 | 25.0 | 27.1 | 24.1 | 22.1 |
| PAPA007 | 2014 | 1 | 18.8 | 43.3 | 25.0 | 26.7 | 24.5 | 22.7 |
| PAPA007 | 2014 | 2 | 20.4 | 47.0 | 27.0 | 28.7 | 25.3 | 23.1 |
| PAPA007 | 2014 | 3 | 20.3 | 42.4 | 26.0 | 27.8 | 25.3 | 23.2 |
| PAPA007 | 2014 | 4 | 20.9 | 39.6 | 27.4 | 29.6 | 26.7 | 23.6 |
| PAPA007 | 2014 | 5 | 20.4 | 41.3 | 26.8 | 28.9 | 25.5 | 23.8 |
| PAPA007 | 2014 | 6 | 23.7 | 59.7 | 32.1 | 32.5 | 28.3 | 26.1 |
| PAPA007 | 2014 | 7 | 22.1 | 57.8 | 33.7 | 32.0 | 27.2 | 25.3 |
| PAPA007 | 2014 | 8 | 20.7 | 66.7 | 38.2 | 33.4 | 28.3 | 25.2 |
| PAPA007 | 2014 | 9 | 20.2 | 61.5 | 32.0 | 31.3 | 26.2 | 23.2 |
| PAPA007 | 2014 | 10 | 20.1 | 68.3 | 34.0 | 31.2 | 25.3 | 22.4 |
| PAPA007 | 2014 | 11 | 19.8 | 57.1 | 28.8 | 29.1 | 23.6 | 21.3 |
| PAPA007 | 2014 | 12 | 18.6 | 65.9 | 40.0 | 31.9 | 25.0 | 21.3 |
| PAPA007 | 2014 | 13 | 20.7 | 55.5 | 40.6 | 44.6 | 37.5 | 24.0 |

| Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA007 | 2014 | 14 | 28.8 | 58.9 | 43.7 | 47.3 | 41.0 | 35.4 |
| PAPA007 | 2014 | 15 | 29.6 | 59.6 | 43.6 | 47.1 | 41.2 | 35.5 |
| PAPA007 | 2014 | 16 | 21.8 | 58.6 | 39.0 | 37.1 | 32.7 | 29.0 |
| PAPA007 | 2014 | 17 | 20.4 | 60.6 | 35.3 | 37.4 | 32.6 | 28.4 |
| PAPA007 | 2014 | 18 | 19.0 | 59.2 | 34.3 | 36.8 | 32.5 | 29.0 |
| PAPA007 | 2014 | 19 | 20.6 | 53.6 | 32.8 | 35.3 | 27.9 | 24.4 |
| PAPA007 | 2014 | 20 | 22.7 | 53.3 | 33.5 | 36.6 | 31.0 | 26.6 |
| PAPA007 | 2014 | 21 | 21.0 | 48.6 | 29.5 | 31.5 | 27.8 | 25.3 |
| PAPA007 | 2014 | 22 | 20.1 | 47.5 | 28.4 | 31.0 | 26.1 | 23.5 |
| PAPA007 | 2014 | 23 | 17.3 | 41.7 | 24.9 | 27.0 | 23.9 | 21.6 |
| PAPA008 | 2014 | 0 | 18.6 | 42.0 | 23.0 | 24.2 | 21.5 | 20.5 |
| PAPA008 | 2014 | 1 | 18.0 | 48.9 | 23.8 | 25.3 | 22.7 | 21.2 |
| PAPA008 | 2014 | 2 | 17.9 | 45.5 | 25.7 | 27.9 | 24.3 | 22.3 |
| PAPA008 | 2014 | 3 | 18.3 | 42.8 | 26.0 | 28.2 | 24.7 | 22.5 |
| PAPA008 | 2014 | 4 | 19.1 | 43.6 | 26.7 | 28.7 | 25.1 | 22.7 |
| PAPA008 | 2014 | 5 | 19.7 | 50.7 | 33.7 | 37.4 | 28.7 | 23.5 |
| PAPA008 | 2014 | 6 | 18.9 | 49.2 | 27.6 | 29.4 | 25.7 | 23.6 |
| PAPA008 | 2014 | 7 | 20.5 | 49.0 | 28.7 | 31.1 | 27.4 | 24.3 |
| PAPA008 | 2014 | 8 | 19.2 | 52.0 | 31.5 | 34.2 | 29.5 | 26.0 |
| PAPA008 | 2014 | 9 | 20.1 | 54.5 | 33.5 | 37.0 | 29.9 | 25.3 |
| PAPA008 | 2014 | 10 | 17.9 | 58.0 | 32.8 | 35.9 | 30.2 | 25.9 |
| PAPA008 | 2014 | 11 | 17.1 | 58.3 | 32.9 | 35.8 | 30.9 | 26.1 |
| PAPA008 | 2014 | 12 | 17.0 | 59.0 | 35.1 | 36.8 | 29.6 | 25.3 |
| PAPA008 | 2014 | 13 | 17.1 | 58.6 | 37.1 | 40.8 | 34.2 | 27.6 |
| PAPA008 | 2014 | 14 | 16.4 | 58.3 | 38.1 | 40.6 | 33.6 | 27.2 |
| PAPA008 | 2014 | 15 | 17.1 | 60.0 | 35.2 | 38.7 | 32.0 | 26.6 |
| PAPA008 | 2014 | 16 | 15.7 | 60.3 | 41.6 | 45.2 | 38.8 | 32.5 |
| PAPA008 | 2014 | 17 | 15.4 | 58.5 | 32.8 | 36.7 | 29.5 | 22.6 |
| PAPA008 | 2014 | 18 | 15.5 | 59.3 | 23.1 | 25.2 | 20.4 | 18.2 |
| PAPA008 | 2014 | 19 | 16.2 | 53.0 | 28.0 | 28.7 | 23.1 | 20.2 |
| PAPA008 | 2014 | 20 | 17.0 | 51.1 | 31.9 | 36.2 | 22.1 | 19.3 |
| PAPA008 | 2014 | 21 | 16.7 | 45.1 | 25.9 | 28.1 | 23.7 | 20.7 |
| PAPA008 | 2014 | 22 | 16.2 | 41.8 | 25.1 | 27.0 | 23.5 | 20.6 |
| PAPA008 | 2014 | 23 | 19.4 | 39.5 | 24.0 | 25.4 | 23.1 | 21.7 |
| PAPA009 | 2014 | 0 | 19.1 | 32.6 | 24.6 | 26.2 | 24.4 | 22.6 |
| PAPA009 | 2014 | 1 | 18.3 | 35.7 | 24.5 | 26.6 | 23.7 | 21.7 |
| PAPA009 | 2014 | 2 | 18.4 | 36.6 | 25.3 | 27.2 | 24.8 | 23.0 |
| PAPA009 | 2014 | 3 | 17.6 | 38.0 | 26.7 | 29.3 | 25.6 | 23.0 |
| PAPA009 | 2014 | 4 | 19.5 | 40.4 | 29.0 | 31.9 | 27.3 | 24.4 |
| PAPA009 | 2014 | 5 | 24.8 | 46.7 | 31.4 | 33.5 | 29.7 | 27.8 |

| Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA009 | 2014 | 6 | 23.5 | 42.8 | 30.6 | 33.7 | 28.5 | 26.3 |
| PAPA009 | 2014 | 7 | 20.5 | 34.8 | 27.3 | 28.8 | 26.8 | 25.2 |
| PAPA009 | 2014 | 8 | 17.0 | 40.7 | 27.0 | 29.5 | 25.7 | 23.0 |
| PAPA009 | 2014 | 9 | 15.7 | 53.1 | 25.9 | 26.9 | 24.1 | 22.7 |
| PAPA009 | 2014 | 10 | 16.8 | 45.4 | 24.3 | 25.3 | 22.5 | 20.8 |
| PAPA009 | 2014 | 11 | 16.3 | 46.2 | 24.0 | 27.0 | 21.2 | 18.2 |
| PAPA009 | 2014 | 12 | 16.9 | 55.3 | 30.7 | 31.4 | 22.9 | 19.6 |
| PAPA009 | 2014 | 13 | 17.7 | 56.5 | 30.6 | 30.9 | 22.9 | 19.8 |
| PAPA009 | 2014 | 14 | 17.6 | 62.5 | 29.7 | 33.8 | 25.9 | 20.6 |
| PAPA009 | 2014 | 15 | 16.7 | 48.6 | 26.9 | 29.9 | 24.3 | 19.6 |
| PAPA009 | 2014 | 16 | 17.0 | 65.4 | 32.3 | 35.9 | 29.1 | 22.7 |
| PAPA009 | 2014 | 17 | 15.6 | 53.9 | 32.1 | 35.6 | 28.5 | 22.6 |
| PAPA009 | 2014 | 18 | 15.9 | 54.8 | 28.5 | 31.9 | 26.0 | 21.1 |
| PAPA009 | 2014 | 19 | 15.2 | 51.1 | 25.6 | 29.0 | 21.4 | 18.6 |
| PAPA009 | 2014 | 20 | 15.9 | 60.7 | 27.5 | 30.2 | 25.4 | 21.3 |
| PAPA009 | 2014 | 21 | 17.3 | 58.5 | 24.9 | 26.4 | 24.1 | 22.8 |
| PAPA009 | 2014 | 22 | 17.9 | 55.2 | 23.6 | 25.5 | 23.0 | 21.1 |
| PAPA009 | 2014 | 23 | 17.8 | 46.0 | 24.6 | 26.5 | 24.5 | 21.6 |
| PAPA010 | 2014 | 0 | 20.6 | 47.0 | 30.1 | 32.0 | 29.5 | 25.3 |
| PAPA010 | 2014 | 1 | 18.8 | 39.0 | 28.7 | 31.1 | 27.4 | 25.1 |
| PAPA010 | 2014 | 2 | 18.4 | 39.6 | 28.2 | 30.3 | 27.1 | 23.2 |
| PAPA010 | 2014 | 3 | 20.6 | 42.8 | 29.3 | 32.4 | 27.9 | 24.7 |
| PAPA010 | 2014 | 4 | 20.7 | 44.0 | 30.8 | 33.4 | 29.5 | 26.7 |
| PAPA010 | 2014 | 5 | 23.7 | 49.0 | 33.1 | 36.3 | 31.3 | 27.9 |
| PAPA010 | 2014 | 6 | 20.3 | 42.8 | 31.2 | 33.4 | 30.3 | 28.6 |
| PAPA010 | 2014 | 7 | 22.6 | 39.9 | 31.3 | 33.6 | 30.6 | 28.2 |
| PAPA010 | 2014 | 8 | 19.9 | 42.7 | 32.2 | 35.9 | 30.2 | 26.4 |
| PAPA010 | 2014 | 9 | 19.3 | 51.1 | 32.5 | 35.0 | 30.8 | 27.3 |
| PAPA010 | 2014 | 10 | 19.7 | 58.1 | 33.1 | 35.9 | 30.0 | 25.1 |
| PAPA010 | 2014 | 11 | 19.3 | 94.0 | 35.4 | 37.1 | 31.2 | 25.4 |
| PAPA010 | 2014 | 12 | 20.5 | 62.2 | 37.2 | 37.7 | 31.7 | 25.5 |
| PAPA010 | 2014 | 13 | 20.7 | 70.4 | 37.9 | 37.5 | 32.6 | 27.5 |
| PAPA010 | 2014 | 14 | 20.0 | 55.9 | 33.4 | 36.7 | 30.3 | 25.0 |
| PAPA010 | 2014 | 15 | 18.9 | 56.4 | 32.8 | 35.7 | 27.6 | 23.1 |
| PAPA010 | 2014 | 16 | 19.0 | 61.5 | 36.4 | 39.6 | 29.8 | 24.0 |
| PAPA010 | 2014 | 17 | 17.8 | 53.7 | 32.5 | 36.0 | 29.4 | 24.7 |
| PAPA010 | 2014 | 18 | 17.4 | 58.2 | 30.2 | 33.7 | 27.5 | 22.4 |
| PAPA010 | 2014 | 19 | 16.8 | 53.4 | 29.5 | 32.3 | 26.8 | 23.5 |
| PAPA010 | 2014 | 20 | 17.6 | 45.5 | 29.9 | 32.9 | 29.0 | 21.8 |
| PAPA010 | 2014 | 21 | 18.6 | 51.8 | 30.4 | 32.7 | 29.7 | 27.0 |

| Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA010 | 2014 | 22 | 18.7 | 56.5 | 30.6 | 33.7 | 29.4 | 25.8 |
| PAPA010 | 2014 | 23 | 19.5 | 50.2 | 30.8 | 32.8 | 29.7 | 26.4 |
| PAPA011 | 2014 | 0 | 16.2 | 45.7 | 25.9 | 21.2 | 17.7 | 17.0 |
| PAPA011 | 2014 | 1 | 15.7 | 35.0 | 17.4 | 18.1 | 17.2 | 16.2 |
| PAPA011 | 2014 | 2 | 16.1 | 40.6 | 20.1 | 17.8 | 17.0 | 16.5 |
| PAPA011 | 2014 | 3 | 16.1 | 45.4 | 31.2 | 36.4 | 17.6 | 16.8 |
| PAPA011 | 2014 | 4 | 15.3 | 40.7 | 19.6 | 17.7 | 16.7 | 15.9 |
| PAPA011 | 2014 | 5 | 15.8 | 44.1 | 26.3 | 29.7 | 18.3 | 16.5 |
| PAPA011 | 2014 | 6 | 18.1 | 50.5 | 34.7 | 38.6 | 29.1 | 21.5 |
| PAPA011 | 2014 | 7 | 18.1 | 53.1 | 36.3 | 39.4 | 24.0 | 20.0 |
| PAPA011 | 2014 | 8 | NA | NA | NA | NA | NA | NA |
| PAPA011 | 2014 | 9 | NA | NA | NA | NA | NA | NA |
| PAPA011 | 2014 | 10 | NA | NA | NA | NA | NA | NA |
| PAPA011 | 2014 | 11 | NA | NA | NA | NA | NA | NA |
| PAPA011 | 2014 | 12 | NA | NA | NA | NA | NA | NA |
| PAPA011 | 2014 | 13 | NA | NA | NA | NA | NA | NA |
| PAPA011 | 2014 | 14 | 16.9 | 59.2 | 35.4 | 36.7 | 28.6 | 21.1 |
| PAPA011 | 2014 | 15 | 16.8 | 75.9 | 55.5 | 37.9 | 26.4 | 19.3 |
| PAPA011 | 2014 | 16 | 16.7 | 60.4 | 31.6 | 33.3 | 25.9 | 19.8 |
| PAPA011 | 2014 | 17 | 16.5 | 59.6 | 32.7 | 32.1 | 25.5 | 20.4 |
| PAPA011 | 2014 | 18 | 16.9 | 66.4 | 45.0 | 31.4 | 23.9 | 19.4 |
| PAPA011 | 2014 | 19 | 15.1 | 53.4 | 32.3 | 29.1 | 19.6 | 15.9 |
| PAPA011 | 2014 | 20 | 15.0 | 48.7 | 21.5 | 21.2 | 16.3 | 15.4 |
| PAPA011 | 2014 | 21 | 15.1 | 33.5 | 17.7 | 18.5 | 16.5 | 15.7 |
| PAPA011 | 2014 | 22 | 15.1 | 47.1 | 24.3 | 19.7 | 17.5 | 15.6 |
| PAPA011 | 2014 | 23 | 16.8 | 37.1 | 19.3 | 20.3 | 18.4 | 17.5 |
| PAPA012 | 2014 | 0 | 14.9 | 50.6 | 22.4 | 19.4 | 17.9 | 16.9 |
| PAPA012 | 2014 | 1 | 14.4 | 55.2 | 21.9 | 23.7 | 17.7 | 16.1 |
| PAPA012 | 2014 | 2 | 14.6 | 39.5 | 20.5 | 23.3 | 17.8 | 15.5 |
| PAPA012 | 2014 | 3 | 14.2 | 47.6 | 20.9 | 22.9 | 19.3 | 17.5 |
| PAPA012 | 2014 | 4 | 14.5 | 44.5 | 21.9 | 23.8 | 21.1 | 18.5 |
| PAPA012 | 2014 | 5 | 15.3 | 42.3 | 24.4 | 27.2 | 23.2 | 19.3 |
| PAPA012 | 2014 | 6 | 15.2 | 71.6 | 25.9 | 28.5 | 24.0 | 21.5 |
| PAPA012 | 2014 | 7 | 15.1 | 63.3 | 25.4 | 27.3 | 22.5 | 18.9 |
| PAPA012 | 2014 | 8 | 15.0 | 51.0 | 29.3 | 29.9 | 21.4 | 17.2 |
| PAPA012 | 2014 | 9 | 15.3 | 64.2 | 27.5 | 29.0 | 17.3 | 16.2 |
| PAPA012 | 2014 | 10 | 14.9 | 54.3 | 27.3 | 26.7 | 17.3 | 16.4 |
| PAPA012 | 2014 | 11 | 15.2 | 45.9 | 22.2 | 21.4 | 18.3 | 16.5 |
| PAPA012 | 2014 | 12 | 15.2 | 56.8 | 27.3 | 25.0 | 18.4 | 16.6 |
| PAPA012 | 2014 | 13 | 15.9 | 59.8 | 31.4 | 29.1 | 22.1 | 18.6 |

| Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA012 | 2014 | 14 | 15.4 | 51.7 | 32.2 | 32.0 | 24.8 | 19.0 |
| PAPA012 | 2014 | 15 | 15.6 | 49.5 | 27.8 | 31.8 | 23.3 | 18.5 |
| PAPA012 | 2014 | 16 | 14.5 | 53.7 | 28.0 | 29.4 | 23.1 | 19.2 |
| PAPA012 | 2014 | 17 | 14.2 | 66.3 | 26.2 | 29.5 | 23.0 | 18.4 |
| PAPA012 | 2014 | 18 | 14.4 | 68.8 | 24.5 | 23.6 | 18.1 | 16.1 |
| PAPA012 | 2014 | 19 | 14.7 | 47.7 | 24.3 | 23.8 | 19.7 | 17.8 |
| PAPA012 | 2014 | 20 | 14.3 | 46.5 | 22.9 | 18.5 | 16.3 | 15.1 |
| PAPA012 | 2014 | 21 | 14.5 | 41.2 | 21.2 | 22.8 | 18.0 | 16.6 |
| PAPA012 | 2014 | 22 | 14.2 | 61.3 | 22.2 | 23.2 | 17.1 | 15.8 |
| PAPA012 | 2014 | 23 | 14.7 | 44.0 | 23.8 | 21.0 | 18.7 | 16.3 |
| PAPA013 | 2014 | 0 | 22.0 | 44.8 | 29.1 | 31.4 | 27.6 | 24.5 |
| PAPA013 | 2014 | 1 | 20.4 | 38.5 | 27.1 | 29.0 | 26.7 | 24.7 |
| PAPA013 | 2014 | 2 | 20.8 | 43.3 | 29.7 | 32.5 | 28.8 | 25.8 |
| PAPA013 | 2014 | 3 | 16.7 | 50.5 | 27.2 | 30.1 | 25.9 | 23.7 |
| PAPA013 | 2014 | 4 | 16.7 | 40.7 | 29.1 | 31.3 | 27.8 | 25.5 |
| PAPA013 | 2014 | 5 | 17.3 | 41.2 | 28.1 | 30.4 | 27.0 | 23.8 |
| PAPA013 | 2014 | 6 | 17.3 | 48.0 | 29.3 | 30.8 | 27.4 | 24.7 |
| PAPA013 | 2014 | 7 | 15.7 | 70.9 | 42.1 | 30.1 | 25.7 | 24.2 |
| PAPA013 | 2014 | 8 | 15.2 | 60.5 | 33.0 | 31.0 | 24.8 | 19.3 |
| PAPA013 | 2014 | 9 | 15.2 | 53.6 | 27.6 | 27.3 | 20.1 | 17.4 |
| PAPA013 | 2014 | 10 | 15.7 | 54.7 | 26.6 | 24.8 | 17.7 | 16.8 |
| PAPA013 | 2014 | 11 | 16.7 | 65.8 | 21.4 | 22.3 | 19.5 | 18.0 |
| PAPA013 | 2014 | 12 | 16.8 | 66.4 | 26.8 | 26.1 | 21.8 | 20.0 |
| PAPA013 | 2014 | 13 | 16.6 | 51.1 | 25.8 | 27.1 | 23.5 | 21.6 |
| PAPA013 | 2014 | 14 | 16.3 | 52.7 | 31.8 | 32.9 | 25.9 | 21.4 |
| PAPA013 | 2014 | 15 | 16.2 | 52.6 | 29.2 | 32.2 | 26.6 | 22.1 |
| PAPA013 | 2014 | 16 | 15.9 | 56.5 | 29.1 | 31.3 | 25.7 | 21.5 |
| PAPA013 | 2014 | 17 | 15.1 | 50.3 | 27.4 | 28.6 | 22.3 | 17.7 |
| PAPA013 | 2014 | 18 | 14.5 | 59.9 | 23.1 | 25.1 | 18.9 | 16.5 |
| PAPA013 | 2014 | 19 | 14.3 | 46.8 | 22.4 | 24.8 | 20.4 | 18.2 |
| PAPA013 | 2014 | 20 | 14.9 | 52.9 | 29.4 | 28.8 | 21.6 | 17.3 |
| PAPA013 | 2014 | 21 | 15.8 | 45.4 | 23.0 | 24.6 | 19.9 | 17.7 |
| PAPA013 | 2014 | 22 | 16.8 | 65.1 | 27.6 | 26.2 | 21.4 | 19.2 |
| PAPA013 | 2014 | 23 | 18.0 | 45.8 | 28.7 | 31.0 | 25.4 | 21.8 |
| PAPA014 | 2014 | 0 | 25.1 | 39.7 | 29.7 | 31.5 | 29.1 | 26.8 |
| PAPA014 | 2014 | 1 | 24.7 | 37.4 | 28.6 | 30.2 | 28.3 | 26.6 |
| PAPA014 | 2014 | 2 | 24.5 | 39.4 | 28.3 | 29.7 | 28.0 | 26.5 |
| PAPA014 | 2014 | 3 | 24.9 | 41.3 | 30.1 | 31.8 | 29.6 | 27.1 |
| PAPA014 | 2014 | 4 | 26.3 | 40.4 | 32.0 | 33.4 | 31.7 | 30.3 |
| PAPA014 | 2014 | 5 | 25.8 | 43.4 | 32.7 | 34.8 | 31.9 | 29.7 |

| Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA014 | 2014 | 6 | 27.2 | 44.0 | 30.9 | 32.5 | 30.4 | 28.9 |
| PAPA014 | 2014 | 7 | 26.6 | 43.6 | 34.0 | 36.7 | 33.1 | 30.0 |
| PAPA014 | 2014 | 8 | 27.3 | 43.4 | 32.1 | 34.7 | 31.0 | 28.6 |
| PAPA014 | 2014 | 9 | 23.3 | 41.5 | 28.4 | 30.1 | 27.7 | 25.0 |
| PAPA014 | 2014 | 10 | 21.0 | 30.4 | 25.0 | 26.9 | 25.2 | 21.5 |
| PAPA014 | 2014 | 11 | 21.0 | 34.0 | 22.6 | 23.7 | 22.0 | 21.4 |
| PAPA014 | 2014 | 12 | 21.3 | 38.7 | 24.2 | 26.1 | 22.9 | 21.9 |
| PAPA014 | 2014 | 13 | 21.3 | 59.2 | 32.0 | 34.6 | 23.0 | 22.1 |
| PAPA014 | 2014 | 14 | 22.4 | 60.0 | 36.7 | 38.5 | 35.4 | 31.7 |
| PAPA014 | 2014 | 15 | 21.6 | 63.7 | 36.5 | 38.7 | 35.2 | 30.1 |
| PAPA014 | 2014 | 16 | 21.9 | 65.2 | 39.8 | 40.0 | 35.6 | 30.9 |
| PAPA014 | 2014 | 17 | 21.9 | 61.6 | 35.6 | 37.9 | 34.5 | 30.5 |
| PAPA014 | 2014 | 18 | 21.8 | 62.1 | 37.9 | 39.1 | 32.4 | 28.1 |
| PAPA014 | 2014 | 19 | 23.3 | 63.3 | 39.1 | 42.6 | 37.1 | 28.6 |
| PAPA014 | 2014 | 20 | 25.5 | 59.7 | 38.3 | 41.4 | 35.4 | 29.8 |
| PAPA014 | 2014 | 21 | 26.0 | 56.6 | 36.6 | 39.7 | 33.9 | 29.4 |
| PAPA014 | 2014 | 22 | 23.8 | 48.4 | 30.3 | 32.1 | 29.1 | 27.1 |
| PAPA014 | 2014 | 23 | 24.2 | 42.7 | 30.3 | 31.7 | 29.6 | 28.1 |
| PAPA015 | 2014 | 0 | 13.5 | 38.0 | 18.1 | 19.2 | 17.2 | 16.2 |
| PAPA015 | 2014 | 1 | 13.6 | 42.4 | 21.3 | 20.3 | 17.5 | 16.1 |
| PAPA015 | 2014 | 2 | 13.5 | 40.8 | 18.4 | 17.6 | 16.0 | 14.5 |
| PAPA015 | 2014 | 3 | 13.7 | 37.5 | 17.5 | 18.6 | 17.0 | 15.2 |
| PAPA015 | 2014 | 4 | 15.7 | 24.8 | 18.4 | 19.5 | 18.2 | 17.0 |
| PAPA015 | 2014 | 5 | 15.8 | 41.8 | 21.2 | 22.7 | 19.4 | 17.7 |
| PAPA015 | 2014 | 6 | 16.2 | 59.8 | 30.7 | 26.8 | 21.2 | 18.7 |
| PAPA015 | 2014 | 7 | 15.3 | 38.3 | 24.3 | 27.8 | 20.1 | 18.2 |
| PAPA015 | 2014 | 8 | 16.7 | 37.7 | 24.0 | 27.0 | 20.2 | 18.2 |
| PAPA015 | 2014 | 9 | 17.1 | 56.2 | 32.8 | 32.2 | 22.1 | 18.7 |
| PAPA015 | 2014 | 10 | 15.5 | 39.8 | 20.2 | 21.4 | 17.7 | 16.2 |
| PAPA015 | 2014 | 11 | 15.1 | 62.0 | 33.3 | 23.4 | 17.2 | 15.9 |
| PAPA015 | 2014 | 12 | 15.2 | 59.0 | 33.5 | 33.4 | 23.7 | 17.7 |
| PAPA015 | 2014 | 13 | 15.2 | 51.1 | 31.7 | 35.4 | 26.0 | 18.9 |
| PAPA015 | 2014 | 14 | 15.9 | 51.9 | 32.6 | 36.4 | 27.4 | 19.9 |
| PAPA015 | 2014 | 15 | 15.6 | 56.4 | 35.6 | 39.0 | 31.3 | 22.5 |
| PAPA015 | 2014 | 16 | 19.8 | 54.2 | 36.9 | 40.5 | 33.2 | 26.8 |
| PAPA015 | 2014 | 17 | 16.4 | 49.9 | 34.5 | 38.2 | 30.9 | 24.6 |
| PAPA015 | 2014 | 18 | 16.5 | 47.0 | 32.7 | 36.2 | 29.8 | 24.1 |
| PAPA015 | 2014 | 19 | 13.8 | 57.5 | 27.4 | 29.6 | 19.2 | 14.4 |
| PAPA015 | 2014 | 20 | 13.7 | 40.8 | 15.6 | 16.0 | 14.5 | 14.0 |
| PAPA015 | 2014 | 21 | 13.6 | 42.7 | 19.5 | 15.8 | 14.4 | 13.9 |

| Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA015 | 2014 | 22 | 13.5 | 52.3 | 22.5 | 19.5 | 14.9 | 13.9 |
| PAPA015 | 2014 | 23 | 13.6 | 33.8 | 17.9 | 18.9 | 17.3 | 16.3 |
| PAPA016 | 2014 | 0 | 14.7 | 49.7 | 20.5 | 22.8 | 18.5 | 16.3 |
| PAPA016 | 2014 | 1 | 15.2 | 50.2 | 23.3 | 27.0 | 19.9 | 16.5 |
| PAPA016 | 2014 | 2 | 15.2 | 44.4 | 21.7 | 24.2 | 20.6 | 17.9 |
| PAPA016 | 2014 | 3 | 15.1 | 42.5 | 20.3 | 22.8 | 18.4 | 17.5 |
| PAPA016 | 2014 | 4 | 15.1 | 41.4 | 20.9 | 23.3 | 18.8 | 16.5 |
| PAPA016 | 2014 | 5 | 15.2 | 43.4 | 27.7 | 29.5 | 23.9 | 19.7 |
| PAPA016 | 2014 | 6 | 15.3 | 49.8 | 23.7 | 25.3 | 22.3 | 19.7 |
| PAPA016 | 2014 | 7 | 15.6 | 70.5 | 30.1 | 27.3 | 25.1 | 23.0 |
| PAPA016 | 2014 | 8 | 16.0 | 47.5 | 29.1 | 31.7 | 26.1 | 23.1 |
| PAPA016 | 2014 | 9 | 16.2 | 55.7 | 28.8 | 31.3 | 27.2 | 23.7 |
| PAPA016 | 2014 | 10 | 17.5 | 55.4 | 33.5 | 36.9 | 30.6 | 21.3 |
| PAPA016 | 2014 | 11 | 17.5 | 55.5 | 36.6 | 40.1 | 33.3 | 27.0 |
| PAPA016 | 2014 | 12 | 17.0 | 57.5 | 33.3 | 35.9 | 29.9 | 26.0 |
| PAPA016 | 2014 | 13 | 16.4 | 91.5 | 43.7 | 47.3 | 34.2 | 26.6 |
| PAPA016 | 2014 | 14 | 16.4 | 81.5 | 42.3 | 42.4 | 33.4 | 27.7 |
| PAPA016 | 2014 | 15 | 16.7 | 55.7 | 36.1 | 38.2 | 34.0 | 29.6 |
| PAPA016 | 2014 | 16 | 15.6 | 73.2 | 41.0 | 39.9 | 33.0 | 28.0 |
| PAPA016 | 2014 | 17 | 15.4 | 92.8 | 41.7 | 42.1 | 29.8 | 24.3 |
| PAPA016 | 2014 | 18 | 16.2 | 56.6 | 29.5 | 32.2 | 25.7 | 21.0 |
| PAPA016 | 2014 | 19 | 15.3 | 52.5 | 25.3 | 28.1 | 23.1 | 19.4 |
| PAPA016 | 2014 | 20 | 15.1 | 57.2 | 25.8 | 27.4 | 20.6 | 17.1 |
| PAPA016 | 2014 | 21 | 14.9 | 49.2 | 25.4 | 24.5 | 19.3 | 16.4 |
| PAPA016 | 2014 | 22 | 14.8 | 46.1 | 24.9 | 23.9 | 18.2 | 16.1 |
| PAPA016 | 2014 | 23 | 14.8 | 46.0 | 21.3 | 20.6 | 17.3 | 15.8 |
| PAPA017 | 2014 | 0 | 23.5 | 40.7 | 31.5 | 33.2 | 31.1 | 29.3 |
| PAPA017 | 2014 | 1 | 24.4 | 40.9 | 31.8 | 33.7 | 31.4 | 29.3 |
| PAPA017 | 2014 | 2 | 27.7 | 45.8 | 33.6 | 35.3 | 33.3 | 31.4 |
| PAPA017 | 2014 | 3 | 28.1 | 43.4 | 34.5 | 37.0 | 33.5 | 31.7 |
| PAPA017 | 2014 | 4 | 26.3 | 45.3 | 34.1 | 36.5 | 32.9 | 30.6 |
| PAPA017 | 2014 | 5 | 29.5 | 42.6 | 34.8 | 36.3 | 34.4 | 32.8 |
| PAPA017 | 2014 | 6 | 28.9 | 55.9 | 36.4 | 37.9 | 35.1 | 32.8 |
| PAPA017 | 2014 | 7 | 29.9 | 59.0 | 36.2 | 37.2 | 35.0 | 33.3 |
| PAPA017 | 2014 | 8 | 28.5 | 56.9 | 36.2 | 37.9 | 35.1 | 32.2 |
| PAPA017 | 2014 | 9 | 22.9 | 52.9 | 31.9 | 32.9 | 28.7 | 26.3 |
| PAPA017 | 2014 | 10 | 17.4 | 51.3 | 29.1 | 30.7 | 26.2 | 24.5 |
| PAPA017 | 2014 | 11 | 16.7 | 68.0 | 31.3 | 28.3 | 22.8 | 21.2 |
| PAPA017 | 2014 | 12 | 17.9 | 61.8 | 36.1 | 31.3 | 24.7 | 20.7 |
| PAPA017 | 2014 | 13 | 19.4 | 62.5 | 36.2 | 36.2 | 28.8 | 23.8 |

| Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA017 | 2014 | 14 | 18.9 | 48.0 | 29.9 | 33.2 | 26.4 | 22.1 |
| PAPA017 | 2014 | 15 | 17.6 | 47.0 | 24.3 | 26.1 | 22.8 | 20.1 |
| PAPA017 | 2014 | 16 | 18.3 | 54.9 | 29.8 | 31.5 | 26.4 | 22.8 |
| PAPA017 | 2014 | 17 | 17.9 | 64.0 | 32.0 | 30.0 | 24.1 | 21.0 |
| PAPA017 | 2014 | 18 | 16.9 | 51.5 | 28.4 | 29.5 | 22.9 | 20.3 |
| PAPA017 | 2014 | 19 | 15.2 | 53.8 | 29.8 | 29.7 | 23.1 | 20.4 |
| PAPA017 | 2014 | 20 | 18.2 | 49.0 | 29.3 | 29.8 | 25.9 | 24.3 |
| PAPA017 | 2014 | 21 | 19.9 | 45.2 | 28.7 | 30.1 | 26.6 | 25.0 |
| PAPA017 | 2014 | 22 | 21.8 | 38.2 | 29.4 | 31.2 | 28.9 | 26.7 |
| PAPA017 | 2014 | 23 | 24.4 | 38.5 | 32.0 | 34.0 | 31.7 | 29.3 |
| PAPA018 | 2014 | 0 | 13.8 | 44.6 | 20.8 | 22.7 | 18.1 | 15.1 |
| PAPA018 | 2014 | 1 | 13.5 | 37.9 | 18.0 | 19.4 | 16.6 | 15.0 |
| PAPA018 | 2014 | 2 | 13.6 | 20.2 | 15.2 | 16.0 | 15.1 | 14.6 |
| PAPA018 | 2014 | 3 | 13.6 | 26.9 | 15.8 | 16.7 | 15.2 | 14.7 |
| PAPA018 | 2014 | 4 | 13.8 | 32.9 | 16.4 | 17.4 | 15.6 | 14.5 |
| PAPA018 | 2014 | 5 | 14.0 | 34.2 | 17.3 | 18.9 | 16.1 | 15.0 |
| PAPA018 | 2014 | 6 | 15.8 | 45.1 | 28.9 | 32.7 | 25.6 | 19.8 |
| PAPA018 | 2014 | 7 | 15.6 | 66.6 | 38.4 | 36.6 | 26.3 | 20.7 |
| PAPA018 | 2014 | 8 | 16.9 | 64.5 | 36.9 | 32.6 | 22.8 | 19.4 |
| PAPA018 | 2014 | 9 | 15.9 | 73.1 | 53.9 | 38.8 | 20.5 | 18.1 |
| PAPA018 | 2014 | 10 | 15.3 | 51.0 | 26.7 | 27.6 | 19.2 | 16.5 |
| PAPA018 | 2014 | 11 | 15.4 | 46.8 | 24.8 | 26.7 | 20.1 | 17.5 |
| PAPA018 | 2014 | 12 | 16.7 | 51.3 | 30.0 | 32.2 | 24.9 | 19.9 |
| PAPA018 | 2014 | 13 | 16.0 | 48.0 | 27.9 | 31.4 | 23.9 | 19.2 |
| PAPA018 | 2014 | 14 | 16.6 | 49.5 | 32.0 | 35.9 | 28.1 | 22.1 |
| PAPA018 | 2014 | 15 | 15.9 | 49.9 | 31.2 | 34.9 | 27.5 | 21.3 |
| PAPA018 | 2014 | 16 | 15.9 | 48.8 | 31.6 | 34.3 | 26.7 | 21.2 |
| PAPA018 | 2014 | 17 | 15.6 | 46.1 | 30.0 | 33.4 | 25.4 | 20.0 |
| PAPA018 | 2014 | 18 | 14.7 | 56.2 | 31.2 | 31.6 | 23.9 | 20.1 |
| PAPA018 | 2014 | 19 | 14.0 | 50.2 | 27.3 | 27.7 | 20.2 | 16.5 |
| PAPA018 | 2014 | 20 | 14.8 | 62.8 | 30.0 | 30.0 | 18.9 | 16.7 |
| PAPA018 | 2014 | 21 | 14.4 | 45.0 | 22.3 | 22.2 | 18.7 | 15.5 |
| PAPA018 | 2014 | 22 | 14.1 | 46.3 | 21.6 | 23.8 | 16.5 | 15.1 |
| PAPA018 | 2014 | 23 | 13.9 | 22.4 | 17.3 | 19.0 | 16.9 | 15.4 |
| PAPA019 | 2014 | 0 | 14.5 | 48.3 | 25.2 | 26.6 | 21.3 | 16.1 |
| PAPA019 | 2014 | 1 | 14.5 | 44.9 | 21.4 | 23.3 | 18.0 | 16.4 |
| PAPA019 | 2014 | 2 | 14.5 | 28.7 | 16.3 | 17.3 | 15.9 | 15.2 |
| PAPA019 | 2014 | 3 | 14.5 | 33.6 | 16.3 | 16.3 | 15.2 | 14.8 |
| PAPA019 | 2014 | 4 | 14.6 | 28.5 | 15.7 | 16.0 | 15.3 | 14.9 |
| PAPA019 | 2014 | 5 | 14.7 | 54.5 | 22.3 | 17.6 | 15.5 | 15.0 |

| Appendix C. Hourly dBA Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Hour | Lmin | Lmax | Leq | L10 | L50 | L90 |
| PAPA019 | 2014 | 6 | 15.9 | 50.4 | 31.0 | 32.6 | 20.7 | 17.7 |
| PAPA019 | 2014 | 7 | 15.7 | 67.3 | 38.8 | 30.9 | 21.8 | 17.9 |
| PAPA019 | 2014 | 8 | 16.1 | 53.6 | 32.4 | 29.7 | 18.5 | 17.1 |
| PAPA019 | 2014 | 9 | 16.2 | 55.3 | 32.0 | 27.8 | 18.6 | 17.1 |
| PAPA019 | 2014 | 10 | 16.5 | 60.1 | 36.7 | 25.6 | 19.7 | 17.6 |
| PAPA019 | 2014 | 11 | 16.4 | 45.4 | 28.9 | 32.5 | 20.8 | 17.8 |
| PAPA019 | 2014 | 12 | 16.1 | 52.2 | 31.7 | 34.1 | 25.8 | 20.3 |
| PAPA019 | 2014 | 13 | 15.8 | 59.3 | 33.5 | 31.4 | 23.5 | 19.2 |
| PAPA019 | 2014 | 14 | 16.2 | 52.4 | 33.2 | 35.4 | 27.8 | 21.7 |
| PAPA019 | 2014 | 15 | 15.8 | 51.0 | 31.0 | 34.8 | 26.6 | 20.4 |
| PAPA019 | 2014 | 16 | 15.9 | 47.9 | 30.5 | 33.9 | 26.6 | 20.7 |
| PAPA019 | 2014 | 17 | 15.4 | 55.0 | 33.1 | 33.7 | 26.3 | 21.0 |
| PAPA019 | 2014 | 18 | 15.3 | 54.9 | 31.9 | 29.6 | 23.0 | 19.1 |
| PAPA019 | 2014 | 19 | 15.1 | 47.3 | 24.3 | 24.1 | 17.3 | 15.7 |
| PAPA019 | 2014 | 20 | 14.8 | 37.6 | 19.2 | 20.7 | 16.8 | 15.5 |
| PAPA019 | 2014 | 21 | 14.7 | 40.9 | 21.2 | 18.7 | 15.8 | 15.2 |
| PAPA019 | 2014 | 22 | 14.6 | 51.9 | 21.2 | 21.4 | 15.2 | 14.8 |
| PAPA019 | 2014 | 23 | 14.6 | 26.7 | 16.2 | 17.0 | 16.0 | 15.1 |

## Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013.

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA001 | 2013 | 12.5 | 44.9 | 48.2 | 43.3 | 38.7 | 22.0 | 73.0 |
| PAPA001 | 2013 | 15.8 | 47.0 | 49.6 | 46.0 | 42.2 | 27.0 | 70.5 |
| PAPA001 | 2013 | 20 | 53.2 | 56.0 | 52.2 | 48.1 | 34.6 | 74.0 |
| PAPA001 | 2013 | 25 | 50.6 | 53.2 | 49.0 | 45.7 | 34.9 | 67.2 |
| PAPA001 | 2013 | 31.5 | 63.0 | 66.4 | 61.5 | 56.1 | 40.2 | 75.0 |
| PAPA001 | 2013 | 40 | 50.2 | 52.5 | 49.8 | 47.3 | 32.8 | 66.1 |
| PAPA001 | 2013 | 50 | 53.3 | 55.5 | 52.9 | 50.1 | 35.5 | 68.7 |
| PAPA001 | 2013 | 63 | 52.5 | 54.8 | 52.0 | 49.6 | 34.9 | 69.5 |
| PAPA001 | 2013 | 80 | 49.5 | 51.4 | 48.3 | 45.9 | 29.0 | 71.7 |
| PAPA001 | 2013 | 100 | 47.2 | 49.4 | 45.9 | 43.0 | 28.8 | 66.5 |
| PAPA001 | 2013 | 125 | 42.8 | 44.6 | 40.4 | 37.6 | 23.7 | 67.1 |
| PAPA001 | 2013 | 160 | 39.7 | 41.3 | 36.7 | 32.2 | 19.5 | 67.1 |
| PAPA001 | 2013 | 200 | 38.8 | 39.8 | 35.4 | 30.1 | 17.7 | 66.6 |
| PAPA001 | 2013 | 250 | 37.1 | 38.3 | 33.2 | 28.5 | 13.7 | 61.5 |
| PAPA001 | 2013 | 315 | 34.2 | 36.3 | 31.6 | 26.1 | 10.8 | 57.2 |
| PAPA001 | 2013 | 400 | 32.7 | 35.0 | 30.4 | 24.8 | 8.0 | 55.6 |
| PAPA001 | 2013 | 500 | 24.9 | 27.6 | 22.7 | 16.5 | 3.5 | 53.2 |
| PAPA001 | 2013 | 630 | 22.1 | 23.0 | 18.5 | 13.5 | 1.8 | 50.8 |
| PAPA001 | 2013 | 800 | 22.7 | 24.5 | 19.8 | 14.7 | 2.1 | 49.8 |
| PAPA001 | 2013 | 1000 | 24.4 | 26.0 | 21.0 | 15.8 | 2.4 | 48.3 |
| PAPA001 | 2013 | 1250 | 23.2 | 26.3 | 20.7 | 14.9 | 2.2 | 46.8 |
| PAPA001 | 2013 | 1600 | 21.7 | 24.5 | 19.4 | 13.1 | 1.6 | 44.8 |
| PAPA001 | 2013 | 2000 | 20.5 | 21.8 | 17.3 | 12.6 | 1.8 | 58.6 |
| PAPA001 | 2013 | 2500 | 12.8 | 15.2 | 10.2 | 6.3 | 2.3 | 63.1 |
| PAPA001 | 2013 | 3150 | 8.6 | 9.7 | 5.2 | 4.1 | 3.0 | 57.3 |
| PAPA001 | 2013 | 4000 | 5.3 | 5.2 | 4.5 | 4.2 | 3.7 | 47.8 |
| PAPA001 | 2013 | 5000 | 5.4 | 5.3 | 5.0 | 4.8 | 4.3 | 47.3 |
| PAPA001 | 2013 | 6300 | 5.4 | 5.5 | 5.3 | 5.2 | 4.2 | 44.6 |
| PAPA001 | 2013 | 8000 | 5.4 | 5.5 | 5.3 | 5.2 | 3.4 | 43.8 |
| PAPA001 | 2013 | 10000 | 5.0 | 5.1 | 5.0 | 4.8 | 2.3 | 41.6 |
| PAPA001 | 2013 | 12500 | 4.2 | 4.3 | 4.2 | 4.1 | 1.6 | 39.8 |
| PAPA001 | 2013 | 16000 | 3.2 | 3.3 | 3.2 | 3.1 | 0.6 | 37.4 |
| PAPA001 | 2013 | 20000 | 1.8 | 1.9 | 1.8 | 1.7 | 1.3 | 33.4 |
| PAPA002 | 2013 | 12.5 | 50.8 | 54.5 | 47.3 | 41.0 | 23.9 | 78.7 |
| PAPA002 | 2013 | 15.8 | 49.3 | 51.9 | 48.1 | 44.3 | 29.8 | 75.3 |
| PAPA002 | 2013 | 20 | 55.9 | 58.2 | 54.8 | 50.6 | 36.9 | 77.4 |
| PAPA002 | 2013 | 25 | 51.7 | 55.7 | 46.5 | 42.7 | 30.4 | 74.0 |
| PAPA002 | 2013 | 31.5 | 48.9 | 52.2 | 47.1 | 43.0 | 31.2 | 72.5 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA002 | 2013 | 40 | 44.3 | 46.5 | 43.5 | 40.8 | 29.4 | 70.4 |
| PAPA002 | 2013 | 50 | 44.2 | 46.2 | 43.3 | 40.8 | 30.6 | 67.4 |
| PAPA002 | 2013 | 63 | 41.9 | 44.2 | 40.2 | 37.0 | 27.7 | 65.6 |
| PAPA002 | 2013 | 80 | 39.6 | 42.5 | 37.2 | 34.0 | 23.3 | 71.6 |
| PAPA002 | 2013 | 100 | 37.6 | 39.9 | 35.6 | 32.2 | 21.6 | 70.5 |
| PAPA002 | 2013 | 125 | 35.6 | 37.2 | 32.9 | 30.0 | 18.9 | 62.4 |
| PAPA002 | 2013 | 160 | 35.3 | 36.5 | 31.5 | 27.4 | 16.7 | 62.1 |
| PAPA002 | 2013 | 200 | 31.5 | 32.5 | 28.8 | 25.4 | 13.6 | 59.3 |
| PAPA002 | 2013 | 250 | 28.7 | 31.4 | 25.9 | 22.2 | 12.2 | 55.4 |
| PAPA002 | 2013 | 315 | 26.3 | 29.0 | 24.5 | 20.8 | 10.3 | 55.0 |
| PAPA002 | 2013 | 400 | 23.6 | 25.8 | 20.9 | 16.4 | 5.0 | 54.0 |
| PAPA002 | 2013 | 500 | 19.7 | 21.5 | 16.7 | 12.2 | 1.0 | 51.5 |
| PAPA002 | 2013 | 630 | 17.1 | 19.9 | 13.4 | 9.0 | -0.7 | 46.9 |
| PAPA002 | 2013 | 800 | 14.6 | 18.0 | 9.9 | 5.5 | -1.5 | 42.0 |
| PAPA002 | 2013 | 1000 | 12.7 | 15.2 | 7.1 | 2.8 | -1.3 | 42.5 |
| PAPA002 | 2013 | 1250 | 9.7 | 10.6 | 4.0 | 1.5 | -0.9 | 40.5 |
| PAPA002 | 2013 | 1600 | 6.1 | 8.1 | 2.5 | 1.5 | -0.2 | 41.8 |
| PAPA002 | 2013 | 2000 | 3.9 | 4.5 | 2.5 | 1.8 | 0.6 | 42.4 |
| PAPA002 | 2013 | 2500 | 4.3 | 4.4 | 2.9 | 2.5 | 1.5 | 44.2 |
| PAPA002 | 2013 | 3150 | 4.0 | 4.1 | 3.4 | 3.1 | 2.3 | 41.9 |
| PAPA002 | 2013 | 4000 | 5.7 | 4.8 | 4.0 | 3.7 | 3.1 | 43.5 |
| PAPA002 | 2013 | 5000 | 6.7 | 5.1 | 4.4 | 4.2 | 3.7 | 53.6 |
| PAPA002 | 2013 | 6300 | 5.4 | 4.9 | 4.6 | 4.4 | 2.7 | 53.7 |
| PAPA002 | 2013 | 8000 | 4.6 | 4.7 | 4.5 | 4.4 | 2.1 | 38.2 |
| PAPA002 | 2013 | 10000 | 4.3 | 4.4 | 4.3 | 4.1 | 1.8 | 36.1 |
| PAPA002 | 2013 | 12500 | 3.8 | 3.9 | 3.8 | 3.6 | 0.4 | 35.8 |
| PAPA002 | 2013 | 16000 | 3.0 | 3.1 | 3.0 | 2.9 | 0.3 | 34.9 |
| PAPA002 | 2013 | 20000 | 1.8 | 1.8 | 1.8 | 1.7 | 1.1 | 34.8 |
| PAPA003 | 2013 | 12.5 | 49.1 | 51.4 | 44.9 | 39.1 | 21.8 | 81.6 |
| PAPA003 | 2013 | 15.8 | 48.8 | 51.3 | 46.5 | 42.0 | 29.0 | 77.8 |
| PAPA003 | 2013 | 20 | 53.1 | 56.2 | 51.3 | 47.0 | 34.9 | 74.4 |
| PAPA003 | 2013 | 25 | 48.5 | 51.9 | 46.2 | 42.3 | 31.3 | 73.2 |
| PAPA003 | 2013 | 31.5 | 52.7 | 56.1 | 51.5 | 46.3 | 33.3 | 68.2 |
| PAPA003 | 2013 | 40 | 45.1 | 47.8 | 44.1 | 40.0 | 27.5 | 66.4 |
| PAPA003 | 2013 | 50 | 43.4 | 45.8 | 42.1 | 37.7 | 26.9 | 64.8 |
| PAPA003 | 2013 | 63 | 42.9 | 45.4 | 41.1 | 37.2 | 24.8 | 67.1 |
| PAPA003 | 2013 | 80 | 40.9 | 43.4 | 39.0 | 34.1 | 14.5 | 69.1 |
| PAPA003 | 2013 | 100 | 38.6 | 40.8 | 36.4 | 32.3 | 16.9 | 70.5 |
| PAPA003 | 2013 | 125 | 36.5 | 38.0 | 33.9 | 30.5 | 16.4 | 63.0 |
| PAPA003 | 2013 | 160 | 35.0 | 36.0 | 31.5 | 27.8 | 16.0 | 65.3 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA003 | 2013 | 200 | 32.4 | 33.1 | 29.1 | 25.3 | 13.7 | 60.1 |
| PAPA003 | 2013 | 250 | 29.2 | 31.2 | 25.9 | 22.7 | 8.7 | 56.4 |
| PAPA003 | 2013 | 315 | 27.2 | 29.1 | 24.5 | 20.3 | 7.3 | 53.8 |
| PAPA003 | 2013 | 400 | 23.9 | 26.4 | 21.0 | 17.0 | 2.9 | 50.7 |
| PAPA003 | 2013 | 500 | 21.0 | 22.8 | 16.8 | 12.4 | -0.1 | 50.8 |
| PAPA003 | 2013 | 630 | 18.3 | 20.2 | 13.9 | 8.6 | -1.4 | 47.6 |
| PAPA003 | 2013 | 800 | 15.0 | 17.7 | 10.7 | 5.3 | -2.0 | 41.6 |
| PAPA003 | 2013 | 1000 | 12.7 | 15.2 | 8.5 | 3.5 | -1.5 | 39.4 |
| PAPA003 | 2013 | 1250 | 9.7 | 12.2 | 5.1 | 1.8 | -1.0 | 39.4 |
| PAPA003 | 2013 | 1600 | 6.8 | 9.3 | 2.8 | 1.5 | -0.2 | 36.4 |
| PAPA003 | 2013 | 2000 | 5.0 | 7.1 | 2.4 | 1.8 | 0.5 | 39.4 |
| PAPA003 | 2013 | 2500 | 3.8 | 4.8 | 3.0 | 2.5 | 1.5 | 39.6 |
| PAPA003 | 2013 | 3150 | 5.0 | 4.4 | 3.5 | 3.2 | 2.3 | 38.6 |
| PAPA003 | 2013 | 4000 | 5.7 | 5.0 | 4.2 | 4.0 | 3.3 | 50.8 |
| PAPA003 | 2013 | 5000 | 6.1 | 5.4 | 4.8 | 4.6 | 3.6 | 57.9 |
| PAPA003 | 2013 | 6300 | 5.5 | 5.4 | 5.1 | 4.9 | 3.5 | 48.8 |
| PAPA003 | 2013 | 8000 | 5.3 | 5.3 | 5.1 | 5.0 | 1.7 | 41.3 |
| PAPA003 | 2013 | 10000 | 4.9 | 5.0 | 4.8 | 4.7 | 1.4 | 38.4 |
| PAPA003 | 2013 | 12500 | 4.2 | 4.3 | 4.2 | 4.1 | 1.1 | 37.8 |
| PAPA003 | 2013 | 16000 | 3.3 | 3.4 | 3.3 | 3.2 | 0.4 | 35.7 |
| PAPA003 | 2013 | 20000 | 2.0 | 2.1 | 1.9 | 1.8 | 0.9 | 31.8 |
| PAPA004 | 2013 | 12.5 | 45.3 | 47.7 | 41.6 | 37.4 | 15.8 | 81.6 |
| PAPA004 | 2013 | 15.8 | 44.6 | 47.0 | 42.3 | 38.9 | 24.7 | 78.0 |
| PAPA004 | 2013 | 20 | 55.1 | 58.6 | 52.9 | 46.8 | 31.2 | 75.9 |
| PAPA004 | 2013 | 25 | 42.3 | 44.9 | 40.4 | 36.4 | 24.2 | 72.8 |
| PAPA004 | 2013 | 31.5 | 47.1 | 50.5 | 42.5 | 36.4 | 22.3 | 70.6 |
| PAPA004 | 2013 | 40 | 41.0 | 43.8 | 38.6 | 34.2 | 21.9 | 69.3 |
| PAPA004 | 2013 | 50 | 39.9 | 42.4 | 36.8 | 32.8 | 18.8 | 67.9 |
| PAPA004 | 2013 | 63 | 38.3 | 40.8 | 35.4 | 31.7 | 15.4 | 66.3 |
| PAPA004 | 2013 | 80 | 36.1 | 38.5 | 33.6 | 30.2 | 11.8 | 69.1 |
| PAPA004 | 2013 | 100 | 36.4 | 38.7 | 33.2 | 29.0 | 10.8 | 69.4 |
| PAPA004 | 2013 | 125 | 35.0 | 37.0 | 31.4 | 27.6 | 9.0 | 65.8 |
| PAPA004 | 2013 | 160 | 31.0 | 33.3 | 28.5 | 24.7 | 5.0 | 61.9 |
| PAPA004 | 2013 | 200 | 29.6 | 32.5 | 27.1 | 23.2 | 4.5 | 62.8 |
| PAPA004 | 2013 | 250 | 26.5 | 29.1 | 24.4 | 20.6 | 2.0 | 58.9 |
| PAPA004 | 2013 | 315 | 24.2 | 27.1 | 22.3 | 18.0 | 0.7 | 53.3 |
| PAPA004 | 2013 | 400 | 22.2 | 24.7 | 19.8 | 15.5 | -1.0 | 50.3 |
| PAPA004 | 2013 | 500 | 18.8 | 21.5 | 15.9 | 12.2 | -3.0 | 47.4 |
| PAPA004 | 2013 | 630 | 15.5 | 18.3 | 11.2 | 7.6 | -3.5 | 44.3 |
| PAPA004 | 2013 | 800 | 12.2 | 14.8 | 8.5 | 5.1 | -3.2 | 47.1 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA004 | 2013 | 1000 | 12.8 | 12.8 | 5.7 | 2.4 | -2.6 | 51.1 |
| PAPA004 | 2013 | 1250 | 9.9 | 10.5 | 4.7 | 1.2 | -1.5 | 50.7 |
| PAPA004 | 2013 | 1600 | 6.5 | 7.2 | 2.2 | 1.1 | -0.6 | 52.2 |
| PAPA004 | 2013 | 2000 | 6.4 | 5.8 | 2.2 | 1.7 | 0.3 | 53.5 |
| PAPA004 | 2013 | 2500 | 5.8 | 5.8 | 2.9 | 2.5 | 1.2 | 43.2 |
| PAPA004 | 2013 | 3150 | 4.3 | 5.1 | 3.5 | 3.2 | 2.1 | 39.7 |
| PAPA004 | 2013 | 4000 | 4.4 | 4.8 | 4.1 | 3.8 | 1.2 | 37.2 |
| PAPA004 | 2013 | 5000 | 4.7 | 4.8 | 4.5 | 4.3 | 0.3 | 35.5 |
| PAPA004 | 2013 | 6300 | 4.7 | 4.9 | 4.7 | 4.5 | -0.1 | 33.7 |
| PAPA004 | 2013 | 8000 | 4.6 | 4.7 | 4.6 | 4.4 | -0.6 | 36.3 |
| PAPA004 | 2013 | 10000 | 4.2 | 4.3 | 4.2 | 4.0 | -0.4 | 29.5 |
| PAPA004 | 2013 | 12500 | 3.5 | 3.7 | 3.5 | 3.4 | -0.5 | 27.8 |
| PAPA004 | 2013 | 16000 | 2.6 | 2.7 | 2.5 | 2.4 | -1.1 | 25.9 |
| PAPA004 | 2013 | 20000 | 0.9 | 1.1 | 0.8 | 0.7 | -0.8 | 20.2 |
| PAPA005 | 2013 | 12.5 | 43.2 | 45.8 | 41.8 | 37.8 | 23.5 | 78.5 |
| PAPA005 | 2013 | 15.8 | 48.0 | 50.2 | 46.3 | 42.5 | 29.2 | 78.0 |
| PAPA005 | 2013 | 20 | 59.0 | 62.9 | 57.0 | 51.6 | 36.4 | 73.6 |
| PAPA005 | 2013 | 25 | 45.7 | 48.0 | 44.0 | 40.5 | 29.7 | 71.2 |
| PAPA005 | 2013 | 31.5 | 48.3 | 51.2 | 45.3 | 41.1 | 29.3 | 67.9 |
| PAPA005 | 2013 | 40 | 44.9 | 47.1 | 43.1 | 40.3 | 29.1 | 66.7 |
| PAPA005 | 2013 | 50 | 46.0 | 48.4 | 45.2 | 41.3 | 24.8 | 63.8 |
| PAPA005 | 2013 | 63 | 42.8 | 45.2 | 41.0 | 37.2 | 22.5 | 68.5 |
| PAPA005 | 2013 | 80 | 40.6 | 42.8 | 37.9 | 33.3 | 18.6 | 77.5 |
| PAPA005 | 2013 | 100 | 39.6 | 42.0 | 36.7 | 33.1 | 16.2 | 73.8 |
| PAPA005 | 2013 | 125 | 36.7 | 38.4 | 34.6 | 31.0 | 15.7 | 72.4 |
| PAPA005 | 2013 | 160 | 33.6 | 36.2 | 31.3 | 27.6 | 9.6 | 64.1 |
| PAPA005 | 2013 | 200 | 32.6 | 35.2 | 30.7 | 26.8 | 7.1 | 60.0 |
| PAPA005 | 2013 | 250 | 29.4 | 31.8 | 27.7 | 24.3 | 4.3 | 62.9 |
| PAPA005 | 2013 | 315 | 27.0 | 30.1 | 25.6 | 21.6 | 1.4 | 56.3 |
| PAPA005 | 2013 | 400 | 24.7 | 28.0 | 22.5 | 18.3 | -0.4 | 53.0 |
| PAPA005 | 2013 | 500 | 23.0 | 25.5 | 19.5 | 13.2 | -1.9 | 56.4 |
| PAPA005 | 2013 | 630 | 20.5 | 23.5 | 16.5 | 10.2 | -2.4 | 53.7 |
| PAPA005 | 2013 | 800 | 20.1 | 23.5 | 15.6 | 8.5 | -2.4 | 45.3 |
| PAPA005 | 2013 | 1000 | 19.5 | 22.9 | 14.1 | 7.5 | -1.4 | 44.7 |
| PAPA005 | 2013 | 1250 | 16.9 | 20.4 | 12.0 | 5.6 | -0.9 | 43.0 |
| PAPA005 | 2013 | 1600 | 13.9 | 16.8 | 8.6 | 3.2 | -0.2 | 44.7 |
| PAPA005 | 2013 | 2000 | 8.7 | 9.3 | 4.1 | 2.7 | 0.9 | 44.1 |
| PAPA005 | 2013 | 2500 | 6.6 | 6.3 | 3.4 | 3.0 | 1.9 | 43.0 |
| PAPA005 | 2013 | 3150 | 5.7 | 5.7 | 4.1 | 3.7 | 2.8 | 42.2 |
| PAPA005 | 2013 | 4000 | 6.0 | 5.5 | 4.7 | 4.4 | 3.7 | 40.7 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA005 | 2013 | 5000 | 7.6 | 5.8 | 5.2 | 5.0 | 4.4 | 62.1 |
| PAPA005 | 2013 | 6300 | 6.0 | 5.8 | 5.5 | 5.4 | 3.3 | 66.6 |
| PAPA005 | 2013 | 8000 | 5.6 | 5.8 | 5.6 | 5.4 | 3.1 | 45.7 |
| PAPA005 | 2013 | 10000 | 5.4 | 5.5 | 5.3 | 5.2 | 2.5 | 41.9 |
| PAPA005 | 2013 | 12500 | 4.8 | 4.9 | 4.8 | 4.7 | 2.0 | 50.9 |
| PAPA005 | 2013 | 16000 | 4.0 | 4.1 | 4.0 | 3.9 | 1.6 | 31.7 |
| PAPA005 | 2013 | 20000 | 2.9 | 3.0 | 2.8 | 2.7 | 1.9 | 31.8 |
| PAPA006 | 2013 | 12.5 | 46.7 | 48.5 | 44.5 | 40.3 | 27.7 | 74.8 |
| PAPA006 | 2013 | 15.8 | 50.5 | 52.3 | 48.4 | 45.1 | 33.9 | 74.2 |
| PAPA006 | 2013 | 20 | 60.0 | 63.4 | 58.5 | 54.6 | 42.2 | 75.8 |
| PAPA006 | 2013 | 25 | 50.2 | 52.5 | 49.0 | 46.1 | 35.8 | 70.1 |
| PAPA006 | 2013 | 31.5 | 56.0 | 59.0 | 55.1 | 48.4 | 36.2 | 71.1 |
| PAPA006 | 2013 | 40 | 50.2 | 52.7 | 49.0 | 46.0 | 33.2 | 75.1 |
| PAPA006 | 2013 | 50 | 48.2 | 50.4 | 46.1 | 43.0 | 29.5 | 73.6 |
| PAPA006 | 2013 | 63 | 47.2 | 49.4 | 45.7 | 42.3 | 28.5 | 69.4 |
| PAPA006 | 2013 | 80 | 42.2 | 43.7 | 39.7 | 36.7 | 22.9 | 75.3 |
| PAPA006 | 2013 | 100 | 39.8 | 41.9 | 38.1 | 35.3 | 23.6 | 72.5 |
| PAPA006 | 2013 | 125 | 37.9 | 39.4 | 35.9 | 32.0 | 22.4 | 72.2 |
| PAPA006 | 2013 | 160 | 35.3 | 36.7 | 33.7 | 30.8 | 14.2 | 66.4 |
| PAPA006 | 2013 | 200 | 34.2 | 35.8 | 32.2 | 28.7 | 11.1 | 66.5 |
| PAPA006 | 2013 | 250 | 30.9 | 32.5 | 29.2 | 26.4 | 8.0 | 60.7 |
| PAPA006 | 2013 | 315 | 27.4 | 29.3 | 26.1 | 23.4 | 6.3 | 56.6 |
| PAPA006 | 2013 | 400 | 24.8 | 27.3 | 23.5 | 20.4 | 3.8 | 52.1 |
| PAPA006 | 2013 | 500 | 21.5 | 23.6 | 19.5 | 16.1 | 0.4 | 52.9 |
| PAPA006 | 2013 | 630 | 18.3 | 21.4 | 16.4 | 12.6 | -0.9 | 50.3 |
| PAPA006 | 2013 | 800 | 18.3 | 21.1 | 15.8 | 11.8 | -0.6 | 53.4 |
| PAPA006 | 2013 | 1000 | 19.0 | 22.3 | 15.3 | 11.1 | -0.4 | 52.0 |
| PAPA006 | 2013 | 1250 | 18.5 | 20.4 | 12.9 | 8.3 | 0.1 | 54.8 |
| PAPA006 | 2013 | 1600 | 15.8 | 17.5 | 10.7 | 6.0 | 0.5 | 53.9 |
| PAPA006 | 2013 | 2000 | 12.9 | 14.9 | 7.5 | 4.3 | 0.9 | 54.6 |
| PAPA006 | 2013 | 2500 | 10.1 | 11.1 | 5.5 | 3.7 | 1.6 | 51.3 |
| PAPA006 | 2013 | 3150 | 8.2 | 7.3 | 4.4 | 3.8 | 2.4 | 51.2 |
| PAPA006 | 2013 | 4000 | 5.9 | 6.0 | 4.6 | 4.3 | 3.4 | 47.0 |
| PAPA006 | 2013 | 5000 | 5.5 | 5.3 | 5.0 | 4.9 | 3.5 | 41.7 |
| PAPA006 | 2013 | 6300 | 5.5 | 5.6 | 5.4 | 5.2 | 3.5 | 38.3 |
| PAPA006 | 2013 | 8000 | 5.6 | 5.6 | 5.4 | 5.3 | 2.9 | 40.8 |
| PAPA006 | 2013 | 10000 | 5.2 | 5.3 | 5.2 | 5.0 | 1.5 | 39.6 |
| PAPA006 | 2013 | 12500 | 4.6 | 4.7 | 4.6 | 4.4 | 1.2 | 40.0 |
| PAPA006 | 2013 | 16000 | 3.7 | 3.9 | 3.7 | 3.5 | 0.5 | 37.1 |
| PAPA006 | 2013 | 20000 | 2.4 | 2.6 | 2.4 | 2.2 | 1.0 | 34.8 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA007 | 2013 | 12.5 | 51.1 | 53.8 | 47.2 | 41.8 | 24.4 | 78.3 |
| PAPA007 | 2013 | 15.8 | 48.3 | 50.9 | 45.4 | 41.2 | 29.0 | 76.0 |
| PAPA007 | 2013 | 20 | 55.7 | 58.3 | 54.8 | 50.5 | 36.8 | 73.9 |
| PAPA007 | 2013 | 25 | 48.1 | 50.6 | 46.6 | 43.1 | 33.9 | 70.6 |
| PAPA007 | 2013 | 31.5 | 46.3 | 49.3 | 43.2 | 39.2 | 30.4 | 69.3 |
| PAPA007 | 2013 | 40 | 42.7 | 44.5 | 40.6 | 37.3 | 27.8 | 68.6 |
| PAPA007 | 2013 | 50 | 40.2 | 42.5 | 38.1 | 35.2 | 26.5 | 75.7 |
| PAPA007 | 2013 | 63 | 39.5 | 41.8 | 36.9 | 34.2 | 23.9 | 80.7 |
| PAPA007 | 2013 | 80 | 37.5 | 39.6 | 34.6 | 31.5 | 22.1 | 85.3 |
| PAPA007 | 2013 | 100 | 35.5 | 37.5 | 33.3 | 30.2 | 20.7 | 83.3 |
| PAPA007 | 2013 | 125 | 34.4 | 36.7 | 32.6 | 29.4 | 20.8 | 73.3 |
| PAPA007 | 2013 | 160 | 30.8 | 33.0 | 29.3 | 26.3 | 14.5 | 73.6 |
| PAPA007 | 2013 | 200 | 28.6 | 30.4 | 26.6 | 24.1 | 11.9 | 78.8 |
| PAPA007 | 2013 | 250 | 25.2 | 27.3 | 23.5 | 21.0 | 10.3 | 63.6 |
| PAPA007 | 2013 | 315 | 22.2 | 25.1 | 20.5 | 17.6 | 7.1 | 65.9 |
| PAPA007 | 2013 | 400 | 19.1 | 20.6 | 15.8 | 12.7 | 1.2 | 68.6 |
| PAPA007 | 2013 | 500 | 16.8 | 19.2 | 12.7 | 8.8 | -1.5 | 65.3 |
| PAPA007 | 2013 | 630 | 14.8 | 17.7 | 10.0 | 5.4 | -2.4 | 56.9 |
| PAPA007 | 2013 | 800 | 14.2 | 17.3 | 9.0 | 3.9 | -2.4 | 53.8 |
| PAPA007 | 2013 | 1000 | 12.4 | 14.9 | 7.0 | 2.2 | -1.9 | 49.6 |
| PAPA007 | 2013 | 1250 | 10.7 | 11.6 | 4.6 | 1.1 | -1.2 | 48.6 |
| PAPA007 | 2013 | 1600 | 9.0 | 10.4 | 4.3 | 1.8 | -0.2 | 43.8 |
| PAPA007 | 2013 | 2000 | 8.4 | 9.7 | 3.5 | 2.1 | 0.5 | 41.5 |
| PAPA007 | 2013 | 2500 | 7.4 | 8.2 | 3.7 | 2.8 | 1.3 | 38.4 |
| PAPA007 | 2013 | 3150 | 7.1 | 7.7 | 3.8 | 3.4 | 2.3 | 46.6 |
| PAPA007 | 2013 | 4000 | 6.4 | 6.3 | 4.3 | 4.0 | 2.0 | 46.8 |
| PAPA007 | 2013 | 5000 | 6.6 | 5.2 | 4.6 | 4.4 | 1.3 | 41.7 |
| PAPA007 | 2013 | 6300 | 5.1 | 5.0 | 4.7 | 4.5 | 0.2 | 34.4 |
| PAPA007 | 2013 | 8000 | 4.7 | 4.9 | 4.6 | 4.4 | 0.1 | 25.5 |
| PAPA007 | 2013 | 10000 | 4.4 | 4.5 | 4.3 | 4.0 | -0.6 | 23.5 |
| PAPA007 | 2013 | 12500 | 3.8 | 4.0 | 3.7 | 3.4 | -1.3 | 21.9 |
| PAPA007 | 2013 | 16000 | 3.0 | 3.2 | 2.8 | 2.5 | -1.3 | 21.1 |
| PAPA007 | 2013 | 20000 | 1.6 | 2.0 | 1.2 | 0.9 | -1.2 | 25.8 |
| PAPA008 | 2013 | 12.5 | 50.6 | 53.5 | 47.5 | 41.7 | 26.7 | 78.6 |
| PAPA008 | 2013 | 15.8 | 49.5 | 52.2 | 46.2 | 41.0 | 24.1 | 75.8 |
| PAPA008 | 2013 | 20 | 53.0 | 55.5 | 51.2 | 47.3 | 32.2 | 73.6 |
| PAPA008 | 2013 | 25 | 47.7 | 50.7 | 45.0 | 41.4 | 28.7 | 71.0 |
| PAPA008 | 2013 | 31.5 | 45.6 | 48.1 | 44.1 | 41.0 | 28.9 | 69.1 |
| PAPA008 | 2013 | 40 | 43.3 | 45.7 | 42.0 | 38.8 | 29.7 | 66.8 |
| PAPA008 | 2013 | 50 | 39.2 | 41.2 | 37.5 | 34.9 | 26.1 | 66.7 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA008 | 2013 | 63 | 39.1 | 41.9 | 37.6 | 34.6 | 24.3 | 85.0 |
| PAPA008 | 2013 | 80 | 36.2 | 38.4 | 34.1 | 31.0 | 22.7 | 84.1 |
| PAPA008 | 2013 | 100 | 34.5 | 37.1 | 33.2 | 30.2 | 21.1 | 79.3 |
| PAPA008 | 2013 | 125 | 33.1 | 35.5 | 31.7 | 29.0 | 20.0 | 66.9 |
| PAPA008 | 2013 | 160 | 30.2 | 32.4 | 28.4 | 25.6 | 16.9 | 70.4 |
| PAPA008 | 2013 | 200 | 28.7 | 31.2 | 27.1 | 24.0 | 14.9 | 65.3 |
| PAPA008 | 2013 | 250 | 26.0 | 28.3 | 24.0 | 21.3 | 13.0 | 53.3 |
| PAPA008 | 2013 | 315 | 22.7 | 25.0 | 21.2 | 18.2 | 9.8 | 46.0 |
| PAPA008 | 2013 | 400 | 19.1 | 21.3 | 16.5 | 12.9 | 4.9 | 47.5 |
| PAPA008 | 2013 | 500 | 17.6 | 19.1 | 14.3 | 10.4 | 1.6 | 52.4 |
| PAPA008 | 2013 | 630 | 15.4 | 17.4 | 11.2 | 6.5 | -1.9 | 48.6 |
| PAPA008 | 2013 | 800 | 14.8 | 16.7 | 9.5 | 4.4 | -1.7 | 43.5 |
| PAPA008 | 2013 | 1000 | 12.9 | 16.0 | 7.9 | 3.3 | -1.0 | 46.5 |
| PAPA008 | 2013 | 1250 | 11.9 | 14.8 | 5.5 | 1.5 | -0.9 | 48.7 |
| PAPA008 | 2013 | 1600 | 10.0 | 12.6 | 4.1 | 1.6 | -0.2 | 36.1 |
| PAPA008 | 2013 | 2000 | 7.3 | 9.7 | 3.3 | 2.2 | 0.5 | 36.7 |
| PAPA008 | 2013 | 2500 | 6.2 | 8.1 | 3.4 | 3.0 | 1.5 | 35.9 |
| PAPA008 | 2013 | 3150 | 6.4 | 7.2 | 4.1 | 3.7 | 2.4 | 34.8 |
| PAPA008 | 2013 | 4000 | 5.4 | 5.9 | 4.7 | 4.4 | 2.2 | 49.3 |
| PAPA008 | 2013 | 5000 | 6.4 | 6.4 | 5.2 | 4.8 | 2.3 | 52.5 |
| PAPA008 | 2013 | 6300 | 5.9 | 5.9 | 5.4 | 5.1 | 2.6 | 38.1 |
| PAPA008 | 2013 | 8000 | 5.6 | 5.9 | 5.4 | 5.2 | 2.2 | 26.1 |
| PAPA008 | 2013 | 10000 | 5.4 | 5.6 | 5.2 | 4.9 | 0.7 | 28.8 |
| PAPA008 | 2013 | 12500 | 4.9 | 5.1 | 4.7 | 4.4 | 0.4 | 23.9 |
| PAPA008 | 2013 | 16000 | 4.1 | 4.4 | 3.9 | 3.5 | -0.3 | 22.7 |
| PAPA008 | 2013 | 20000 | 2.9 | 3.4 | 2.7 | 2.3 | 0.5 | 22.3 |
| PAPA009 | 2013 | 12.5 | 53.8 | 56.9 | 50.5 | 45.6 | 26.6 | 77.2 |
| PAPA009 | 2013 | 15.8 | 52.5 | 55.3 | 50.6 | 45.7 | 30.2 | 73.1 |
| PAPA009 | 2013 | 20 | 52.9 | 55.4 | 50.8 | 46.6 | 33.0 | 71.5 |
| PAPA009 | 2013 | 25 | 48.8 | 51.5 | 47.2 | 43.4 | 30.5 | 68.1 |
| PAPA009 | 2013 | 31.5 | 47.7 | 50.7 | 45.8 | 41.4 | 30.7 | 66.9 |
| PAPA009 | 2013 | 40 | 43.4 | 45.5 | 41.8 | 38.2 | 28.8 | 64.0 |
| PAPA009 | 2013 | 50 | 40.7 | 42.7 | 38.0 | 33.6 | 24.0 | 73.6 |
| PAPA009 | 2013 | 63 | 40.2 | 42.5 | 37.9 | 34.1 | 24.6 | 75.9 |
| PAPA009 | 2013 | 80 | 38.2 | 40.1 | 35.5 | 31.7 | 21.6 | 75.3 |
| PAPA009 | 2013 | 100 | 35.8 | 38.0 | 34.2 | 31.2 | 20.5 | 73.8 |
| PAPA009 | 2013 | 125 | 35.1 | 37.7 | 32.6 | 29.7 | 19.6 | 66.0 |
| PAPA009 | 2013 | 160 | 31.5 | 33.7 | 30.1 | 27.8 | 16.0 | 68.3 |
| PAPA009 | 2013 | 200 | 29.5 | 31.7 | 27.5 | 24.9 | 13.8 | 66.1 |
| PAPA009 | 2013 | 250 | 26.0 | 28.3 | 24.6 | 21.6 | 11.6 | 56.4 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA009 | 2013 | 315 | 22.3 | 25.0 | 20.8 | 16.8 | 5.9 | 45.9 |
| PAPA009 | 2013 | 400 | 19.7 | 22.6 | 17.5 | 13.4 | 2.2 | 43.4 |
| PAPA009 | 2013 | 500 | 17.3 | 19.8 | 14.0 | 9.7 | -0.2 | 49.1 |
| PAPA009 | 2013 | 630 | 13.5 | 15.5 | 9.7 | 5.5 | -1.9 | 45.4 |
| PAPA009 | 2013 | 800 | 12.1 | 14.0 | 7.0 | 3.3 | -2.3 | 40.7 |
| PAPA009 | 2013 | 1000 | 10.5 | 13.1 | 5.7 | 1.9 | -1.6 | 37.3 |
| PAPA009 | 2013 | 1250 | 10.4 | 12.4 | 3.4 | 1.5 | -1.1 | 40.3 |
| PAPA009 | 2013 | 1600 | 8.8 | 11.1 | 2.4 | 1.7 | -0.2 | 40.0 |
| PAPA009 | 2013 | 2000 | 6.6 | 9.0 | 2.8 | 2.4 | 0.7 | 35.6 |
| PAPA009 | 2013 | 2500 | 6.0 | 7.7 | 3.5 | 3.1 | 1.7 | 34.6 |
| PAPA009 | 2013 | 3150 | 5.5 | 6.9 | 4.1 | 3.8 | 2.5 | 41.4 |
| PAPA009 | 2013 | 4000 | 6.1 | 5.8 | 4.6 | 4.4 | 1.7 | 35.4 |
| PAPA009 | 2013 | 5000 | 6.1 | 5.6 | 4.9 | 4.6 | 0.2 | 46.6 |
| PAPA009 | 2013 | 6300 | 5.3 | 5.3 | 5.0 | 4.6 | -0.1 | 42.6 |
| PAPA009 | 2013 | 8000 | 5.1 | 5.2 | 4.9 | 4.5 | -0.9 | 33.4 |
| PAPA009 | 2013 | 10000 | 4.8 | 5.0 | 4.7 | 4.3 | -0.7 | 23.6 |
| PAPA009 | 2013 | 12500 | 4.5 | 4.7 | 4.4 | 3.9 | -0.6 | 25.4 |
| PAPA009 | 2013 | 16000 | 4.0 | 4.4 | 3.9 | 3.4 | -0.8 | 25.1 |
| PAPA009 | 2013 | 20000 | 3.0 | 4.1 | 2.8 | 2.5 | -0.3 | 22.5 |
| PAPA010 | 2013 | 12.5 | 52.2 | 55.3 | 49.9 | 45.1 | 25.2 | 76.7 |
| PAPA010 | 2013 | 15.8 | 53.1 | 55.7 | 52.0 | 47.6 | 33.0 | 74.8 |
| PAPA010 | 2013 | 20 | 53.7 | 56.5 | 51.9 | 47.3 | 34.8 | 74.5 |
| PAPA010 | 2013 | 25 | 50.2 | 53.0 | 48.1 | 44.4 | 31.6 | 73.6 |
| PAPA010 | 2013 | 31.5 | 48.1 | 50.7 | 46.9 | 42.9 | 32.9 | 69.6 |
| PAPA010 | 2013 | 40 | 43.4 | 45.5 | 42.5 | 39.1 | 29.9 | 65.6 |
| PAPA010 | 2013 | 50 | 42.6 | 45.4 | 40.8 | 37.6 | 25.0 | 64.1 |
| PAPA010 | 2013 | 63 | 40.0 | 41.9 | 38.4 | 35.4 | 24.6 | 61.2 |
| PAPA010 | 2013 | 80 | 37.5 | 39.5 | 35.5 | 32.6 | 21.9 | 70.4 |
| PAPA010 | 2013 | 100 | 35.9 | 37.6 | 34.0 | 31.4 | 18.9 | 66.3 |
| PAPA010 | 2013 | 125 | 33.9 | 36.4 | 32.7 | 29.8 | 18.6 | 69.5 |
| PAPA010 | 2013 | 160 | 31.4 | 33.6 | 30.4 | 27.6 | 15.4 | 63.9 |
| PAPA010 | 2013 | 200 | 30.8 | 33.2 | 29.2 | 26.4 | 14.1 | 59.4 |
| PAPA010 | 2013 | 250 | 27.8 | 30.8 | 26.4 | 23.4 | 11.5 | 55.1 |
| PAPA010 | 2013 | 315 | 24.0 | 27.4 | 22.6 | 19.0 | 5.9 | 44.7 |
| PAPA010 | 2013 | 400 | 21.7 | 25.7 | 19.5 | 16.1 | 3.1 | 43.4 |
| PAPA010 | 2013 | 500 | 18.5 | 20.8 | 14.7 | 11.4 | 0.0 | 48.9 |
| PAPA010 | 2013 | 630 | 16.0 | 18.8 | 12.5 | 8.3 | -1.7 | 43.8 |
| PAPA010 | 2013 | 800 | 14.1 | 16.1 | 9.7 | 5.5 | -1.3 | 41.1 |
| PAPA010 | 2013 | 1000 | 13.7 | 16.5 | 8.6 | 4.8 | -1.1 | 40.8 |
| PAPA010 | 2013 | 1250 | 12.4 | 15.5 | 7.2 | 3.6 | -0.4 | 37.5 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA010 | 2013 | 1600 | 10.2 | 13.0 | 5.1 | 2.9 | 0.2 | 36.5 |
| PAPA010 | 2013 | 2000 | 7.7 | 9.7 | 3.7 | 2.9 | 1.2 | 41.2 |
| PAPA010 | 2013 | 2500 | 8.1 | 8.6 | 3.8 | 3.4 | 2.0 | 58.5 |
| PAPA010 | 2013 | 3150 | 6.6 | 7.0 | 4.5 | 4.1 | 3.0 | 50.0 |
| PAPA010 | 2013 | 4000 | 6.4 | 6.8 | 5.1 | 4.8 | 3.3 | 42.6 |
| PAPA010 | 2013 | 5000 | 7.2 | 6.4 | 5.5 | 5.3 | 1.4 | 50.8 |
| PAPA010 | 2013 | 6300 | 6.0 | 6.1 | 5.8 | 5.5 | 1.6 | 42.0 |
| PAPA010 | 2013 | 8000 | 5.8 | 6.0 | 5.7 | 5.5 | -0.2 | 27.3 |
| PAPA010 | 2013 | 10000 | 5.5 | 5.7 | 5.4 | 5.2 | -0.3 | 23.9 |
| PAPA010 | 2013 | 12500 | 4.9 | 5.2 | 4.8 | 4.5 | -0.6 | 22.8 |
| PAPA010 | 2013 | 16000 | 4.1 | 4.5 | 3.9 | 3.6 | -0.9 | 20.7 |
| PAPA010 | 2013 | 20000 | 2.7 | 3.1 | 2.5 | 2.2 | -1.1 | 19.4 |
| PAPA011 | 2013 | 12.5 | 48.3 | 52.0 | 40.4 | 34.7 | 19.3 | 77.8 |
| PAPA011 | 2013 | 15.8 | 45.7 | 48.0 | 40.3 | 34.6 | 20.7 | 76.6 |
| PAPA011 | 2013 | 20 | 46.1 | 49.0 | 42.4 | 37.2 | 21.2 | 77.6 |
| PAPA011 | 2013 | 25 | 39.5 | 41.5 | 35.2 | 30.8 | 17.3 | 71.3 |
| PAPA011 | 2013 | 31.5 | 42.7 | 45.0 | 39.0 | 33.3 | 17.8 | 69.6 |
| PAPA011 | 2013 | 40 | 34.9 | 37.1 | 32.7 | 29.2 | 13.6 | 67.4 |
| PAPA011 | 2013 | 50 | 34.4 | 37.0 | 32.2 | 28.7 | 13.4 | 65.7 |
| PAPA011 | 2013 | 63 | 34.2 | 36.9 | 31.5 | 28.4 | 12.8 | 64.5 |
| PAPA011 | 2013 | 80 | 32.0 | 34.2 | 29.9 | 26.5 | 13.1 | 69.3 |
| PAPA011 | 2013 | 100 | 34.7 | 36.7 | 31.5 | 27.1 | 12.5 | 68.1 |
| PAPA011 | 2013 | 125 | 29.3 | 31.5 | 26.7 | 23.0 | 10.3 | 73.3 |
| PAPA011 | 2013 | 160 | 28.1 | 30.4 | 24.7 | 20.0 | 6.2 | 62.7 |
| PAPA011 | 2013 | 200 | 26.6 | 29.2 | 23.2 | 18.7 | 4.2 | 55.9 |
| PAPA011 | 2013 | 250 | 24.2 | 26.6 | 19.7 | 13.7 | 0.0 | 60.0 |
| PAPA011 | 2013 | 315 | 22.4 | 25.2 | 17.8 | 10.7 | -2.3 | 55.8 |
| PAPA011 | 2013 | 400 | 19.4 | 23.0 | 15.2 | 7.2 | -3.4 | 50.1 |
| PAPA011 | 2013 | 500 | 16.1 | 19.0 | 11.8 | 3.2 | -3.8 | 44.7 |
| PAPA011 | 2013 | 630 | 12.6 | 16.3 | 7.4 | 0.6 | -3.5 | 44.5 |
| PAPA011 | 2013 | 800 | 10.5 | 14.3 | 5.1 | -0.1 | -3.1 | 41.5 |
| PAPA011 | 2013 | 1000 | 10.0 | 14.0 | 4.0 | 0.0 | -2.1 | 34.6 |
| PAPA011 | 2013 | 1250 | 9.2 | 13.1 | 3.9 | 0.5 | -1.2 | 34.1 |
| PAPA011 | 2013 | 1600 | 8.8 | 11.8 | 3.4 | 1.3 | -0.3 | 35.1 |
| PAPA011 | 2013 | 2000 | 7.4 | 10.2 | 3.4 | 1.9 | 0.7 | 34.7 |
| PAPA011 | 2013 | 2500 | 6.6 | 8.7 | 3.8 | 2.7 | 1.6 | 34.6 |
| PAPA011 | 2013 | 3150 | 6.7 | 7.7 | 4.4 | 3.4 | 2.2 | 38.6 |
| PAPA011 | 2013 | 4000 | 6.3 | 6.3 | 4.6 | 4.2 | 1.6 | 45.5 |
| PAPA011 | 2013 | 5000 | 6.0 | 6.1 | 5.0 | 4.7 | 1.5 | 49.2 |
| PAPA011 | 2013 | 6300 | 5.6 | 5.8 | 5.3 | 5.0 | 1.5 | 41.2 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA011 | 2013 | 8000 | 5.5 | 5.7 | 5.3 | 5.1 | 1.0 | 23.4 |
| PAPA011 | 2013 | 10000 | 5.2 | 5.4 | 5.1 | 4.9 | 0.7 | 27.3 |
| PAPA011 | 2013 | 12500 | 4.8 | 5.0 | 4.6 | 4.3 | 0.4 | 26.8 |
| PAPA011 | 2013 | 16000 | 4.2 | 4.5 | 3.8 | 3.6 | 0.2 | 28.5 |
| PAPA011 | 2013 | 20000 | 3.4 | 4.1 | 2.7 | 2.4 | 0.4 | 27.2 |
| PAPA012 | 2013 | 12.5 | 45.6 | 48.5 | 43.2 | 38.1 | 20.7 | 73.9 |
| PAPA012 | 2013 | 15.8 | 44.4 | 47.1 | 42.3 | 38.7 | 23.0 | 70.9 |
| PAPA012 | 2013 | 20 | 47.6 | 50.5 | 46.1 | 41.8 | 25.3 | 69.0 |
| PAPA012 | 2013 | 25 | 41.1 | 44.3 | 38.6 | 35.1 | 21.3 | 67.2 |
| PAPA012 | 2013 | 31.5 | 42.5 | 45.5 | 40.3 | 35.8 | 21.8 | 67.6 |
| PAPA012 | 2013 | 40 | 35.8 | 38.0 | 34.2 | 31.3 | 16.2 | 63.5 |
| PAPA012 | 2013 | 50 | 35.0 | 37.3 | 33.6 | 30.9 | 15.2 | 59.7 |
| PAPA012 | 2013 | 63 | 35.2 | 38.3 | 33.9 | 30.7 | 15.8 | 57.6 |
| PAPA012 | 2013 | 80 | 33.5 | 35.3 | 31.5 | 28.5 | 14.6 | 66.2 |
| PAPA012 | 2013 | 100 | 33.2 | 34.9 | 31.3 | 28.3 | 12.6 | 73.4 |
| PAPA012 | 2013 | 125 | 30.4 | 32.0 | 28.4 | 25.5 | 11.8 | 77.0 |
| PAPA012 | 2013 | 160 | 27.9 | 30.0 | 25.6 | 22.8 | 9.2 | 70.0 |
| PAPA012 | 2013 | 200 | 26.5 | 28.5 | 23.6 | 20.5 | 7.4 | 68.1 |
| PAPA012 | 2013 | 250 | 23.8 | 26.1 | 20.6 | 16.5 | 3.3 | 66.7 |
| PAPA012 | 2013 | 315 | 20.7 | 23.7 | 17.4 | 12.4 | -0.3 | 60.5 |
| PAPA012 | 2013 | 400 | 16.5 | 20.0 | 12.5 | 6.9 | -3.0 | 56.7 |
| PAPA012 | 2013 | 500 | 13.3 | 15.5 | 8.0 | 2.1 | -3.8 | 55.1 |
| PAPA012 | 2013 | 630 | 11.0 | 13.8 | 5.8 | -0.3 | -3.7 | 53.2 |
| PAPA012 | 2013 | 800 | 12.2 | 16.1 | 6.3 | -1.0 | -3.7 | 56.5 |
| PAPA012 | 2013 | 1000 | 12.6 | 17.1 | 6.4 | -0.9 | -2.9 | 54.9 |
| PAPA012 | 2013 | 1250 | 12.4 | 16.6 | 5.3 | -0.5 | -2.2 | 51.2 |
| PAPA012 | 2013 | 1600 | 11.5 | 15.0 | 3.6 | 0.3 | -1.4 | 45.2 |
| PAPA012 | 2013 | 2000 | 9.8 | 12.7 | 2.8 | 0.8 | -0.7 | 42.8 |
| PAPA012 | 2013 | 2500 | 7.9 | 10.3 | 2.3 | 1.4 | 0.4 | 41.9 |
| PAPA012 | 2013 | 3150 | 5.3 | 7.1 | 2.6 | 2.2 | 1.3 | 42.3 |
| PAPA012 | 2013 | 4000 | 5.2 | 5.7 | 3.3 | 3.0 | 1.4 | 43.5 |
| PAPA012 | 2013 | 5000 | 4.8 | 4.9 | 4.0 | 3.7 | 1.4 | 41.0 |
| PAPA012 | 2013 | 6300 | 5.0 | 5.0 | 4.6 | 4.4 | 1.0 | 43.5 |
| PAPA012 | 2013 | 8000 | 5.3 | 5.3 | 5.1 | 4.9 | 0.4 | 46.2 |
| PAPA012 | 2013 | 10000 | 5.4 | 5.5 | 5.3 | 5.1 | 0.1 | 38.4 |
| PAPA012 | 2013 | 12500 | 5.0 | 5.2 | 4.9 | 4.7 | 0.3 | 39.7 |
| PAPA012 | 2013 | 16000 | 3.1 | 3.4 | 2.8 | 2.7 | -0.4 | 36.7 |
| PAPA012 | 2013 | 20000 | 0.8 | 2.1 | 0.3 | 0.1 | -0.7 | 29.3 |
| PAPA013 | 2013 | 12.5 | 53.0 | 56.1 | 49.9 | 43.8 | 23.7 | 79.5 |
| PAPA013 | 2013 | 15.8 | 51.6 | 54.8 | 47.0 | 41.3 | 27.0 | 76.5 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA013 | 2013 | 20 | 50.8 | 53.6 | 48.3 | 42.4 | 29.2 | 73.1 |
| PAPA013 | 2013 | 25 | 47.5 | 50.6 | 45.5 | 40.6 | 24.3 | 71.3 |
| PAPA013 | 2013 | 31.5 | 48.3 | 51.1 | 46.4 | 41.7 | 28.3 | 68.3 |
| PAPA013 | 2013 | 40 | 41.6 | 44.3 | 40.0 | 36.7 | 25.6 | 65.9 |
| PAPA013 | 2013 | 50 | 38.2 | 40.2 | 35.8 | 32.5 | 24.0 | 65.1 |
| PAPA013 | 2013 | 63 | 37.3 | 39.7 | 35.3 | 32.2 | 24.1 | 61.9 |
| PAPA013 | 2013 | 80 | 34.7 | 37.1 | 33.3 | 30.1 | 20.6 | 61.8 |
| PAPA013 | 2013 | 100 | 36.7 | 37.8 | 33.9 | 30.5 | 18.7 | 63.9 |
| PAPA013 | 2013 | 125 | 33.6 | 35.1 | 31.2 | 27.5 | 16.3 | 66.3 |
| PAPA013 | 2013 | 160 | 30.5 | 32.1 | 28.4 | 24.7 | 15.1 | 70.2 |
| PAPA013 | 2013 | 200 | 29.4 | 31.9 | 27.8 | 23.5 | 13.4 | 55.5 |
| PAPA013 | 2013 | 250 | 27.0 | 29.9 | 25.3 | 21.2 | 9.7 | 57.3 |
| PAPA013 | 2013 | 315 | 24.1 | 27.2 | 22.3 | 17.2 | 6.4 | 51.2 |
| PAPA013 | 2013 | 400 | 21.7 | 25.2 | 19.8 | 14.5 | 2.6 | 50.5 |
| PAPA013 | 2013 | 500 | 19.0 | 22.8 | 17.1 | 11.2 | -0.7 | 49.2 |
| PAPA013 | 2013 | 630 | 16.9 | 20.0 | 13.5 | 7.5 | -2.6 | 42.7 |
| PAPA013 | 2013 | 800 | 16.3 | 20.0 | 12.3 | 5.5 | -2.8 | 38.2 |
| PAPA013 | 2013 | 1000 | 17.2 | 21.1 | 12.5 | 5.4 | -1.9 | 38.1 |
| PAPA013 | 2013 | 1250 | 14.1 | 18.1 | 8.2 | 2.4 | -1.6 | 38.5 |
| PAPA013 | 2013 | 1600 | 12.6 | 15.8 | 6.2 | 2.0 | -0.7 | 39.4 |
| PAPA013 | 2013 | 2000 | 10.7 | 11.8 | 3.6 | 1.7 | 0.4 | 44.9 |
| PAPA013 | 2013 | 2500 | 11.1 | 10.1 | 3.2 | 2.4 | 1.3 | 62.8 |
| PAPA013 | 2013 | 3150 | 8.8 | 8.8 | 3.6 | 3.1 | 2.1 | 71.2 |
| PAPA013 | 2013 | 4000 | 6.8 | 7.0 | 4.1 | 3.8 | 3.1 | 69.5 |
| PAPA013 | 2013 | 5000 | 6.3 | 6.1 | 4.5 | 4.2 | 2.7 | 45.2 |
| PAPA013 | 2013 | 6300 | 5.3 | 5.3 | 4.7 | 4.5 | 1.6 | 46.7 |
| PAPA013 | 2013 | 8000 | 4.9 | 4.8 | 4.6 | 4.4 | 1.6 | 57.9 |
| PAPA013 | 2013 | 10000 | 4.5 | 4.4 | 4.2 | 4.1 | 0.3 | 38.0 |
| PAPA013 | 2013 | 12500 | 3.7 | 3.8 | 3.5 | 3.3 | 0.1 | 34.6 |
| PAPA013 | 2013 | 16000 | 2.9 | 3.0 | 2.6 | 2.4 | -0.3 | 35.7 |
| PAPA013 | 2013 | 20000 | 1.5 | 1.9 | 1.0 | 0.7 | -1.1 | 29.5 |
| PAPA014 | 2013 | 12.5 | 43.7 | 45.7 | 41.4 | 35.5 | 20.5 | 73.7 |
| PAPA014 | 2013 | 15.8 | 48.8 | 50.6 | 44.4 | 40.1 | 24.6 | 71.1 |
| PAPA014 | 2013 | 20 | 57.8 | 61.4 | 52.6 | 48.4 | 31.0 | 76.1 |
| PAPA014 | 2013 | 25 | 43.2 | 46.0 | 42.4 | 39.2 | 23.6 | 66.3 |
| PAPA014 | 2013 | 31.5 | 48.6 | 51.8 | 47.5 | 42.6 | 26.3 | 66.1 |
| PAPA014 | 2013 | 40 | 44.9 | 47.0 | 44.0 | 41.1 | 25.6 | 64.0 |
| PAPA014 | 2013 | 50 | 43.0 | 45.2 | 41.4 | 38.8 | 25.9 | 67.6 |
| PAPA014 | 2013 | 63 | 42.0 | 43.8 | 40.0 | 36.5 | 25.1 | 68.3 |
| PAPA014 | 2013 | 80 | 38.1 | 40.3 | 36.1 | 33.3 | 22.8 | 70.9 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA014 | 2013 | 100 | 37.9 | 39.7 | 36.2 | 33.0 | 22.2 | 72.8 |
| PAPA014 | 2013 | 125 | 38.8 | 40.3 | 36.8 | 34.1 | 21.6 | 70.4 |
| PAPA014 | 2013 | 160 | 32.6 | 34.8 | 31.5 | 28.0 | 19.1 | 65.4 |
| PAPA014 | 2013 | 200 | 30.5 | 32.9 | 28.1 | 24.2 | 8.6 | 66.2 |
| PAPA014 | 2013 | 250 | 27.3 | 29.7 | 25.2 | 21.4 | 5.8 | 62.0 |
| PAPA014 | 2013 | 315 | 24.7 | 28.2 | 22.6 | 18.9 | 3.4 | 57.5 |
| PAPA014 | 2013 | 400 | 21.3 | 23.7 | 19.0 | 15.5 | 0.3 | 50.6 |
| PAPA014 | 2013 | 500 | 19.2 | 22.9 | 15.3 | 10.6 | -1.6 | 48.6 |
| PAPA014 | 2013 | 630 | 14.9 | 18.3 | 10.3 | 5.8 | -2.9 | 46.9 |
| PAPA014 | 2013 | 800 | 15.4 | 19.4 | 8.7 | 5.4 | -2.1 | 41.9 |
| PAPA014 | 2013 | 1000 | 16.1 | 20.4 | 8.7 | 4.7 | -1.8 | 38.4 |
| PAPA014 | 2013 | 1250 | 17.7 | 21.8 | 11.7 | 5.1 | -1.4 | 42.4 |
| PAPA014 | 2013 | 1600 | 18.2 | 22.1 | 11.0 | 4.2 | -0.9 | 48.6 |
| PAPA014 | 2013 | 2000 | 14.3 | 17.6 | 8.2 | 2.8 | -0.4 | 51.8 |
| PAPA014 | 2013 | 2500 | 10.5 | 12.8 | 5.2 | 2.1 | 0.3 | 53.9 |
| PAPA014 | 2013 | 3150 | 9.4 | 12.2 | 4.5 | 2.9 | 1.3 | 52.6 |
| PAPA014 | 2013 | 4000 | 4.8 | 4.6 | 3.4 | 3.0 | 2.2 | 52.8 |
| PAPA014 | 2013 | 5000 | 4.6 | 4.3 | 3.9 | 3.7 | 1.9 | 57.1 |
| PAPA014 | 2013 | 6300 | 4.8 | 4.7 | 4.5 | 4.4 | 1.1 | 43.7 |
| PAPA014 | 2013 | 8000 | 5.2 | 5.2 | 5.0 | 4.9 | 0.6 | 40.0 |
| PAPA014 | 2013 | 10000 | 5.3 | 5.5 | 5.3 | 5.2 | -0.2 | 31.8 |
| PAPA014 | 2013 | 12500 | 4.9 | 5.0 | 4.9 | 4.7 | -0.5 | 33.1 |
| PAPA014 | 2013 | 16000 | 2.8 | 2.9 | 2.8 | 2.6 | -1.1 | 29.3 |
| PAPA014 | 2013 | 20000 | 0.2 | 0.5 | 0.2 | 0.1 | -1.0 | 22.6 |
| PAPA015 | 2013 | 12.5 | 40.9 | 43.0 | 38.5 | 34.1 | 16.0 | 78.4 |
| PAPA015 | 2013 | 15.8 | 44.0 | 46.4 | 41.9 | 35.8 | 16.8 | 76.1 |
| PAPA015 | 2013 | 20 | 48.7 | 51.6 | 44.6 | 37.4 | 18.3 | 74.0 |
| PAPA015 | 2013 | 25 | 38.3 | 40.9 | 35.0 | 29.0 | 14.2 | 71.8 |
| PAPA015 | 2013 | 31.5 | 39.8 | 42.6 | 35.2 | 29.1 | 13.4 | 68.3 |
| PAPA015 | 2013 | 40 | 32.5 | 34.7 | 28.9 | 24.8 | 11.5 | 65.4 |
| PAPA015 | 2013 | 50 | 31.5 | 33.6 | 27.8 | 23.9 | 9.5 | 64.3 |
| PAPA015 | 2013 | 63 | 30.8 | 33.0 | 27.2 | 23.2 | 8.9 | 66.8 |
| PAPA015 | 2013 | 80 | 30.3 | 32.0 | 24.6 | 20.9 | 7.3 | 72.0 |
| PAPA015 | 2013 | 100 | 28.0 | 29.9 | 23.4 | 19.1 | 3.6 | 71.5 |
| PAPA015 | 2013 | 125 | 27.2 | 28.4 | 21.8 | 17.2 | 1.6 | 67.9 |
| PAPA015 | 2013 | 160 | 24.8 | 25.8 | 19.0 | 13.5 | -0.5 | 60.3 |
| PAPA015 | 2013 | 200 | 23.2 | 23.7 | 17.2 | 11.3 | -1.2 | 59.2 |
| PAPA015 | 2013 | 250 | 19.7 | 21.8 | 12.4 | 6.9 | -3.2 | 53.3 |
| PAPA015 | 2013 | 315 | 16.5 | 17.8 | 8.5 | 3.5 | -3.8 | 45.8 |
| PAPA015 | 2013 | 400 | 14.9 | 13.3 | 5.0 | 1.7 | -3.7 | 47.9 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA015 | 2013 | 500 | 13.5 | 9.5 | 3.3 | 0.1 | -4.0 | 50.0 |
| PAPA015 | 2013 | 630 | 11.5 | 7.0 | 1.0 | -0.8 | -3.8 | 46.0 |
| PAPA015 | 2013 | 800 | 7.8 | 5.0 | -0.5 | -1.4 | -3.8 | 41.4 |
| PAPA015 | 2013 | 1000 | 3.2 | 1.9 | -0.6 | -1.3 | -3.3 | 37.7 |
| PAPA015 | 2013 | 1250 | 1.0 | 0.4 | -0.7 | -1.1 | -2.6 | 37.1 |
| PAPA015 | 2013 | 1600 | 1.0 | 1.0 | 0.0 | -0.5 | -1.9 | 38.1 |
| PAPA015 | 2013 | 2000 | 2.2 | 1.6 | 0.9 | 0.5 | -0.8 | 39.8 |
| PAPA015 | 2013 | 2500 | 2.3 | 2.4 | 1.8 | 1.3 | 0.0 | 39.8 |
| PAPA015 | 2013 | 3150 | 3.1 | 3.2 | 2.5 | 2.2 | 1.2 | 41.0 |
| PAPA015 | 2013 | 4000 | 4.0 | 3.9 | 3.4 | 3.2 | 2.3 | 38.3 |
| PAPA015 | 2013 | 5000 | 4.7 | 4.7 | 4.3 | 4.1 | 3.4 | 43.2 |
| PAPA015 | 2013 | 6300 | 5.2 | 5.4 | 5.0 | 4.8 | 3.8 | 39.0 |
| PAPA015 | 2013 | 8000 | 5.8 | 5.9 | 5.5 | 5.4 | 3.4 | 39.4 |
| PAPA015 | 2013 | 10000 | 5.9 | 6.1 | 5.8 | 5.5 | 3.3 | 45.7 |
| PAPA015 | 2013 | 12500 | 5.4 | 5.5 | 5.2 | 4.8 | 3.0 | 44.1 |
| PAPA015 | 2013 | 16000 | 3.6 | 3.7 | 3.3 | 2.8 | 1.8 | 38.5 |
| PAPA015 | 2013 | 20000 | 0.9 | 1.6 | 0.6 | 0.2 | -0.5 | 35.6 |
| PAPA016 | 2013 | 12.5 | 39.5 | 40.6 | 35.7 | 31.1 | 16.5 | 74.5 |
| PAPA016 | 2013 | 15.8 | 41.2 | 43.4 | 37.0 | 32.4 | 22.3 | 71.8 |
| PAPA016 | 2013 | 20 | 46.2 | 49.1 | 41.6 | 36.3 | 22.9 | 68.9 |
| PAPA016 | 2013 | 25 | 37.9 | 39.6 | 33.6 | 29.9 | 20.2 | 65.2 |
| PAPA016 | 2013 | 31.5 | 38.9 | 41.3 | 34.3 | 29.8 | 18.0 | 65.9 |
| PAPA016 | 2013 | 40 | 34.7 | 35.9 | 30.6 | 27.0 | 15.8 | 58.3 |
| PAPA016 | 2013 | 50 | 33.4 | 36.4 | 29.8 | 25.2 | 13.9 | 58.7 |
| PAPA016 | 2013 | 63 | 34.0 | 36.6 | 29.9 | 24.9 | 12.7 | 66.1 |
| PAPA016 | 2013 | 80 | 33.3 | 35.7 | 28.9 | 25.0 | 9.2 | 71.4 |
| PAPA016 | 2013 | 100 | 32.6 | 34.6 | 28.3 | 24.6 | 7.0 | 75.7 |
| PAPA016 | 2013 | 125 | 30.5 | 32.7 | 26.6 | 23.1 | 4.4 | 73.4 |
| PAPA016 | 2013 | 160 | 28.4 | 29.3 | 23.7 | 20.2 | 2.2 | 64.3 |
| PAPA016 | 2013 | 200 | 25.6 | 27.8 | 21.9 | 17.7 | 0.2 | 56.5 |
| PAPA016 | 2013 | 250 | 20.7 | 21.4 | 17.1 | 12.4 | -3.3 | 52.6 |
| PAPA016 | 2013 | 315 | 15.4 | 17.3 | 13.3 | 7.7 | -4.4 | 46.4 |
| PAPA016 | 2013 | 400 | 12.9 | 13.1 | 8.6 | 2.5 | -4.5 | 52.3 |
| PAPA016 | 2013 | 500 | 11.0 | 9.1 | 2.5 | -0.8 | -4.5 | 48.1 |
| PAPA016 | 2013 | 630 | 9.7 | 9.2 | 1.1 | -1.4 | -4.0 | 40.4 |
| PAPA016 | 2013 | 800 | 6.4 | 9.4 | 1.5 | -1.0 | -3.2 | 42.0 |
| PAPA016 | 2013 | 1000 | 5.7 | 8.3 | 1.2 | -0.5 | -2.4 | 38.5 |
| PAPA016 | 2013 | 1250 | 5.6 | 6.9 | 1.0 | -0.1 | -1.6 | 38.7 |
| PAPA016 | 2013 | 1600 | 5.1 | 6.2 | 1.5 | 0.8 | -0.6 | 48.1 |
| PAPA016 | 2013 | 2000 | 4.0 | 4.4 | 2.1 | 1.5 | 0.4 | 37.8 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA016 | 2013 | 2500 | 3.4 | 3.8 | 2.8 | 2.3 | 1.3 | 35.5 |
| PAPA016 | 2013 | 3150 | 3.8 | 4.1 | 3.5 | 3.1 | 2.2 | 35.0 |
| PAPA016 | 2013 | 4000 | 4.5 | 4.7 | 4.1 | 3.9 | 3.2 | 33.2 |
| PAPA016 | 2013 | 5000 | 5.2 | 5.3 | 4.8 | 4.5 | 3.6 | 37.7 |
| PAPA016 | 2013 | 6300 | 5.4 | 5.6 | 5.2 | 5.0 | 3.5 | 38.0 |
| PAPA016 | 2013 | 8000 | 5.4 | 5.6 | 5.3 | 5.1 | 3.6 | 41.3 |
| PAPA016 | 2013 | 10000 | 5.1 | 5.4 | 5.0 | 4.8 | 3.1 | 35.5 |
| PAPA016 | 2013 | 12500 | 4.4 | 4.7 | 4.3 | 4.1 | 2.8 | 35.7 |
| PAPA016 | 2013 | 16000 | 3.4 | 3.8 | 3.3 | 3.1 | 2.5 | 33.5 |
| PAPA016 | 2013 | 20000 | 2.2 | 2.6 | 2.0 | 1.7 | 1.2 | 32.9 |
| PAPA017 | 2013 | 12.5 | 48.5 | 50.6 | 44.1 | 39.3 | 25.3 | 78.3 |
| PAPA017 | 2013 | 15.8 | 46.8 | 49.7 | 44.1 | 39.3 | 25.1 | 77.6 |
| PAPA017 | 2013 | 20 | 56.3 | 60.8 | 50.8 | 46.2 | 29.6 | 75.9 |
| PAPA017 | 2013 | 25 | 47.7 | 50.3 | 46.3 | 42.8 | 27.6 | 70.6 |
| PAPA017 | 2013 | 31.5 | 54.5 | 58.2 | 52.7 | 46.8 | 26.1 | 69.4 |
| PAPA017 | 2013 | 40 | 42.7 | 45.1 | 41.8 | 38.0 | 24.6 | 64.5 |
| PAPA017 | 2013 | 50 | 39.1 | 41.5 | 37.7 | 34.8 | 24.1 | 63.8 |
| PAPA017 | 2013 | 63 | 37.9 | 40.0 | 36.8 | 33.7 | 21.8 | 62.8 |
| PAPA017 | 2013 | 80 | 34.1 | 36.7 | 32.8 | 29.2 | 17.2 | 68.7 |
| PAPA017 | 2013 | 100 | 32.7 | 35.5 | 30.1 | 26.7 | 13.4 | 69.9 |
| PAPA017 | 2013 | 125 | 31.8 | 34.8 | 29.2 | 25.6 | 7.5 | 74.7 |
| PAPA017 | 2013 | 160 | 30.0 | 32.3 | 27.6 | 24.0 | 4.5 | 71.3 |
| PAPA017 | 2013 | 200 | 28.5 | 30.6 | 26.5 | 22.5 | 4.5 | 57.8 |
| PAPA017 | 2013 | 250 | 24.5 | 26.9 | 23.0 | 19.2 | 1.1 | 55.1 |
| PAPA017 | 2013 | 315 | 20.6 | 23.5 | 18.9 | 15.6 | -1.1 | 47.9 |
| PAPA017 | 2013 | 400 | 17.2 | 19.1 | 15.1 | 11.1 | -3.0 | 49.2 |
| PAPA017 | 2013 | 500 | 13.8 | 14.8 | 9.3 | 6.1 | -3.4 | 47.3 |
| PAPA017 | 2013 | 630 | 8.5 | 10.7 | 4.9 | 1.2 | -3.4 | 41.4 |
| PAPA017 | 2013 | 800 | 6.7 | 8.5 | 2.9 | -0.1 | -3.1 | 39.4 |
| PAPA017 | 2013 | 1000 | 6.1 | 9.1 | 1.7 | -0.1 | -2.1 | 50.9 |
| PAPA017 | 2013 | 1250 | 5.2 | 7.7 | 1.3 | 0.3 | -1.3 | 42.2 |
| PAPA017 | 2013 | 1600 | 4.7 | 5.6 | 1.6 | 1.0 | -0.5 | 37.5 |
| PAPA017 | 2013 | 2000 | 3.8 | 3.8 | 2.3 | 1.7 | 0.6 | 33.7 |
| PAPA017 | 2013 | 2500 | 3.6 | 3.6 | 2.9 | 2.5 | 1.6 | 35.2 |
| PAPA017 | 2013 | 3150 | 3.9 | 4.1 | 3.7 | 3.3 | 2.5 | 48.5 |
| PAPA017 | 2013 | 4000 | 4.8 | 4.8 | 4.4 | 4.1 | 3.2 | 38.5 |
| PAPA017 | 2013 | 5000 | 5.6 | 5.3 | 4.9 | 4.7 | 2.7 | 45.2 |
| PAPA017 | 2013 | 6300 | 5.5 | 5.5 | 5.2 | 5.0 | 2.7 | 41.5 |
| PAPA017 | 2013 | 8000 | 5.3 | 5.5 | 5.3 | 5.1 | 2.2 | 29.5 |
| PAPA017 | 2013 | 10000 | 5.1 | 5.2 | 5.0 | 4.9 | 2.4 | 26.2 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA017 | 2013 | 12500 | 4.6 | 4.7 | 4.5 | 4.3 | 1.9 | 26.2 |
| PAPA017 | 2013 | 16000 | 3.8 | 3.9 | 3.6 | 3.5 | 1.8 | 23.6 |
| PAPA017 | 2013 | 20000 | 2.6 | 3.0 | 2.4 | 2.3 | 1.7 | 20.5 |
| PAPA018 | 2013 | 12.5 | 46.5 | 47.9 | 41.8 | 36.8 | 19.0 | 78.4 |
| PAPA018 | 2013 | 15.8 | 47.7 | 50.1 | 44.7 | 38.4 | 23.7 | 75.3 |
| PAPA018 | 2013 | 20 | 54.0 | 58.5 | 49.3 | 45.1 | 29.4 | 75.1 |
| PAPA018 | 2013 | 25 | 43.3 | 45.5 | 41.0 | 36.5 | 22.0 | 70.9 |
| PAPA018 | 2013 | 31.5 | 48.1 | 51.6 | 45.4 | 39.5 | 23.7 | 69.4 |
| PAPA018 | 2013 | 40 | 40.6 | 42.7 | 37.8 | 34.3 | 21.0 | 65.1 |
| PAPA018 | 2013 | 50 | 38.1 | 40.6 | 36.0 | 32.1 | 20.6 | 64.2 |
| PAPA018 | 2013 | 63 | 38.0 | 40.8 | 34.7 | 30.7 | 17.8 | 66.0 |
| PAPA018 | 2013 | 80 | 34.9 | 37.8 | 31.5 | 26.4 | 14.1 | 68.8 |
| PAPA018 | 2013 | 100 | 34.6 | 37.3 | 29.8 | 25.2 | 12.9 | 77.6 |
| PAPA018 | 2013 | 125 | 32.2 | 35.0 | 28.8 | 24.0 | 11.6 | 76.8 |
| PAPA018 | 2013 | 160 | 30.8 | 32.7 | 26.1 | 22.4 | 8.4 | 60.3 |
| PAPA018 | 2013 | 200 | 29.6 | 32.4 | 26.2 | 21.8 | 7.6 | 68.3 |
| PAPA018 | 2013 | 250 | 24.8 | 28.0 | 22.7 | 18.0 | 2.7 | 63.9 |
| PAPA018 | 2013 | 315 | 21.8 | 24.3 | 19.3 | 15.0 | -0.1 | 52.9 |
| PAPA018 | 2013 | 400 | 16.6 | 19.1 | 13.9 | 9.8 | -3.3 | 57.8 |
| PAPA018 | 2013 | 500 | 11.5 | 14.6 | 9.1 | 4.7 | -3.8 | 59.7 |
| PAPA018 | 2013 | 630 | 8.7 | 10.8 | 5.0 | 1.0 | -3.9 | 52.9 |
| PAPA018 | 2013 | 800 | 7.7 | 10.7 | 2.8 | -0.3 | -3.6 | 39.9 |
| PAPA018 | 2013 | 1000 | 6.0 | 8.3 | 0.5 | -1.1 | -2.9 | 38.3 |
| PAPA018 | 2013 | 1250 | 4.4 | 6.8 | -0.2 | -0.9 | -2.4 | 34.1 |
| PAPA018 | 2013 | 1600 | 3.5 | 3.8 | 0.2 | -0.4 | -1.5 | 35.5 |
| PAPA018 | 2013 | 2000 | 2.6 | 3.0 | 0.9 | 0.3 | -0.7 | 37.3 |
| PAPA018 | 2013 | 2500 | 2.4 | 2.6 | 1.5 | 1.1 | 0.2 | 36.9 |
| PAPA018 | 2013 | 3150 | 2.7 | 2.8 | 2.2 | 1.9 | 1.2 | 34.4 |
| PAPA018 | 2013 | 4000 | 3.4 | 3.4 | 3.0 | 2.8 | 2.2 | 43.8 |
| PAPA018 | 2013 | 5000 | 4.4 | 4.1 | 3.8 | 3.6 | 2.9 | 47.8 |
| PAPA018 | 2013 | 6300 | 4.7 | 4.7 | 4.5 | 4.4 | 2.8 | 54.3 |
| PAPA018 | 2013 | 8000 | 5.1 | 5.2 | 5.1 | 4.9 | 2.6 | 55.8 |
| PAPA018 | 2013 | 10000 | 5.4 | 5.5 | 5.3 | 5.2 | 2.7 | 36.8 |
| PAPA018 | 2013 | 12500 | 5.0 | 5.2 | 4.8 | 4.7 | 2.5 | 28.0 |
| PAPA018 | 2013 | 16000 | 2.9 | 3.2 | 2.8 | 2.6 | 1.6 | 33.5 |
| PAPA018 | 2013 | 20000 | 0.4 | 0.7 | 0.2 | 0.0 | -0.4 | 19.2 |
| PAPA019 | 2013 | 12.5 | 41.5 | 43.7 | 38.5 | 33.9 | 16.2 | 73.2 |
| PAPA019 | 2013 | 15.8 | 42.2 | 44.9 | 40.0 | 34.9 | 19.9 | 69.7 |
| PAPA019 | 2013 | 20 | 49.9 | 52.9 | 43.9 | 39.5 | 22.6 | 71.7 |
| PAPA019 | 2013 | 25 | 39.6 | 42.2 | 36.7 | 32.1 | 20.7 | 63.8 |

| Appendix D. One-third Octave Band Metrics, PAPA Leks, April 2013. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA019 | 2013 | 31.5 | 42.2 | 45.2 | 39.5 | 33.6 | 20.7 | 63.6 |
| PAPA019 | 2013 | 40 | 36.8 | 39.1 | 34.3 | 29.6 | 18.5 | 60.9 |
| PAPA019 | 2013 | 50 | 36.1 | 39.0 | 33.1 | 28.8 | 16.6 | 59.7 |
| PAPA019 | 2013 | 63 | 36.4 | 38.6 | 32.9 | 28.5 | 18.5 | 65.6 |
| PAPA019 | 2013 | 80 | 34.0 | 36.8 | 30.8 | 26.7 | 14.5 | 76.9 |
| PAPA019 | 2013 | 100 | 32.7 | 35.3 | 28.8 | 24.9 | 14.3 | 74.5 |
| PAPA019 | 2013 | 125 | 31.0 | 33.1 | 27.1 | 22.5 | 11.3 | 71.6 |
| PAPA019 | 2013 | 160 | 28.6 | 29.4 | 24.5 | 20.0 | 7.8 | 60.1 |
| PAPA019 | 2013 | 200 | 25.6 | 27.6 | 22.5 | 18.2 | 4.8 | 68.0 |
| PAPA019 | 2013 | 250 | 21.1 | 23.4 | 18.5 | 14.9 | 1.1 | 65.3 |
| PAPA019 | 2013 | 315 | 18.0 | 20.5 | 14.7 | 10.8 | -1.9 | 52.1 |
| PAPA019 | 2013 | 400 | 13.1 | 16.1 | 10.0 | 5.8 | -3.3 | 56.2 |
| PAPA019 | 2013 | 500 | 9.8 | 12.2 | 5.4 | 1.0 | -3.9 | 56.8 |
| PAPA019 | 2013 | 630 | 7.4 | 8.6 | 1.9 | -1.4 | -3.6 | 52.4 |
| PAPA019 | 2013 | 800 | 5.9 | 8.2 | 0.5 | -1.5 | -3.3 | 48.5 |
| PAPA019 | 2013 | 1000 | 6.6 | 7.7 | 0.2 | -1.0 | -2.4 | 50.7 |
| PAPA019 | 2013 | 1250 | 6.2 | 6.9 | 0.4 | -0.3 | -1.6 | 53.4 |
| PAPA019 | 2013 | 1600 | 4.8 | 5.9 | 1.1 | 0.5 | -0.7 | 54.4 |
| PAPA019 | 2013 | 2000 | 3.0 | 3.5 | 1.8 | 1.3 | 0.3 | 49.9 |
| PAPA019 | 2013 | 2500 | 2.8 | 3.1 | 2.5 | 2.0 | 1.3 | 43.8 |
| PAPA019 | 2013 | 3150 | 3.4 | 3.7 | 3.2 | 2.9 | 2.1 | 35.2 |
| PAPA019 | 2013 | 4000 | 4.0 | 4.3 | 3.9 | 3.6 | 2.0 | 37.0 |
| PAPA019 | 2013 | 5000 | 4.5 | 4.7 | 4.4 | 4.2 | 2.4 | 35.9 |
| PAPA019 | 2013 | 6300 | 4.8 | 4.9 | 4.7 | 4.5 | 1.4 | 37.7 |
| PAPA019 | 2013 | 8000 | 4.7 | 4.8 | 4.6 | 4.4 | 1.1 | 29.6 |
| PAPA019 | 2013 | 10000 | 4.2 | 4.5 | 4.2 | 4.0 | 0.5 | 32.1 |
| PAPA019 | 2013 | 12500 | 3.6 | 3.8 | 3.5 | 3.3 | 0.0 | 28.3 |
| PAPA019 | 2013 | 16000 | 2.7 | 2.9 | 2.5 | 2.3 | -0.4 | 26.5 |
| PAPA019 | 2013 | 20000 | 1.1 | 1.4 | 0.9 | 0.6 | -0.3 | 26.4 |

## Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA001 | 2014 | 12.5 | 47.9 | 50.3 | 44.9 | 39.9 | 25.2 | 83.9 |
| PAPA001 | 2014 | 15.8 | 54.6 | 57.4 | 53.8 | 49.6 | 30.7 | 79.1 |
| PAPA001 | 2014 | 20 | 56.9 | 59.3 | 55.7 | 51.9 | 35.8 | 81.9 |
| PAPA001 | 2014 | 25 | 51.2 | 53.2 | 50.1 | 47.5 | 34.2 | 73.0 |
| PAPA001 | 2014 | 31.5 | 61.9 | 65.3 | 60.8 | 54.2 | 37.5 | 78.1 |
| PAPA001 | 2014 | 40 | 44.4 | 46.5 | 43.1 | 40.4 | 28.4 | 68.2 |
| PAPA001 | 2014 | 50 | 40.4 | 42.8 | 39.4 | 36.9 | 20.4 | 63.2 |
| PAPA001 | 2014 | 63 | 40.3 | 43.4 | 38.2 | 34.3 | 18.5 | 69.5 |
| PAPA001 | 2014 | 80 | 37.4 | 38.6 | 31.5 | 29.1 | 13.3 | 69.5 |
| PAPA001 | 2014 | 100 | 34.2 | 36.2 | 31.8 | 28.2 | 11.0 | 72.3 |
| PAPA001 | 2014 | 125 | 31.3 | 33.2 | 28.6 | 25.1 | 7.7 | 62.2 |
| PAPA001 | 2014 | 160 | 27.8 | 28.5 | 23.6 | 20.9 | 4.7 | 58.9 |
| PAPA001 | 2014 | 200 | 26.0 | 26.5 | 22.2 | 18.9 | 0.0 | 60.8 |
| PAPA001 | 2014 | 250 | 23.8 | 23.9 | 18.9 | 16.3 | 0.0 | 55.9 |
| PAPA001 | 2014 | 315 | 21.3 | 19.8 | 16.8 | 14.2 | 0.0 | 51.8 |
| PAPA001 | 2014 | 400 | 19.1 | 18.6 | 14.2 | 11.9 | 0.0 | 57.4 |
| PAPA001 | 2014 | 500 | 16.5 | 16.2 | 10.7 | 7.7 | 0.0 | 53.6 |
| PAPA001 | 2014 | 630 | 13.9 | 15.1 | 8.3 | 4.7 | 0.0 | 48.7 |
| PAPA001 | 2014 | 800 | 12.6 | 14.5 | 8.3 | 5.9 | 0.0 | 43.8 |
| PAPA001 | 2014 | 1000 | 11.2 | 12.2 | 7.7 | 5.9 | 0.0 | 49.2 |
| PAPA001 | 2014 | 1250 | 8.0 | 9.4 | 5.9 | 4.7 | 2.9 | 50.3 |
| PAPA001 | 2014 | 1600 | 7.2 | 8.3 | 5.9 | 4.7 | 2.9 | 37.9 |
| PAPA001 | 2014 | 2000 | 7.3 | 7.7 | 6.9 | 5.9 | 4.7 | 51.9 |
| PAPA001 | 2014 | 2500 | 7.6 | 7.7 | 6.9 | 6.9 | 5.9 | 50.5 |
| PAPA001 | 2014 | 3150 | 8.3 | 8.3 | 7.7 | 7.7 | 6.9 | 41.8 |
| PAPA001 | 2014 | 4000 | 8.7 | 8.9 | 8.3 | 8.3 | 7.7 | 37.7 |
| PAPA001 | 2014 | 5000 | 9.1 | 9.4 | 8.9 | 8.9 | 8.3 | 37.7 |
| PAPA001 | 2014 | 6300 | 9.4 | 9.4 | 9.4 | 8.9 | 8.3 | 46.4 |
| PAPA001 | 2014 | 8000 | 9.3 | 9.4 | 9.4 | 8.9 | 8.9 | 40.7 |
| PAPA001 | 2014 | 10000 | 9.2 | 9.4 | 8.9 | 8.9 | 8.3 | 34.7 |
| PAPA001 | 2014 | 12500 | 9.3 | 9.4 | 9.4 | 8.9 | 8.9 | 35.8 |
| PAPA001 | 2014 | 16000 | 9.9 | 9.9 | 9.9 | 9.4 | 8.9 | 37.2 |
| PAPA001 | 2014 | 20000 | 12.9 | 13.1 | 12.9 | 12.7 | 11.9 | 44.7 |
| PAPA002 | 2014 | 12.5 | 53.4 | 56.0 | 49.0 | 41.9 | 25.9 | 90.6 |
| PAPA002 | 2014 | 15.8 | 55.0 | 57.8 | 53.3 | 49.0 | 32.2 | 88.0 |
| PAPA002 | 2014 | 20 | 57.2 | 59.8 | 56.4 | 52.7 | 35.1 | 85.6 |
| PAPA002 | 2014 | 25 | 49.9 | 53.7 | 45.0 | 41.1 | 30.3 | 82.7 |
| PAPA002 | 2014 | 31.5 | 48.0 | 51.0 | 46.3 | 41.8 | 28.5 | 77.7 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA002 | 2014 | 40 | 41.7 | 44.4 | 40.5 | 36.6 | 25.6 | 75.7 |
| PAPA002 | 2014 | 50 | 39.4 | 41.8 | 37.9 | 34.6 | 23.4 | 71.0 |
| PAPA002 | 2014 | 63 | 36.8 | 39.0 | 34.2 | 31.5 | 20.0 | 68.0 |
| PAPA002 | 2014 | 80 | 33.7 | 36.2 | 31.2 | 28.0 | 14.6 | 74.9 |
| PAPA002 | 2014 | 100 | 32.3 | 33.6 | 28.6 | 25.2 | 11.9 | 66.1 |
| PAPA002 | 2014 | 125 | 30.4 | 31.8 | 26.2 | 23.3 | 9.5 | 60.4 |
| PAPA002 | 2014 | 160 | 27.1 | 28.7 | 23.5 | 20.2 | 6.5 | 56.6 |
| PAPA002 | 2014 | 200 | 25.8 | 26.9 | 21.9 | 18.6 | 5.3 | 58.2 |
| PAPA002 | 2014 | 250 | 23.3 | 25.4 | 19.0 | 15.5 | 3.5 | 55.6 |
| PAPA002 | 2014 | 315 | 20.7 | 22.9 | 17.8 | 14.3 | 0.0 | 55.8 |
| PAPA002 | 2014 | 400 | 20.1 | 18.5 | 13.5 | 9.5 | 0.0 | 56.5 |
| PAPA002 | 2014 | 500 | 19.1 | 16.4 | 8.9 | 5.3 | 0.0 | 59.5 |
| PAPA002 | 2014 | 630 | 16.2 | 15.0 | 7.5 | 3.5 | 0.0 | 55.3 |
| PAPA002 | 2014 | 800 | 11.6 | 13.3 | 6.5 | 3.5 | 0.0 | 45.6 |
| PAPA002 | 2014 | 1000 | 7.7 | 10.5 | 5.3 | 3.5 | 0.0 | 42.6 |
| PAPA002 | 2014 | 1250 | 6.2 | 7.5 | 5.3 | 3.5 | 0.0 | 43.0 |
| PAPA002 | 2014 | 1600 | 7.0 | 7.5 | 5.3 | 5.3 | 3.5 | 47.5 |
| PAPA002 | 2014 | 2000 | 7.6 | 8.3 | 6.5 | 6.5 | 3.5 | 57.6 |
| PAPA002 | 2014 | 2500 | 8.1 | 8.3 | 7.5 | 7.5 | 5.3 | 57.7 |
| PAPA002 | 2014 | 3150 | 8.6 | 8.9 | 8.3 | 8.3 | 6.5 | 47.5 |
| PAPA002 | 2014 | 4000 | 9.6 | 9.5 | 8.9 | 8.9 | 7.5 | 48.1 |
| PAPA002 | 2014 | 5000 | 10.4 | 9.5 | 9.5 | 8.9 | 8.3 | 48.7 |
| PAPA002 | 2014 | 6300 | 9.8 | 10.0 | 9.5 | 9.5 | 8.3 | 49.2 |
| PAPA002 | 2014 | 8000 | 10.0 | 10.0 | 9.5 | 9.5 | 8.3 | 50.4 |
| PAPA002 | 2014 | 10000 | 9.9 | 10.0 | 10.0 | 9.5 | 8.3 | 37.3 |
| PAPA002 | 2014 | 12500 | 10.0 | 10.0 | 10.0 | 9.5 | 8.9 | 37.7 |
| PAPA002 | 2014 | 16000 | 10.4 | 10.5 | 10.0 | 10.0 | 9.5 | 38.3 |
| PAPA002 | 2014 | 20000 | 13.0 | 12.8 | 12.8 | 12.5 | 12.2 | 44.4 |
| PAPA003 | 2014 | 12.5 | 49.1 | 52.2 | 46.4 | 41.1 | 22.4 | 76.9 |
| PAPA003 | 2014 | 15.8 | 54.4 | 57.4 | 53.5 | 48.5 | 29.6 | 76.1 |
| PAPA003 | 2014 | 20 | 57.0 | 59.4 | 55.5 | 51.8 | 35.9 | 73.4 |
| PAPA003 | 2014 | 25 | 51.5 | 54.5 | 48.9 | 44.0 | 30.4 | 71.9 |
| PAPA003 | 2014 | 31.5 | 53.3 | 56.4 | 52.4 | 48.2 | 34.4 | 71.3 |
| PAPA003 | 2014 | 40 | 45.4 | 47.6 | 44.4 | 40.8 | 32.3 | 69.0 |
| PAPA003 | 2014 | 50 | 45.4 | 48.1 | 43.8 | 40.5 | 31.0 | 67.2 |
| PAPA003 | 2014 | 63 | 45.5 | 48.4 | 43.8 | 39.8 | 28.7 | 66.1 |
| PAPA003 | 2014 | 80 | 41.4 | 43.1 | 37.4 | 34.3 | 22.8 | 75.0 |
| PAPA003 | 2014 | 100 | 40.2 | 41.4 | 36.0 | 32.3 | 21.1 | 70.4 |
| PAPA003 | 2014 | 125 | 37.2 | 39.1 | 34.5 | 30.6 | 17.5 | 65.2 |
| PAPA003 | 2014 | 160 | 34.1 | 36.3 | 31.1 | 27.4 | 16.3 | 63.8 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA003 | 2014 | 200 | 31.2 | 33.4 | 28.6 | 25.0 | 14.2 | 64.7 |
| PAPA003 | 2014 | 250 | 28.3 | 30.5 | 25.9 | 22.2 | 12.0 | 56.9 |
| PAPA003 | 2014 | 315 | 25.9 | 28.2 | 23.8 | 20.0 | 9.5 | 51.3 |
| PAPA003 | 2014 | 400 | 22.6 | 24.7 | 20.0 | 16.2 | 6.0 | 48.6 |
| PAPA003 | 2014 | 500 | 19.8 | 20.7 | 16.1 | 12.0 | 1.8 | 50.4 |
| PAPA003 | 2014 | 630 | 16.6 | 17.4 | 12.9 | 8.7 | -0.5 | 47.1 |
| PAPA003 | 2014 | 800 | 12.5 | 14.1 | 9.2 | 4.5 | -1.8 | 47.7 |
| PAPA003 | 2014 | 1000 | 9.5 | 11.2 | 6.1 | 1.8 | -1.8 | 45.7 |
| PAPA003 | 2014 | 1250 | 5.3 | 7.8 | 3.1 | 0.4 | -1.3 | 37.1 |
| PAPA003 | 2014 | 1600 | 3.6 | 4.6 | 1.3 | 0.6 | -0.7 | 40.4 |
| PAPA003 | 2014 | 2000 | 3.5 | 5.3 | 1.7 | 1.2 | 0.0 | 35.3 |
| PAPA003 | 2014 | 2500 | 3.7 | 5.0 | 2.3 | 1.8 | -0.1 | 42.3 |
| PAPA003 | 2014 | 3150 | 3.5 | 3.9 | 2.7 | 2.3 | -0.1 | 36.0 |
| PAPA003 | 2014 | 4000 | 5.0 | 4.7 | 3.0 | 2.6 | -0.8 | 41.2 |
| PAPA003 | 2014 | 5000 | 6.2 | 4.3 | 3.1 | 2.8 | -1.2 | 45.8 |
| PAPA003 | 2014 | 6300 | 3.9 | 3.5 | 3.2 | 2.9 | -1.5 | 42.3 |
| PAPA003 | 2014 | 8000 | 3.2 | 3.4 | 3.2 | 3.1 | -1.6 | 28.4 |
| PAPA003 | 2014 | 10000 | 3.6 | 3.7 | 3.6 | 3.4 | -1.6 | 31.1 |
| PAPA003 | 2014 | 12500 | 3.8 | 3.9 | 3.8 | 3.5 | -1.5 | 31.7 |
| PAPA003 | 2014 | 16000 | 1.9 | 2.0 | 1.9 | 1.8 | -1.7 | 32.0 |
| PAPA003 | 2014 | 20000 | -1.5 | -1.3 | -1.6 | -1.7 | -2.2 | 29.3 |
| PAPA004 | 2014 | 12.5 | 48.8 | 51.3 | 43.9 | 36.1 | 21.7 | 76.8 |
| PAPA004 | 2014 | 15.8 | 49.7 | 52.5 | 45.2 | 39.1 | 26.1 | 73.9 |
| PAPA004 | 2014 | 20 | 51.8 | 54.7 | 49.0 | 45.2 | 30.1 | 75.6 |
| PAPA004 | 2014 | 25 | 45.3 | 47.9 | 40.2 | 36.4 | 23.8 | 71.0 |
| PAPA004 | 2014 | 31.5 | 46.9 | 50.2 | 44.1 | 38.5 | 23.9 | 71.4 |
| PAPA004 | 2014 | 40 | 40.8 | 43.4 | 38.4 | 34.2 | 21.6 | 67.3 |
| PAPA004 | 2014 | 50 | 38.7 | 41.2 | 34.9 | 31.5 | 17.8 | 66.2 |
| PAPA004 | 2014 | 63 | 36.9 | 39.4 | 34.5 | 30.3 | 18.2 | 67.0 |
| PAPA004 | 2014 | 80 | 35.4 | 37.5 | 32.3 | 29.0 | 13.7 | 68.0 |
| PAPA004 | 2014 | 100 | 34.2 | 36.5 | 31.8 | 28.2 | 15.1 | 79.5 |
| PAPA004 | 2014 | 125 | 33.0 | 34.2 | 29.3 | 26.2 | 10.4 | 80.5 |
| PAPA004 | 2014 | 160 | 30.2 | 31.5 | 26.0 | 22.7 | 7.7 | 76.3 |
| PAPA004 | 2014 | 200 | 27.5 | 29.7 | 23.8 | 20.1 | 4.6 | 69.2 |
| PAPA004 | 2014 | 250 | 25.5 | 26.3 | 22.1 | 17.8 | 4.2 | 69.5 |
| PAPA004 | 2014 | 315 | 22.3 | 22.8 | 18.8 | 15.1 | -0.3 | 63.1 |
| PAPA004 | 2014 | 400 | 19.1 | 19.4 | 15.1 | 12.1 | -2.2 | 66.0 |
| PAPA004 | 2014 | 500 | 14.1 | 15.0 | 10.3 | 6.7 | -3.1 | 68.8 |
| PAPA004 | 2014 | 630 | 10.9 | 13.5 | 6.6 | 3.2 | -3.3 | 66.1 |
| PAPA004 | 2014 | 800 | 11.8 | 15.6 | 4.7 | 0.8 | -3.1 | 60.7 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA004 | 2014 | 1000 | 13.3 | 15.1 | 3.4 | 0.1 | -2.5 | 54.4 |
| PAPA004 | 2014 | 1250 | 12.3 | 12.7 | 2.7 | 0.4 | -1.7 | 57.5 |
| PAPA004 | 2014 | 1600 | 10.1 | 10.3 | 2.1 | 0.8 | -0.8 | 52.8 |
| PAPA004 | 2014 | 2000 | 7.8 | 9.6 | 2.3 | 1.3 | 0.1 | 53.4 |
| PAPA004 | 2014 | 2500 | 6.7 | 6.3 | 2.7 | 2.0 | 1.0 | 50.5 |
| PAPA004 | 2014 | 3150 | 7.9 | 5.1 | 3.1 | 2.8 | 1.5 | 59.9 |
| PAPA004 | 2014 | 4000 | 5.3 | 4.3 | 3.9 | 3.7 | 0.9 | 51.9 |
| PAPA004 | 2014 | 5000 | 5.1 | 4.9 | 4.7 | 4.5 | 1.4 | 39.9 |
| PAPA004 | 2014 | 6300 | 5.4 | 5.5 | 5.3 | 5.2 | 1.2 | 30.7 |
| PAPA004 | 2014 | 8000 | 5.9 | 6.0 | 5.8 | 5.7 | 1.5 | 28.8 |
| PAPA004 | 2014 | 10000 | 6.3 | 6.4 | 6.2 | 6.1 | 0.6 | 29.5 |
| PAPA004 | 2014 | 12500 | 6.3 | 6.4 | 6.2 | 6.0 | 0.7 | 30.1 |
| PAPA004 | 2014 | 16000 | 5.6 | 5.9 | 5.6 | 5.4 | 0.8 | 31.3 |
| PAPA004 | 2014 | 20000 | 3.8 | 4.5 | 3.6 | 3.3 | 0.6 | 25.3 |
| PAPA005 | 2014 | 12.5 | 44.3 | 47.3 | 41.1 | 36.4 | 21.6 | 78.3 |
| PAPA005 | 2014 | 15.8 | 48.6 | 51.2 | 47.0 | 42.7 | 27.0 | 75.9 |
| PAPA005 | 2014 | 20 | 57.5 | 59.5 | 56.3 | 52.4 | 33.6 | 73.9 |
| PAPA005 | 2014 | 25 | 60.9 | 63.5 | 59.7 | 55.7 | 27.6 | 76.1 |
| PAPA005 | 2014 | 31.5 | 48.5 | 51.6 | 46.4 | 41.6 | 27.7 | 70.6 |
| PAPA005 | 2014 | 40 | 43.6 | 45.7 | 41.7 | 39.3 | 25.7 | 68.6 |
| PAPA005 | 2014 | 50 | 46.3 | 49.1 | 46.2 | 40.4 | 27.6 | 66.8 |
| PAPA005 | 2014 | 63 | 39.7 | 42.4 | 37.9 | 34.6 | 23.7 | 69.6 |
| PAPA005 | 2014 | 80 | 37.7 | 40.2 | 34.4 | 31.0 | 21.4 | 74.5 |
| PAPA005 | 2014 | 100 | 36.4 | 35.9 | 31.2 | 28.5 | 17.0 | 78.1 |
| PAPA005 | 2014 | 125 | 33.8 | 34.9 | 29.4 | 25.7 | 12.9 | 76.5 |
| PAPA005 | 2014 | 160 | 31.3 | 32.7 | 27.5 | 23.2 | 10.1 | 74.5 |
| PAPA005 | 2014 | 200 | 29.0 | 30.3 | 24.9 | 20.6 | 6.5 | 64.1 |
| PAPA005 | 2014 | 250 | 26.6 | 27.8 | 21.5 | 18.4 | 4.4 | 67.3 |
| PAPA005 | 2014 | 315 | 23.0 | 24.7 | 19.1 | 15.5 | 1.8 | 61.5 |
| PAPA005 | 2014 | 400 | 18.6 | 20.8 | 14.4 | 11.3 | -0.2 | 61.2 |
| PAPA005 | 2014 | 500 | 17.2 | 17.4 | 10.4 | 6.9 | -2.3 | 64.7 |
| PAPA005 | 2014 | 630 | 14.3 | 15.0 | 7.0 | 3.2 | -2.9 | 63.2 |
| PAPA005 | 2014 | 800 | 9.0 | 11.2 | 3.6 | 0.7 | -2.9 | 57.0 |
| PAPA005 | 2014 | 1000 | 4.7 | 6.0 | 1.6 | 0.1 | -2.3 | 45.6 |
| PAPA005 | 2014 | 1250 | 2.6 | 3.1 | 0.9 | 0.4 | -1.6 | 47.6 |
| PAPA005 | 2014 | 1600 | 2.8 | 3.2 | 1.3 | 0.7 | -0.8 | 41.4 |
| PAPA005 | 2014 | 2000 | 7.7 | 8.5 | 2.4 | 1.8 | 0.1 | 41.8 |
| PAPA005 | 2014 | 2500 | 8.5 | 9.3 | 3.2 | 2.6 | 1.0 | 47.4 |
| PAPA005 | 2014 | 3150 | 9.7 | 6.5 | 3.8 | 3.3 | 1.9 | 55.1 |
| PAPA005 | 2014 | 4000 | 12.5 | 7.4 | 4.5 | 4.0 | 1.3 | 53.0 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA005 | 2014 | 5000 | 11.3 | 7.6 | 5.0 | 4.6 | 1.4 | 61.6 |
| PAPA005 | 2014 | 6300 | 7.8 | 6.1 | 5.4 | 5.2 | 1.3 | 50.2 |
| PAPA005 | 2014 | 8000 | 6.1 | 6.1 | 5.9 | 5.7 | 0.5 | 41.4 |
| PAPA005 | 2014 | 10000 | 6.4 | 6.4 | 6.2 | 6.1 | 0.2 | 31.3 |
| PAPA005 | 2014 | 12500 | 6.5 | 6.5 | 6.3 | 6.1 | 0.0 | 31.9 |
| PAPA005 | 2014 | 16000 | 5.9 | 5.9 | 5.7 | 5.5 | 0.3 | 33.1 |
| PAPA005 | 2014 | 20000 | 3.7 | 3.8 | 3.6 | 3.5 | 0.0 | 35.2 |
| PAPA006 | 2014 | 12.5 | 51.9 | 55.2 | 48.1 | 42.3 | 27.3 | 96.7 |
| PAPA006 | 2014 | 15.8 | 53.6 | 56.0 | 52.9 | 48.7 | 32.9 | 93.4 |
| PAPA006 | 2014 | 20 | 61.3 | 63.3 | 61.0 | 57.6 | 43.2 | 94.5 |
| PAPA006 | 2014 | 25 | 56.3 | 57.8 | 55.6 | 52.4 | 40.9 | 89.1 |
| PAPA006 | 2014 | 31.5 | 51.9 | 53.9 | 50.8 | 46.8 | 35.1 | 86.2 |
| PAPA006 | 2014 | 40 | 50.1 | 52.2 | 48.7 | 45.0 | 34.9 | 86.7 |
| PAPA006 | 2014 | 50 | 47.1 | 48.6 | 45.8 | 42.1 | 34.4 | 79.4 |
| PAPA006 | 2014 | 63 | 45.0 | 47.0 | 44.4 | 42.0 | 33.1 | 79.1 |
| PAPA006 | 2014 | 80 | 41.7 | 43.2 | 40.6 | 37.8 | 29.4 | 76.1 |
| PAPA006 | 2014 | 100 | 40.6 | 42.6 | 39.9 | 37.2 | 26.9 | 71.3 |
| PAPA006 | 2014 | 125 | 37.8 | 39.4 | 36.9 | 34.1 | 25.4 | 69.0 |
| PAPA006 | 2014 | 160 | 34.9 | 36.5 | 33.9 | 31.2 | 21.6 | 64.7 |
| PAPA006 | 2014 | 200 | 32.1 | 33.9 | 31.0 | 28.4 | 18.1 | 66.6 |
| PAPA006 | 2014 | 250 | 29.0 | 31.1 | 27.6 | 24.9 | 14.5 | 63.9 |
| PAPA006 | 2014 | 315 | 28.7 | 30.7 | 27.9 | 25.5 | 11.0 | 59.0 |
| PAPA006 | 2014 | 400 | 24.1 | 25.9 | 22.8 | 19.9 | 7.1 | 59.9 |
| PAPA006 | 2014 | 500 | 17.4 | 18.7 | 15.1 | 12.6 | 2.3 | 64.9 |
| PAPA006 | 2014 | 630 | 13.6 | 15.0 | 9.9 | 7.4 | 0.0 | 60.4 |
| PAPA006 | 2014 | 800 | 11.7 | 13.3 | 6.3 | 4.1 | 0.0 | 51.4 |
| PAPA006 | 2014 | 1000 | 8.5 | 7.7 | 4.1 | 2.3 | 0.0 | 51.6 |
| PAPA006 | 2014 | 1250 | 8.7 | 6.7 | 4.1 | 4.1 | 2.3 | 51.4 |
| PAPA006 | 2014 | 1600 | 11.1 | 8.0 | 5.3 | 4.1 | 4.1 | 51.5 |
| PAPA006 | 2014 | 2000 | 9.5 | 9.3 | 6.3 | 5.3 | 4.1 | 51.0 |
| PAPA006 | 2014 | 2500 | 10.3 | 9.9 | 7.1 | 6.3 | 5.3 | 62.5 |
| PAPA006 | 2014 | 3150 | 8.6 | 8.3 | 7.7 | 7.1 | 6.3 | 65.8 |
| PAPA006 | 2014 | 4000 | 8.7 | 8.3 | 8.3 | 7.7 | 7.1 | 60.4 |
| PAPA006 | 2014 | 5000 | 9.0 | 8.8 | 8.3 | 8.3 | 7.7 | 44.5 |
| PAPA006 | 2014 | 6300 | 8.8 | 8.8 | 8.8 | 8.3 | 8.3 | 42.6 |
| PAPA006 | 2014 | 8000 | 8.9 | 8.8 | 8.8 | 8.3 | 8.3 | 40.0 |
| PAPA006 | 2014 | 10000 | 8.7 | 8.8 | 8.8 | 8.3 | 8.3 | 37.1 |
| PAPA006 | 2014 | 12500 | 8.8 | 8.8 | 8.8 | 8.3 | 8.3 | 36.7 |
| PAPA006 | 2014 | 16000 | 9.7 | 9.3 | 9.3 | 8.8 | 8.8 | 38.3 |
| PAPA006 | 2014 | 20000 | 12.2 | 12.1 | 12.1 | 11.8 | 11.3 | 44.5 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA007 | 2014 | 12.5 | 49.0 | 51.8 | 45.8 | 40.2 | 27.5 | 76.2 |
| PAPA007 | 2014 | 15.8 | 51.0 | 53.7 | 49.0 | 44.8 | 30.0 | 74.3 |
| PAPA007 | 2014 | 20 | 52.0 | 53.8 | 50.7 | 47.5 | 34.6 | 72.0 |
| PAPA007 | 2014 | 25 | 50.2 | 53.7 | 47.7 | 43.7 | 31.1 | 72.1 |
| PAPA007 | 2014 | 31.5 | 49.8 | 52.9 | 48.1 | 43.9 | 32.7 | 69.1 |
| PAPA007 | 2014 | 40 | 44.1 | 46.9 | 42.6 | 39.9 | 29.2 | 67.1 |
| PAPA007 | 2014 | 50 | 44.6 | 47.5 | 40.8 | 37.1 | 28.2 | 69.4 |
| PAPA007 | 2014 | 63 | 40.7 | 43.3 | 38.3 | 35.1 | 24.1 | 70.8 |
| PAPA007 | 2014 | 80 | 39.1 | 41.0 | 35.7 | 32.5 | 23.4 | 76.9 |
| PAPA007 | 2014 | 100 | 37.5 | 40.4 | 35.2 | 31.9 | 21.6 | 66.3 |
| PAPA007 | 2014 | 125 | 34.3 | 36.7 | 32.1 | 28.9 | 20.8 | 65.4 |
| PAPA007 | 2014 | 160 | 31.6 | 34.4 | 29.7 | 26.7 | 16.4 | 58.9 |
| PAPA007 | 2014 | 200 | 29.6 | 32.4 | 28.2 | 25.1 | 13.5 | 57.6 |
| PAPA007 | 2014 | 250 | 26.5 | 28.4 | 25.0 | 22.3 | 10.8 | 56.1 |
| PAPA007 | 2014 | 315 | 23.3 | 25.6 | 22.3 | 18.8 | 4.2 | 54.2 |
| PAPA007 | 2014 | 400 | 20.6 | 23.5 | 19.6 | 16.0 | -0.8 | 50.6 |
| PAPA007 | 2014 | 500 | 16.9 | 19.5 | 14.9 | 11.7 | -2.6 | 45.5 |
| PAPA007 | 2014 | 630 | 11.8 | 15.1 | 10.5 | 5.7 | -3.9 | 42.9 |
| PAPA007 | 2014 | 800 | 9.8 | 11.5 | 7.6 | 2.7 | -3.3 | 39.6 |
| PAPA007 | 2014 | 1000 | 6.8 | 8.5 | 5.4 | 1.7 | -2.7 | 48.0 |
| PAPA007 | 2014 | 1250 | 6.0 | 6.1 | 2.1 | 0.5 | -1.6 | 45.9 |
| PAPA007 | 2014 | 1600 | 5.3 | 6.5 | 2.4 | 1.2 | -0.9 | 36.7 |
| PAPA007 | 2014 | 2000 | 7.5 | 7.8 | 2.0 | 1.3 | -0.6 | 43.9 |
| PAPA007 | 2014 | 2500 | 11.6 | 9.6 | 2.3 | 1.9 | -1.0 | 58.1 |
| PAPA007 | 2014 | 3150 | 8.3 | 6.3 | 2.7 | 2.2 | -1.5 | 63.6 |
| PAPA007 | 2014 | 4000 | 7.7 | 5.1 | 3.0 | 2.5 | -1.8 | 63.7 |
| PAPA007 | 2014 | 5000 | 4.2 | 3.5 | 3.0 | 2.7 | -1.8 | 56.5 |
| PAPA007 | 2014 | 6300 | 4.2 | 3.4 | 3.1 | 2.9 | -1.8 | 51.2 |
| PAPA007 | 2014 | 8000 | 3.3 | 3.4 | 3.2 | 3.0 | -2.0 | 58.4 |
| PAPA007 | 2014 | 10000 | 3.6 | 3.7 | 3.5 | 3.3 | -2.0 | 34.1 |
| PAPA007 | 2014 | 12500 | 3.6 | 3.9 | 3.6 | 3.3 | -2.2 | 31.9 |
| PAPA007 | 2014 | 16000 | 2.1 | 2.3 | 1.9 | 1.5 | -2.7 | 36.4 |
| PAPA007 | 2014 | 20000 | -0.3 | 0.3 | -1.1 | -1.6 | -3.1 | 29.4 |
| PAPA008 | 2014 | 12.5 | 51.0 | 54.5 | 48.0 | 41.8 | 23.2 | 76.0 |
| PAPA008 | 2014 | 15.8 | 53.9 | 57.0 | 52.1 | 46.4 | 28.5 | 73.9 |
| PAPA008 | 2014 | 20 | 54.2 | 57.6 | 52.1 | 47.5 | 34.1 | 72.4 |
| PAPA008 | 2014 | 25 | 48.2 | 51.4 | 46.6 | 42.8 | 27.5 | 71.4 |
| PAPA008 | 2014 | 31.5 | 47.0 | 49.9 | 45.3 | 41.8 | 28.0 | 70.2 |
| PAPA008 | 2014 | 40 | 45.3 | 47.7 | 44.6 | 41.0 | 24.6 | 71.7 |
| PAPA008 | 2014 | 50 | 39.8 | 42.1 | 37.5 | 34.6 | 20.5 | 71.6 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA008 | 2014 | 63 | 38.2 | 40.4 | 36.1 | 33.1 | 18.7 | 69.1 |
| PAPA008 | 2014 | 80 | 36.2 | 38.7 | 33.9 | 30.6 | 17.7 | 67.7 |
| PAPA008 | 2014 | 100 | 36.1 | 38.6 | 34.3 | 31.3 | 15.3 | 68.6 |
| PAPA008 | 2014 | 125 | 32.2 | 34.2 | 29.9 | 27.5 | 13.3 | 63.2 |
| PAPA008 | 2014 | 160 | 29.6 | 31.2 | 27.0 | 24.0 | 11.0 | 61.0 |
| PAPA008 | 2014 | 200 | 27.3 | 29.5 | 25.2 | 22.2 | 9.3 | 60.7 |
| PAPA008 | 2014 | 250 | 24.8 | 26.7 | 22.7 | 19.3 | 6.7 | 54.7 |
| PAPA008 | 2014 | 315 | 21.9 | 24.3 | 19.4 | 16.2 | 2.5 | 52.2 |
| PAPA008 | 2014 | 400 | 18.8 | 21.3 | 15.8 | 12.4 | 0.1 | 49.0 |
| PAPA008 | 2014 | 500 | 16.4 | 17.6 | 12.1 | 8.5 | -1.8 | 47.1 |
| PAPA008 | 2014 | 630 | 13.8 | 15.4 | 9.2 | 5.3 | -2.6 | 44.6 |
| PAPA008 | 2014 | 800 | 11.8 | 14.4 | 8.5 | 4.1 | -2.8 | 46.9 |
| PAPA008 | 2014 | 1000 | 10.3 | 13.0 | 6.8 | 2.4 | -2.1 | 46.2 |
| PAPA008 | 2014 | 1250 | 8.2 | 11.1 | 4.1 | 1.2 | -1.8 | 52.0 |
| PAPA008 | 2014 | 1600 | 6.3 | 9.1 | 2.6 | 1.0 | -0.8 | 46.7 |
| PAPA008 | 2014 | 2000 | 9.3 | 10.0 | 3.0 | 1.6 | -1.5 | 47.9 |
| PAPA008 | 2014 | 2500 | 9.1 | 10.6 | 3.6 | 2.1 | -2.6 | 47.0 |
| PAPA008 | 2014 | 3150 | 8.2 | 8.3 | 3.2 | 2.4 | -2.3 | 44.4 |
| PAPA008 | 2014 | 4000 | 7.5 | 6.7 | 3.0 | 2.6 | -2.4 | 48.5 |
| PAPA008 | 2014 | 5000 | 7.4 | 5.6 | 3.1 | 2.8 | -2.3 | 49.3 |
| PAPA008 | 2014 | 6300 | 5.5 | 4.2 | 3.2 | 2.9 | -2.0 | 43.9 |
| PAPA008 | 2014 | 8000 | 3.7 | 3.6 | 3.3 | 3.1 | -2.2 | 54.5 |
| PAPA008 | 2014 | 10000 | 3.7 | 3.9 | 3.7 | 3.4 | -2.6 | 36.6 |
| PAPA008 | 2014 | 12500 | 3.8 | 4.2 | 3.7 | 3.4 | -3.4 | 35.1 |
| PAPA008 | 2014 | 16000 | 1.8 | 2.3 | 1.8 | 1.2 | -4.4 | 37.1 |
| PAPA008 | 2014 | 20000 | 0.2 | 1.5 | -0.3 | -1.1 | -4.5 | 31.6 |
| PAPA009 | 2014 | 12.5 | 51.5 | 54.3 | 48.7 | 42.3 | 22.7 | 75.9 |
| PAPA009 | 2014 | 15.8 | 53.1 | 56.6 | 51.1 | 46.4 | 29.9 | 74.3 |
| PAPA009 | 2014 | 20 | 56.5 | 59.5 | 55.2 | 50.4 | 33.6 | 73.8 |
| PAPA009 | 2014 | 25 | 48.6 | 51.8 | 46.4 | 41.3 | 27.0 | 72.4 |
| PAPA009 | 2014 | 31.5 | 47.5 | 50.5 | 45.8 | 41.9 | 28.7 | 70.6 |
| PAPA009 | 2014 | 40 | 42.6 | 44.8 | 39.8 | 36.3 | 22.8 | 68.6 |
| PAPA009 | 2014 | 50 | 40.2 | 43.0 | 37.0 | 33.6 | 21.0 | 67.4 |
| PAPA009 | 2014 | 63 | 37.8 | 40.7 | 34.8 | 31.2 | 16.4 | 65.0 |
| PAPA009 | 2014 | 80 | 35.7 | 38.3 | 33.1 | 29.1 | 14.1 | 62.9 |
| PAPA009 | 2014 | 100 | 34.0 | 36.7 | 31.8 | 28.9 | 14.2 | 64.2 |
| PAPA009 | 2014 | 125 | 33.3 | 36.1 | 30.6 | 26.2 | 12.6 | 68.3 |
| PAPA009 | 2014 | 160 | 31.1 | 33.0 | 28.3 | 23.6 | 10.0 | 57.7 |
| PAPA009 | 2014 | 200 | 27.2 | 29.8 | 25.3 | 21.9 | 8.5 | 55.1 |
| PAPA009 | 2014 | 250 | 24.4 | 27.5 | 22.5 | 17.7 | 6.8 | 55.4 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA009 | 2014 | 315 | 21.7 | 24.4 | 19.6 | 15.3 | 1.5 | 50.7 |
| PAPA009 | 2014 | 400 | 19.7 | 22.8 | 17.4 | 12.5 | -1.3 | 48.6 |
| PAPA009 | 2014 | 500 | 14.3 | 17.5 | 11.7 | 7.6 | -3.9 | 47.4 |
| PAPA009 | 2014 | 630 | 10.3 | 13.4 | 7.2 | 2.7 | -4.0 | 45.1 |
| PAPA009 | 2014 | 800 | 8.3 | 11.1 | 5.0 | 1.1 | -3.4 | 42.2 |
| PAPA009 | 2014 | 1000 | 7.0 | 10.9 | 3.1 | 0.7 | -2.6 | 39.3 |
| PAPA009 | 2014 | 1250 | 4.2 | 6.6 | 1.7 | 0.4 | -1.8 | 38.6 |
| PAPA009 | 2014 | 1600 | 5.3 | 6.0 | 1.5 | 0.8 | -0.9 | 39.6 |
| PAPA009 | 2014 | 2000 | 8.0 | 10.6 | 2.4 | 1.5 | -0.1 | 52.0 |
| PAPA009 | 2014 | 2500 | 9.1 | 10.5 | 2.7 | 2.1 | -0.5 | 58.8 |
| PAPA009 | 2014 | 3150 | 5.8 | 7.1 | 2.9 | 2.5 | -1.8 | 52.7 |
| PAPA009 | 2014 | 4000 | 6.1 | 6.3 | 3.1 | 2.7 | -1.5 | 46.1 |
| PAPA009 | 2014 | 5000 | 6.2 | 4.7 | 3.2 | 2.8 | -1.9 | 46.7 |
| PAPA009 | 2014 | 6300 | 3.6 | 3.7 | 3.2 | 2.9 | -1.8 | 39.7 |
| PAPA009 | 2014 | 8000 | 3.4 | 3.5 | 3.3 | 3.1 | -1.8 | 31.8 |
| PAPA009 | 2014 | 10000 | 3.7 | 4.0 | 3.7 | 3.5 | -2.2 | 31.1 |
| PAPA009 | 2014 | 12500 | 3.9 | 4.3 | 3.9 | 3.5 | -2.3 | 26.4 |
| PAPA009 | 2014 | 16000 | 2.1 | 2.5 | 2.0 | 1.5 | -2.7 | 24.2 |
| PAPA009 | 2014 | 20000 | -0.2 | 0.6 | -0.7 | -1.0 | -2.9 | 22.1 |
| PAPA010 | 2014 | 12.5 | 51.8 | 54.8 | 49.2 | 42.2 | 11.7 | 78.9 |
| PAPA010 | 2014 | 15.8 | 54.7 | 57.8 | 52.4 | 47.7 | 9.5 | 76.9 |
| PAPA010 | 2014 | 20 | 59.7 | 62.4 | 58.7 | 53.6 | 16.7 | 73.3 |
| PAPA010 | 2014 | 25 | 48.0 | 50.4 | 45.7 | 41.3 | 2.0 | 72.4 |
| PAPA010 | 2014 | 31.5 | 48.2 | 50.6 | 46.7 | 42.8 | 14.1 | 69.0 |
| PAPA010 | 2014 | 40 | 42.9 | 45.1 | 40.6 | 37.4 | 4.9 | 69.3 |
| PAPA010 | 2014 | 50 | 40.1 | 42.6 | 38.1 | 34.7 | -7.3 | 66.5 |
| PAPA010 | 2014 | 63 | 37.5 | 40.1 | 35.5 | 32.1 | -6.8 | 64.2 |
| PAPA010 | 2014 | 80 | 35.8 | 38.4 | 33.8 | 30.1 | -7.0 | 63.3 |
| PAPA010 | 2014 | 100 | 36.6 | 38.8 | 33.6 | 29.9 | 9.9 | 67.3 |
| PAPA010 | 2014 | 125 | 38.7 | 41.4 | 36.4 | 33.2 | 16.3 | 73.8 |
| PAPA010 | 2014 | 160 | 33.5 | 35.8 | 31.6 | 27.8 | 3.2 | 64.9 |
| PAPA010 | 2014 | 200 | 29.7 | 32.4 | 27.7 | 24.4 | -9.8 | 61.9 |
| PAPA010 | 2014 | 250 | 28.6 | 31.1 | 26.4 | 22.3 | -10.4 | 66.9 |
| PAPA010 | 2014 | 315 | 25.2 | 28.3 | 22.8 | 18.3 | -10.1 | 57.6 |
| PAPA010 | 2014 | 400 | 23.5 | 26.3 | 19.6 | 15.0 | -9.8 | 59.5 |
| PAPA010 | 2014 | 500 | 19.6 | 22.2 | 16.4 | 11.4 | -9.3 | 57.6 |
| PAPA010 | 2014 | 630 | 17.2 | 19.8 | 13.6 | 7.9 | -9.2 | 58.1 |
| PAPA010 | 2014 | 800 | 16.4 | 19.4 | 12.8 | 6.1 | -8.4 | 62.8 |
| PAPA010 | 2014 | 1000 | 14.2 | 17.6 | 11.2 | 4.9 | -8.1 | 88.2 |
| PAPA010 | 2014 | 1250 | 12.2 | 15.8 | 8.7 | 2.9 | -7.6 | 69.2 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA010 | 2014 | 1600 | 8.8 | 11.2 | 4.6 | 1.8 | -7.1 | 71.0 |
| PAPA010 | 2014 | 2000 | 7.9 | 10.8 | 3.8 | 2.1 | -6.2 | 74.6 |
| PAPA010 | 2014 | 2500 | 7.4 | 9.8 | 3.6 | 2.7 | -5.5 | 64.4 |
| PAPA010 | 2014 | 3150 | 8.3 | 8.7 | 4.0 | 3.3 | -4.9 | 76.7 |
| PAPA010 | 2014 | 4000 | 9.1 | 7.6 | 4.5 | 4.1 | -4.4 | 67.3 |
| PAPA010 | 2014 | 5000 | 8.9 | 6.9 | 5.1 | 4.8 | -3.9 | 67.1 |
| PAPA010 | 2014 | 6300 | 6.4 | 6.1 | 5.6 | 5.3 | -3.7 | 62.4 |
| PAPA010 | 2014 | 8000 | 6.1 | 6.2 | 6.0 | 5.7 | -3.6 | 60.3 |
| PAPA010 | 2014 | 10000 | 6.3 | 6.5 | 6.3 | 6.1 | -3.8 | 57.9 |
| PAPA010 | 2014 | 12500 | 6.4 | 6.6 | 6.4 | 6.1 | -4.2 | 57.6 |
| PAPA010 | 2014 | 16000 | 5.9 | 6.2 | 5.9 | 5.5 | -4.9 | 60.8 |
| PAPA010 | 2014 | 20000 | 4.1 | 4.5 | 3.9 | 3.6 | -5.6 | 66.3 |
| PAPA011 | 2014 | 12.5 | 44.3 | 47.1 | 42.8 | 37.5 | 21.3 | 79.9 |
| PAPA011 | 2014 | 15.8 | 46.7 | 49.2 | 45.4 | 38.9 | 23.8 | 75.2 |
| PAPA011 | 2014 | 20 | 47.1 | 49.7 | 45.4 | 39.0 | 26.8 | 73.9 |
| PAPA011 | 2014 | 25 | 41.2 | 43.5 | 39.5 | 34.1 | 18.2 | 72.0 |
| PAPA011 | 2014 | 31.5 | 43.7 | 46.8 | 40.4 | 35.1 | 18.7 | 67.8 |
| PAPA011 | 2014 | 40 | 35.8 | 38.1 | 34.8 | 29.8 | 15.7 | 66.8 |
| PAPA011 | 2014 | 50 | 32.3 | 34.5 | 31.1 | 26.9 | 12.6 | 64.1 |
| PAPA011 | 2014 | 63 | 31.0 | 33.6 | 29.2 | 25.4 | 12.2 | 63.8 |
| PAPA011 | 2014 | 80 | 29.2 | 31.7 | 27.5 | 23.5 | 12.9 | 63.3 |
| PAPA011 | 2014 | 100 | 27.3 | 29.5 | 25.2 | 21.7 | 9.3 | 67.0 |
| PAPA011 | 2014 | 125 | 26.1 | 27.5 | 22.0 | 19.7 | 7.4 | 69.4 |
| PAPA011 | 2014 | 160 | 23.2 | 23.5 | 18.0 | 15.8 | 3.8 | 72.2 |
| PAPA011 | 2014 | 200 | 20.8 | 20.3 | 16.7 | 13.8 | 2.0 | 63.8 |
| PAPA011 | 2014 | 250 | 16.1 | 15.6 | 11.9 | 9.0 | -1.1 | 58.2 |
| PAPA011 | 2014 | 315 | 12.9 | 14.1 | 8.8 | 5.7 | -2.1 | 56.5 |
| PAPA011 | 2014 | 400 | 6.9 | 8.3 | 4.1 | 1.6 | -3.3 | 58.9 |
| PAPA011 | 2014 | 500 | 2.6 | 5.0 | 0.1 | -1.5 | -3.8 | 59.8 |
| PAPA011 | 2014 | 630 | -1.2 | -0.3 | -1.7 | -2.3 | -3.7 | 57.8 |
| PAPA011 | 2014 | 800 | -0.9 | -0.2 | -1.4 | -2.0 | -3.3 | 52.3 |
| PAPA011 | 2014 | 1000 | 0.2 | 1.2 | -0.9 | -1.5 | -2.5 | 46.3 |
| PAPA011 | 2014 | 1250 | 1.0 | 1.9 | -0.2 | -0.8 | -1.7 | 46.4 |
| PAPA011 | 2014 | 1600 | 9.0 | 6.9 | 0.7 | 0.2 | -0.9 | 56.4 |
| PAPA011 | 2014 | 2000 | 15.0 | 15.4 | 1.5 | 1.1 | 0.1 | 69.8 |
| PAPA011 | 2014 | 2500 | 20.2 | 15.7 | 2.3 | 2.0 | 1.0 | 70.9 |
| PAPA011 | 2014 | 3150 | 13.5 | 11.6 | 3.1 | 2.9 | 0.8 | 71.0 |
| PAPA011 | 2014 | 4000 | 9.7 | 8.1 | 4.0 | 3.7 | 1.1 | 69.5 |
| PAPA011 | 2014 | 5000 | 6.3 | 6.3 | 4.7 | 4.5 | 0.1 | 64.1 |
| PAPA011 | 2014 | 6300 | 6.2 | 5.8 | 5.4 | 5.0 | 0.0 | 54.5 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA011 | 2014 | 8000 | 6.0 | 6.0 | 5.8 | 5.6 | 0.0 | 57.9 |
| PAPA011 | 2014 | 10000 | 6.3 | 6.4 | 6.2 | 6.0 | 0.5 | 46.8 |
| PAPA011 | 2014 | 12500 | 6.2 | 6.3 | 6.2 | 6.0 | 0.9 | 43.6 |
| PAPA011 | 2014 | 16000 | 5.5 | 5.6 | 5.5 | 5.3 | 1.0 | 40.0 |
| PAPA011 | 2014 | 20000 | 3.3 | 3.4 | 3.3 | 3.3 | 1.5 | 40.6 |
| PAPA012 | 2014 | 12.5 | 44.0 | 46.7 | 41.2 | 36.4 | 18.3 | 72.4 |
| PAPA012 | 2014 | 15.8 | 47.8 | 50.6 | 46.5 | 42.0 | 24.5 | 71.5 |
| PAPA012 | 2014 | 20 | 48.9 | 51.7 | 47.8 | 43.9 | 27.0 | 71.9 |
| PAPA012 | 2014 | 25 | 42.1 | 44.9 | 39.5 | 36.0 | 19.8 | 69.3 |
| PAPA012 | 2014 | 31.5 | 44.5 | 47.7 | 43.1 | 38.5 | 22.2 | 65.6 |
| PAPA012 | 2014 | 40 | 35.6 | 37.8 | 34.2 | 31.1 | 18.9 | 63.6 |
| PAPA012 | 2014 | 50 | 33.1 | 35.7 | 30.4 | 26.6 | 11.3 | 62.0 |
| PAPA012 | 2014 | 63 | 33.2 | 35.7 | 29.9 | 25.8 | 8.1 | 67.7 |
| PAPA012 | 2014 | 80 | 30.6 | 32.6 | 27.6 | 23.4 | 5.7 | 75.2 |
| PAPA012 | 2014 | 100 | 29.3 | 31.2 | 25.7 | 22.2 | 3.8 | 76.5 |
| PAPA012 | 2014 | 125 | 26.6 | 27.6 | 20.2 | 17.2 | 0.4 | 74.9 |
| PAPA012 | 2014 | 160 | 24.7 | 25.6 | 16.2 | 13.1 | -1.4 | 68.8 |
| PAPA012 | 2014 | 200 | 22.9 | 23.4 | 15.1 | 11.6 | -2.1 | 69.1 |
| PAPA012 | 2014 | 250 | 20.2 | 20.5 | 10.7 | 6.9 | -3.3 | 65.3 |
| PAPA012 | 2014 | 315 | 17.5 | 16.2 | 6.3 | 3.5 | -4.0 | 58.6 |
| PAPA012 | 2014 | 400 | 14.6 | 12.7 | 4.2 | 1.4 | -4.5 | 62.2 |
| PAPA012 | 2014 | 500 | 12.2 | 8.1 | 1.3 | -0.9 | -4.2 | 63.7 |
| PAPA012 | 2014 | 630 | 9.7 | 5.5 | -0.1 | -1.6 | -4.1 | 58.3 |
| PAPA012 | 2014 | 800 | 6.4 | 4.2 | -0.5 | -1.7 | -4.1 | 49.2 |
| PAPA012 | 2014 | 1000 | 2.2 | 2.3 | -0.8 | -1.4 | -3.4 | 50.1 |
| PAPA012 | 2014 | 1250 | 1.3 | 1.3 | -0.5 | -1.0 | -2.8 | 44.7 |
| PAPA012 | 2014 | 1600 | 1.9 | 2.2 | 0.2 | -0.3 | -1.9 | 51.3 |
| PAPA012 | 2014 | 2000 | 3.1 | 3.0 | 1.1 | 0.6 | -0.9 | 54.3 |
| PAPA012 | 2014 | 2500 | 4.9 | 4.7 | 1.9 | 1.5 | 0.0 | 59.9 |
| PAPA012 | 2014 | 3150 | 4.6 | 4.3 | 2.7 | 2.3 | 1.1 | 63.5 |
| PAPA012 | 2014 | 4000 | 5.0 | 5.5 | 3.6 | 3.2 | 1.2 | 68.8 |
| PAPA012 | 2014 | 5000 | 5.3 | 5.4 | 4.3 | 4.0 | 1.6 | 62.8 |
| PAPA012 | 2014 | 6300 | 5.6 | 5.2 | 4.9 | 4.7 | 1.5 | 52.6 |
| PAPA012 | 2014 | 8000 | 5.5 | 5.5 | 5.3 | 5.1 | 1.3 | 51.4 |
| PAPA012 | 2014 | 10000 | 5.6 | 5.6 | 5.4 | 5.3 | 0.9 | 49.7 |
| PAPA012 | 2014 | 12500 | 5.1 | 5.2 | 4.9 | 4.7 | 0.8 | 51.7 |
| PAPA012 | 2014 | 16000 | 3.4 | 3.5 | 3.1 | 2.9 | 0.2 | 44.0 |
| PAPA012 | 2014 | 20000 | 0.7 | 0.7 | 0.4 | 0.1 | -0.8 | 47.5 |
| PAPA013 | 2014 | 12.5 | 52.5 | 55.8 | 50.5 | 43.6 | 20.1 | 75.1 |
| PAPA013 | 2014 | 15.8 | 55.7 | 59.4 | 53.9 | 49.0 | 29.0 | 73.0 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA013 | 2014 | 20 | 52.4 | 55.0 | 49.5 | 45.5 | 30.9 | 74.1 |
| PAPA013 | 2014 | 25 | 47.3 | 50.5 | 44.9 | 39.8 | 25.7 | 70.4 |
| PAPA013 | 2014 | 31.5 | 44.4 | 46.8 | 43.0 | 39.2 | 24.6 | 67.7 |
| PAPA013 | 2014 | 40 | 38.6 | 40.8 | 37.3 | 34.3 | 19.6 | 65.1 |
| PAPA013 | 2014 | 50 | 37.0 | 38.8 | 35.2 | 31.9 | 16.7 | 65.3 |
| PAPA013 | 2014 | 63 | 36.9 | 39.1 | 34.4 | 30.6 | 12.2 | 78.8 |
| PAPA013 | 2014 | 80 | 34.3 | 36.4 | 31.6 | 27.3 | 12.2 | 80.0 |
| PAPA013 | 2014 | 100 | 37.0 | 38.3 | 33.0 | 28.6 | 12.0 | 75.3 |
| PAPA013 | 2014 | 125 | 31.3 | 32.9 | 28.2 | 22.7 | 8.9 | 78.5 |
| PAPA013 | 2014 | 160 | 27.9 | 29.5 | 24.5 | 19.2 | 6.1 | 68.6 |
| PAPA013 | 2014 | 200 | 28.4 | 30.4 | 24.3 | 18.6 | 5.2 | 71.1 |
| PAPA013 | 2014 | 250 | 23.3 | 24.6 | 20.2 | 15.5 | 2.2 | 67.3 |
| PAPA013 | 2014 | 315 | 22.0 | 22.1 | 17.1 | 12.2 | -0.8 | 58.6 |
| PAPA013 | 2014 | 400 | 17.7 | 17.7 | 12.5 | 7.2 | -2.4 | 57.2 |
| PAPA013 | 2014 | 500 | 17.0 | 16.9 | 11.0 | 6.2 | -3.5 | 56.4 |
| PAPA013 | 2014 | 630 | 13.7 | 13.5 | 7.7 | 3.6 | -3.4 | 54.0 |
| PAPA013 | 2014 | 800 | 11.9 | 14.2 | 7.4 | 3.4 | -2.7 | 45.8 |
| PAPA013 | 2014 | 1000 | 12.2 | 15.6 | 8.8 | 4.1 | -2.1 | 39.6 |
| PAPA013 | 2014 | 1250 | 6.8 | 9.5 | 3.9 | 1.3 | -1.3 | 40.0 |
| PAPA013 | 2014 | 1600 | 3.9 | 5.7 | 1.9 | 0.9 | -0.9 | 37.7 |
| PAPA013 | 2014 | 2000 | 2.5 | 3.1 | 1.7 | 1.2 | -0.6 | 46.9 |
| PAPA013 | 2014 | 2500 | 3.2 | 2.8 | 2.0 | 1.6 | -0.3 | 62.2 |
| PAPA013 | 2014 | 3150 | 4.0 | 3.5 | 2.5 | 2.2 | -0.6 | 69.0 |
| PAPA013 | 2014 | 4000 | 4.1 | 3.9 | 2.9 | 2.6 | -0.9 | 60.9 |
| PAPA013 | 2014 | 5000 | 4.3 | 4.1 | 3.1 | 2.8 | -1.0 | 56.5 |
| PAPA013 | 2014 | 6300 | 4.1 | 3.7 | 3.2 | 2.9 | -1.5 | 64.9 |
| PAPA013 | 2014 | 8000 | 3.6 | 3.5 | 3.3 | 3.1 | -1.6 | 59.0 |
| PAPA013 | 2014 | 10000 | 3.9 | 3.8 | 3.6 | 3.4 | -1.7 | 40.9 |
| PAPA013 | 2014 | 12500 | 4.2 | 4.3 | 3.9 | 3.6 | -1.5 | 45.5 |
| PAPA013 | 2014 | 16000 | 2.7 | 2.8 | 2.1 | 1.9 | -1.9 | 39.3 |
| PAPA013 | 2014 | 20000 | -0.6 | -0.3 | -1.2 | -1.5 | -2.4 | 42.0 |
| PAPA014 | 2014 | 12.5 | 44.9 | 47.7 | 41.6 | 37.5 | 22.7 | 101.5 |
| PAPA014 | 2014 | 15.8 | 49.6 | 52.0 | 48.0 | 44.7 | 27.7 | 99.4 |
| PAPA014 | 2014 | 20 | 61.5 | 64.0 | 60.9 | 55.2 | 35.9 | 97.4 |
| PAPA014 | 2014 | 25 | 49.9 | 52.2 | 48.2 | 45.4 | 29.2 | 95.5 |
| PAPA014 | 2014 | 31.5 | 51.5 | 54.4 | 50.0 | 44.7 | 28.0 | 90.8 |
| PAPA014 | 2014 | 40 | 47.4 | 49.4 | 46.2 | 42.4 | 23.8 | 89.4 |
| PAPA014 | 2014 | 50 | 46.6 | 48.7 | 44.9 | 39.5 | 24.5 | 87.0 |
| PAPA014 | 2014 | 63 | 44.4 | 45.5 | 42.1 | 39.4 | 26.5 | 81.8 |
| PAPA014 | 2014 | 80 | 39.2 | 40.6 | 38.9 | 35.2 | 22.9 | 78.4 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA014 | 2014 | 100 | 38.9 | 40.5 | 38.0 | 35.6 | 22.6 | 74.5 |
| PAPA014 | 2014 | 125 | 35.5 | 37.7 | 34.8 | 32.1 | 18.3 | 73.7 |
| PAPA014 | 2014 | 160 | 31.8 | 33.8 | 30.8 | 27.8 | 14.6 | 68.3 |
| PAPA014 | 2014 | 200 | 28.6 | 29.9 | 26.6 | 23.9 | 8.1 | 66.7 |
| PAPA014 | 2014 | 250 | 27.9 | 30.2 | 25.2 | 22.7 | 3.3 | 64.0 |
| PAPA014 | 2014 | 315 | 23.3 | 25.4 | 22.0 | 19.3 | 0.0 | 58.4 |
| PAPA014 | 2014 | 400 | 21.2 | 23.4 | 18.3 | 15.3 | 0.0 | 54.1 |
| PAPA014 | 2014 | 500 | 18.5 | 21.3 | 14.6 | 10.7 | 0.0 | 56.0 |
| PAPA014 | 2014 | 630 | 14.2 | 16.1 | 9.8 | 6.3 | 0.0 | 55.1 |
| PAPA014 | 2014 | 800 | 14.6 | 17.5 | 9.3 | 6.3 | 0.0 | 51.7 |
| PAPA014 | 2014 | 1000 | 16.0 | 18.0 | 9.3 | 6.3 | 0.0 | 49.4 |
| PAPA014 | 2014 | 1250 | 19.2 | 23.4 | 10.7 | 7.3 | 3.3 | 50.3 |
| PAPA014 | 2014 | 1600 | 13.9 | 17.8 | 9.3 | 6.3 | 3.3 | 50.7 |
| PAPA014 | 2014 | 2000 | 11.5 | 13.7 | 8.1 | 7.3 | 5.1 | 50.6 |
| PAPA014 | 2014 | 2500 | 8.5 | 9.3 | 8.1 | 7.3 | 6.3 | 49.8 |
| PAPA014 | 2014 | 3150 | 8.7 | 8.7 | 8.7 | 8.1 | 7.3 | 48.3 |
| PAPA014 | 2014 | 4000 | 9.1 | 9.3 | 8.7 | 8.7 | 8.1 | 46.4 |
| PAPA014 | 2014 | 5000 | 9.5 | 9.3 | 9.3 | 9.3 | 8.7 | 44.7 |
| PAPA014 | 2014 | 6300 | 9.6 | 9.8 | 9.8 | 9.3 | 8.7 | 43.7 |
| PAPA014 | 2014 | 8000 | 9.7 | 9.8 | 9.8 | 9.3 | 9.3 | 41.8 |
| PAPA014 | 2014 | 10000 | 9.7 | 9.8 | 9.8 | 9.3 | 9.3 | 40.5 |
| PAPA014 | 2014 | 12500 | 9.8 | 9.8 | 9.8 | 9.8 | 9.3 | 40.0 |
| PAPA014 | 2014 | 16000 | 10.3 | 10.3 | 10.3 | 9.8 | 9.8 | 39.7 |
| PAPA014 | 2014 | 20000 | 12.9 | 13.1 | 12.8 | 12.6 | 12.3 | 44.8 |
| PAPA015 | 2014 | 12.5 | 38.7 | 41.7 | 36.6 | 32.0 | 13.9 | 76.0 |
| PAPA015 | 2014 | 15.8 | 43.6 | 45.9 | 41.5 | 33.5 | 18.7 | 72.1 |
| PAPA015 | 2014 | 20 | 48.9 | 51.4 | 46.8 | 41.6 | 26.2 | 71.3 |
| PAPA015 | 2014 | 25 | 40.3 | 43.1 | 38.0 | 31.7 | 17.1 | 68.1 |
| PAPA015 | 2014 | 31.5 | 45.1 | 48.2 | 37.1 | 30.5 | 15.1 | 66.0 |
| PAPA015 | 2014 | 40 | 36.9 | 39.4 | 33.2 | 27.8 | 9.6 | 65.1 |
| PAPA015 | 2014 | 50 | 36.4 | 38.8 | 31.5 | 26.5 | 9.9 | 62.9 |
| PAPA015 | 2014 | 63 | 35.6 | 38.3 | 30.5 | 26.3 | 10.2 | 65.3 |
| PAPA015 | 2014 | 80 | 34.1 | 36.7 | 29.2 | 24.8 | 8.5 | 72.8 |
| PAPA015 | 2014 | 100 | 30.7 | 32.8 | 27.4 | 22.9 | 6.0 | 71.6 |
| PAPA015 | 2014 | 125 | 27.7 | 28.6 | 24.7 | 20.7 | 4.0 | 67.7 |
| PAPA015 | 2014 | 160 | 25.5 | 25.2 | 20.7 | 16.9 | 1.6 | 64.3 |
| PAPA015 | 2014 | 200 | 20.9 | 21.4 | 17.2 | 13.4 | -0.3 | 65.7 |
| PAPA015 | 2014 | 250 | 18.3 | 18.5 | 14.0 | 9.7 | -1.9 | 57.5 |
| PAPA015 | 2014 | 315 | 14.5 | 14.8 | 9.0 | 5.7 | -3.7 | 49.1 |
| PAPA015 | 2014 | 400 | 12.6 | 10.6 | 5.3 | 1.8 | -4.3 | 53.0 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA015 | 2014 | 500 | 10.7 | 6.8 | 1.8 | -0.9 | -4.5 | 53.6 |
| PAPA015 | 2014 | 630 | 5.3 | 3.7 | -0.6 | -1.8 | -4.5 | 50.1 |
| PAPA015 | 2014 | 800 | 2.7 | 3.2 | -1.0 | -2.0 | -3.6 | 41.6 |
| PAPA015 | 2014 | 1000 | 0.9 | 1.7 | -1.0 | -1.8 | -3.1 | 40.9 |
| PAPA015 | 2014 | 1250 | -0.6 | 0.1 | -0.9 | -1.3 | -2.6 | 44.0 |
| PAPA015 | 2014 | 1600 | 2.2 | 0.5 | -0.2 | -0.6 | -1.7 | 36.3 |
| PAPA015 | 2014 | 2000 | 5.5 | 2.9 | 1.0 | 0.4 | -0.8 | 45.5 |
| PAPA015 | 2014 | 2500 | 11.8 | 5.8 | 1.9 | 1.2 | 0.1 | 53.3 |
| PAPA015 | 2014 | 3150 | 9.1 | 7.5 | 2.5 | 2.0 | 0.7 | 59.3 |
| PAPA015 | 2014 | 4000 | 4.0 | 3.9 | 2.9 | 2.6 | 0.9 | 43.8 |
| PAPA015 | 2014 | 5000 | 4.0 | 3.9 | 3.4 | 3.2 | 0.3 | 52.5 |
| PAPA015 | 2014 | 6300 | 4.3 | 4.2 | 3.9 | 3.8 | 0.0 | 42.3 |
| PAPA015 | 2014 | 8000 | 4.4 | 4.5 | 4.4 | 4.2 | -0.9 | 41.1 |
| PAPA015 | 2014 | 10000 | 4.7 | 4.8 | 4.7 | 4.5 | -0.9 | 41.0 |
| PAPA015 | 2014 | 12500 | 4.1 | 4.2 | 4.1 | 3.9 | -1.1 | 42.5 |
| PAPA015 | 2014 | 16000 | 1.2 | 1.3 | 1.2 | 1.1 | -2.1 | 35.3 |
| PAPA015 | 2014 | 20000 | -1.0 | -0.9 | -1.0 | -1.1 | -2.0 | 34.2 |
| PAPA016 | 2014 | 12.5 | 43.6 | 45.8 | 36.0 | 30.5 | 13.8 | 74.9 |
| PAPA016 | 2014 | 15.8 | 43.3 | 46.2 | 38.0 | 32.3 | 13.4 | 75.8 |
| PAPA016 | 2014 | 20 | 43.4 | 46.8 | 39.2 | 34.2 | 16.6 | 74.1 |
| PAPA016 | 2014 | 25 | 37.3 | 39.5 | 34.1 | 29.8 | 14.1 | 76.6 |
| PAPA016 | 2014 | 31.5 | 39.1 | 42.0 | 37.0 | 31.7 | 14.0 | 76.6 |
| PAPA016 | 2014 | 40 | 35.0 | 37.7 | 32.3 | 28.7 | 12.2 | 76.6 |
| PAPA016 | 2014 | 50 | 34.2 | 36.5 | 31.3 | 27.4 | 10.4 | 78.7 |
| PAPA016 | 2014 | 63 | 34.0 | 36.3 | 31.2 | 27.5 | 8.7 | 79.2 |
| PAPA016 | 2014 | 80 | 32.6 | 35.2 | 29.2 | 25.5 | 8.2 | 79.7 |
| PAPA016 | 2014 | 100 | 31.9 | 34.0 | 28.0 | 24.0 | 6.9 | 78.7 |
| PAPA016 | 2014 | 125 | 30.7 | 32.9 | 26.6 | 22.9 | 4.8 | 81.3 |
| PAPA016 | 2014 | 160 | 28.7 | 30.5 | 24.4 | 20.4 | 1.9 | 79.1 |
| PAPA016 | 2014 | 200 | 27.0 | 28.5 | 22.6 | 19.2 | -0.1 | 79.4 |
| PAPA016 | 2014 | 250 | 24.1 | 25.9 | 20.5 | 16.4 | -1.9 | 79.3 |
| PAPA016 | 2014 | 315 | 20.6 | 22.8 | 17.9 | 12.8 | -3.2 | 75.1 |
| PAPA016 | 2014 | 400 | 17.0 | 19.5 | 14.2 | 9.5 | -3.6 | 72.6 |
| PAPA016 | 2014 | 500 | 15.0 | 16.7 | 9.6 | 4.8 | -3.9 | 75.9 |
| PAPA016 | 2014 | 630 | 14.2 | 15.7 | 5.5 | 1.3 | -3.4 | 77.1 |
| PAPA016 | 2014 | 800 | 13.1 | 14.7 | 4.4 | 0.7 | -2.7 | 76.1 |
| PAPA016 | 2014 | 1000 | 12.0 | 13.4 | 4.3 | 1.2 | -2.0 | 73.5 |
| PAPA016 | 2014 | 1250 | 10.7 | 12.1 | 3.9 | 1.0 | -1.5 | 74.0 |
| PAPA016 | 2014 | 1600 | 8.5 | 10.0 | 2.5 | 1.1 | -0.7 | 72.9 |
| PAPA016 | 2014 | 2000 | 7.7 | 7.5 | 2.4 | 1.6 | 0.1 | 70.5 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA016 | 2014 | 2500 | 6.9 | 6.2 | 3.1 | 2.3 | 1.0 | 69.1 |
| PAPA016 | 2014 | 3150 | 5.3 | 5.4 | 3.6 | 3.0 | 1.4 | 65.9 |
| PAPA016 | 2014 | 4000 | 5.7 | 5.8 | 4.2 | 3.8 | 0.9 | 62.8 |
| PAPA016 | 2014 | 5000 | 6.0 | 6.0 | 4.9 | 4.6 | 1.4 | 59.8 |
| PAPA016 | 2014 | 6300 | 5.8 | 6.0 | 5.4 | 5.2 | 1.4 | 56.6 |
| PAPA016 | 2014 | 8000 | 6.1 | 6.3 | 5.9 | 5.8 | -0.2 | 53.3 |
| PAPA016 | 2014 | 10000 | 6.5 | 6.7 | 6.3 | 6.1 | 0.7 | 50.4 |
| PAPA016 | 2014 | 12500 | 6.5 | 6.8 | 6.4 | 6.2 | 0.0 | 47.4 |
| PAPA016 | 2014 | 16000 | 5.9 | 6.3 | 5.7 | 5.6 | 1.5 | 45.0 |
| PAPA016 | 2014 | 20000 | 3.9 | 4.6 | 3.6 | 3.4 | 0.5 | 53.0 |
| PAPA017 | 2014 | 12.5 | 43.2 | 45.4 | 41.5 | 34.3 | 19.8 | 75.6 |
| PAPA017 | 2014 | 15.8 | 49.2 | 51.8 | 45.3 | 38.0 | 22.0 | 72.0 |
| PAPA017 | 2014 | 20 | 51.0 | 55.0 | 47.6 | 40.6 | 25.1 | 69.2 |
| PAPA017 | 2014 | 25 | 48.5 | 52.0 | 45.4 | 40.2 | 24.0 | 67.6 |
| PAPA017 | 2014 | 31.5 | 57.0 | 60.6 | 54.8 | 48.2 | 25.5 | 73.0 |
| PAPA017 | 2014 | 40 | 47.8 | 51.0 | 45.5 | 41.8 | 20.7 | 64.1 |
| PAPA017 | 2014 | 50 | 46.6 | 49.1 | 45.3 | 41.6 | 20.5 | 63.5 |
| PAPA017 | 2014 | 63 | 42.0 | 44.4 | 40.3 | 37.2 | 19.9 | 67.6 |
| PAPA017 | 2014 | 80 | 39.4 | 41.1 | 37.8 | 34.7 | 17.9 | 72.5 |
| PAPA017 | 2014 | 100 | 39.0 | 39.5 | 35.4 | 31.3 | 16.8 | 81.0 |
| PAPA017 | 2014 | 125 | 35.5 | 36.0 | 31.0 | 27.0 | 10.8 | 77.2 |
| PAPA017 | 2014 | 160 | 33.8 | 34.0 | 28.9 | 24.9 | 5.7 | 71.5 |
| PAPA017 | 2014 | 200 | 30.7 | 32.8 | 27.7 | 23.6 | 3.0 | 63.1 |
| PAPA017 | 2014 | 250 | 28.5 | 29.9 | 25.6 | 21.5 | 1.2 | 63.2 |
| PAPA017 | 2014 | 315 | 25.2 | 27.1 | 22.9 | 18.8 | -1.3 | 64.0 |
| PAPA017 | 2014 | 400 | 22.0 | 24.3 | 19.9 | 15.6 | -2.1 | 56.9 |
| PAPA017 | 2014 | 500 | 19.0 | 20.9 | 15.4 | 11.6 | -3.4 | 54.1 |
| PAPA017 | 2014 | 630 | 15.7 | 18.1 | 12.6 | 7.1 | -3.7 | 52.1 |
| PAPA017 | 2014 | 800 | 13.4 | 15.3 | 10.1 | 4.6 | -3.5 | 49.2 |
| PAPA017 | 2014 | 1000 | 12.0 | 14.0 | 8.1 | 3.1 | -2.7 | 44.8 |
| PAPA017 | 2014 | 1250 | 9.1 | 10.4 | 3.9 | 1.0 | -2.1 | 44.4 |
| PAPA017 | 2014 | 1600 | 6.9 | 6.5 | 2.0 | 0.7 | -1.5 | 50.5 |
| PAPA017 | 2014 | 2000 | 10.4 | 9.5 | 1.9 | 1.1 | -0.5 | 60.8 |
| PAPA017 | 2014 | 2500 | 10.5 | 6.9 | 2.5 | 1.9 | 0.4 | 65.3 |
| PAPA017 | 2014 | 3150 | 7.1 | 5.0 | 3.1 | 2.5 | 0.3 | 61.1 |
| PAPA017 | 2014 | 4000 | 5.0 | 4.2 | 3.6 | 3.3 | -0.2 | 56.1 |
| PAPA017 | 2014 | 5000 | 4.8 | 4.6 | 4.2 | 4.0 | -1.0 | 55.1 |
| PAPA017 | 2014 | 6300 | 5.0 | 5.1 | 4.8 | 4.6 | -1.0 | 50.3 |
| PAPA017 | 2014 | 8000 | 5.3 | 5.5 | 5.3 | 5.1 | -1.1 | 50.7 |
| PAPA017 | 2014 | 10000 | 5.4 | 5.5 | 5.4 | 5.2 | -0.8 | 34.5 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA017 | 2014 | 12500 | 5.0 | 5.1 | 4.9 | 4.6 | -1.2 | 37.9 |
| PAPA017 | 2014 | 16000 | 3.2 | 3.4 | 3.1 | 3.0 | -1.8 | 30.6 |
| PAPA017 | 2014 | 20000 | 0.4 | 0.6 | 0.4 | 0.1 | -1.4 | 28.2 |
| PAPA018 | 2014 | 12.5 | 38.3 | 40.2 | 35.2 | 31.0 | 16.2 | 75.1 |
| PAPA018 | 2014 | 15.8 | 41.2 | 43.7 | 38.9 | 33.4 | 20.5 | 73.5 |
| PAPA018 | 2014 | 20 | 50.2 | 54.2 | 47.3 | 39.9 | 23.1 | 73.4 |
| PAPA018 | 2014 | 25 | 45.7 | 49.2 | 40.5 | 34.2 | 20.1 | 70.0 |
| PAPA018 | 2014 | 31.5 | 41.0 | 44.5 | 38.5 | 33.4 | 19.6 | 67.6 |
| PAPA018 | 2014 | 40 | 36.1 | 38.9 | 33.4 | 28.9 | 18.4 | 65.2 |
| PAPA018 | 2014 | 50 | 33.9 | 36.7 | 30.0 | 26.2 | 15.5 | 62.8 |
| PAPA018 | 2014 | 63 | 32.8 | 35.6 | 29.1 | 24.7 | 10.5 | 63.5 |
| PAPA018 | 2014 | 80 | 30.1 | 32.7 | 26.0 | 21.6 | 4.7 | 71.8 |
| PAPA018 | 2014 | 100 | 29.5 | 31.8 | 25.0 | 20.4 | 3.4 | 68.8 |
| PAPA018 | 2014 | 125 | 26.8 | 29.2 | 23.7 | 19.4 | 3.2 | 67.2 |
| PAPA018 | 2014 | 160 | 25.1 | 27.5 | 21.0 | 15.6 | 1.9 | 67.0 |
| PAPA018 | 2014 | 200 | 22.6 | 24.8 | 18.8 | 13.4 | 0.2 | 57.4 |
| PAPA018 | 2014 | 250 | 19.7 | 22.1 | 16.1 | 11.6 | -0.3 | 56.8 |
| PAPA018 | 2014 | 315 | 17.4 | 18.6 | 13.3 | 8.6 | -2.6 | 51.3 |
| PAPA018 | 2014 | 400 | 13.5 | 14.7 | 9.1 | 5.1 | -3.5 | 47.2 |
| PAPA018 | 2014 | 500 | 11.4 | 11.6 | 4.2 | 1.1 | -4.2 | 51.6 |
| PAPA018 | 2014 | 630 | 6.7 | 6.1 | 0.4 | -1.2 | -4.1 | 54.7 |
| PAPA018 | 2014 | 800 | 3.4 | 3.4 | -0.9 | -1.8 | -3.9 | 52.3 |
| PAPA018 | 2014 | 1000 | 2.0 | 1.8 | -0.8 | -1.6 | -3.1 | 46.5 |
| PAPA018 | 2014 | 1250 | 2.1 | 1.8 | -0.5 | -1.1 | -2.3 | 43.5 |
| PAPA018 | 2014 | 1600 | 4.0 | 2.4 | 0.3 | -0.3 | -1.6 | 46.6 |
| PAPA018 | 2014 | 2000 | 5.9 | 7.5 | 1.5 | 0.8 | -0.6 | 56.1 |
| PAPA018 | 2014 | 2500 | 7.8 | 9.5 | 2.4 | 1.5 | -0.8 | 63.4 |
| PAPA018 | 2014 | 3150 | 11.5 | 11.4 | 2.8 | 2.2 | -1.3 | 69.5 |
| PAPA018 | 2014 | 4000 | 7.7 | 7.5 | 3.1 | 2.8 | -1.4 | 66.3 |
| PAPA018 | 2014 | 5000 | 4.7 | 4.5 | 3.5 | 3.2 | -1.7 | 60.3 |
| PAPA018 | 2014 | 6300 | 4.6 | 4.2 | 3.8 | 3.6 | -1.9 | 62.4 |
| PAPA018 | 2014 | 8000 | 4.3 | 4.4 | 4.2 | 4.0 | -1.9 | 56.0 |
| PAPA018 | 2014 | 10000 | 4.5 | 4.7 | 4.6 | 4.3 | -2.1 | 33.2 |
| PAPA018 | 2014 | 12500 | 4.4 | 4.5 | 4.3 | 4.0 | -2.3 | 40.7 |
| PAPA018 | 2014 | 16000 | 2.1 | 2.1 | 1.9 | 1.7 | -2.6 | 37.6 |
| PAPA018 | 2014 | 20000 | -0.7 | -0.5 | -1.0 | -1.2 | -2.8 | 30.5 |
| PAPA019 | 2014 | 12.5 | 36.6 | 38.3 | 32.1 | 28.1 | 15.3 | 74.4 |
| PAPA019 | 2014 | 15.8 | 36.4 | 38.2 | 33.3 | 29.3 | 15.7 | 73.6 |
| PAPA019 | 2014 | 20 | 44.5 | 47.0 | 41.0 | 33.0 | 17.2 | 72.4 |
| PAPA019 | 2014 | 25 | 38.0 | 40.8 | 35.6 | 29.6 | 15.8 | 66.3 |

| Appendix E. One-third Octave Band Metrics, PAPA Leks, April 2014. | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Freq | Leq | L10 | L50 | L90 | LMin | LMax |
| PAPA019 | 2014 | 31.5 | 33.9 | 36.4 | 30.9 | 26.5 | 14.1 | 65.7 |
| PAPA019 | 2014 | 40 | 31.1 | 33.9 | 27.7 | 23.5 | 10.3 | 63.6 |
| PAPA019 | 2014 | 50 | 30.5 | 33.2 | 25.9 | 21.3 | 8.8 | 60.9 |
| PAPA019 | 2014 | 63 | 30.8 | 33.4 | 25.7 | 22.2 | 7.9 | 68.4 |
| PAPA019 | 2014 | 80 | 30.4 | 31.8 | 23.8 | 19.5 | 4.9 | 69.8 |
| PAPA019 | 2014 | 100 | 29.3 | 29.9 | 22.2 | 19.1 | 2.8 | 70.7 |
| PAPA019 | 2014 | 125 | 27.0 | 28.3 | 21.0 | 17.2 | 2.0 | 66.7 |
| PAPA019 | 2014 | 160 | 24.0 | 25.4 | 18.2 | 14.8 | 0.0 | 65.0 |
| PAPA019 | 2014 | 200 | 21.1 | 22.1 | 14.6 | 10.8 | -1.3 | 54.6 |
| PAPA019 | 2014 | 250 | 18.6 | 18.6 | 11.3 | 8.0 | -2.6 | 56.7 |
| PAPA019 | 2014 | 315 | 15.8 | 17.0 | 9.9 | 5.6 | -3.3 | 51.0 |
| PAPA019 | 2014 | 400 | 12.8 | 13.1 | 6.2 | 2.4 | -3.7 | 49.6 |
| PAPA019 | 2014 | 500 | 12.8 | 11.8 | 3.7 | 0.2 | -3.8 | 51.2 |
| PAPA019 | 2014 | 630 | 7.4 | 5.2 | 0.3 | -1.3 | -3.5 | 50.3 |
| PAPA019 | 2014 | 800 | 4.3 | 4.1 | -0.3 | -1.3 | -3.2 | 48.0 |
| PAPA019 | 2014 | 1000 | 3.1 | 3.6 | 0.1 | -0.8 | -2.5 | 48.2 |
| PAPA019 | 2014 | 1250 | 2.9 | 2.5 | 0.5 | -0.3 | -1.5 | 50.9 |
| PAPA019 | 2014 | 1600 | 3.0 | 2.7 | 1.1 | 0.5 | -0.9 | 44.3 |
| PAPA019 | 2014 | 2000 | 7.3 | 4.4 | 2.0 | 1.5 | 0.1 | 51.5 |
| PAPA019 | 2014 | 2500 | 7.2 | 6.4 | 3.0 | 2.4 | 1.1 | 61.9 |
| PAPA019 | 2014 | 3150 | 6.0 | 6.5 | 3.8 | 3.3 | 1.9 | 63.7 |
| PAPA019 | 2014 | 4000 | 5.0 | 5.0 | 4.2 | 3.9 | 1.9 | 39.5 |
| PAPA019 | 2014 | 5000 | 5.3 | 5.3 | 4.8 | 4.6 | 1.2 | 38.7 |
| PAPA019 | 2014 | 6300 | 5.7 | 5.7 | 5.4 | 5.2 | 0.9 | 47.9 |
| PAPA019 | 2014 | 8000 | 5.9 | 6.0 | 5.9 | 5.7 | 0.9 | 47.6 |
| PAPA019 | 2014 | 10000 | 6.2 | 6.3 | 6.2 | 6.1 | 1.1 | 24.3 |
| PAPA019 | 2014 | 12500 | 6.3 | 6.4 | 6.3 | 6.1 | 1.4 | 29.4 |
| PAPA019 | 2014 | 16000 | 5.8 | 5.9 | 5.7 | 5.6 | 1.6 | 27.6 |
| PAPA019 | 2014 | 20000 | 3.9 | 4.0 | 3.8 | 3.6 | 1.7 | 29.8 |

## Appendix F. Credentials of Authors

The three authors of this report have over 75 years combined experience working in the field of acoustics, sound level measurements, and assessing impacts on wildlife resources. All three were involved in initial measurements National Parks in an effort to determine existing ambient and baseline ambient sound levels in order to assess impacts of anthropogenic sounds on resources. This work involved sound level measurements in remote places with little human activity for long periods of time, and consequently very, very low sound levels. This work required development of new tools and techniques, many of which were pioneered by the authors. In total, these three individuals have collected data at over 250 locations throughout North America.

**Skip Ambrose**
Clemson University, B.S., 1969
Mr. Ambrose worked for the Fish and Wildlife Service in Alaska for 28 years as head of the Endangered Species Program in Fairbanks, AK. Much of this work involved assessing and protecting listed species from human impacts, including impacts from anthropogenic sounds. In 2001, Mr. Ambrose began working for the National Park Service to development the Acoustic Division of the Natural Sounds Program. The work involved developing new tools and techniques to study sound levels in very remote and very quiet places, and working with acousticians from other federal, state, and private organizations. In 2005, Mr. Ambrose retired from the National Park Service and co-founded Sandhill Company, a consulting firm specializing in avian and acoustic studies. Mr. Ambrose has participated in over 50 sound level measurement studies throughout North America, and has authored over 30 reports on sound level measurements in national parks and other rural and remote locations.

**Christine Florian**
Northern Arizona University, B.S., 1994.
Beginning in 1993, Ms. Florian worked for the National Park Service in Arizona surveying and studying wildlife resources in northern Arizona parks, primary avian species. In 1997, she began working in Alaska conducting avian and acoustic surveys in national parks in interior Alaska. In 2001, Ms. Florian started working for the National Park Service's new Natural Sounds Program, and participated in equipment and software development for sound level measurements and acoustic studies in National Parks throughout North America. She retired from the National Park Service in 2005 and co-founded Sandhill Company, a consulting firm specializing in avian and acoustic studies. Ms. Florian has participated in over 50 sound level studies throughout North America, and co-authored over 25 reports on this work.

**John MacDonald**
General Motors Engineering and Management Institute, B.S. Electrical Engineering, 1990
University of Central Florida, Master of Science, Environmental Engineering, 1996
University of Central Florida, Ph.D., Environmental Engineering, 2001
Licensed Professional Engineer; State of Florida; PE# 63038

Dr. MacDonald has been performing engineering tests and analyzing engineering data since 1986 when he worked as an engineer at General Motors in Flint, Michigan. He began performing environmental noise measurements in 1995 and has conducted environmental noise and vibration studies since that time. Dr. MacDonald developed the "Community Noise Model" that was in use at one time in 35 different countries. The CNM was a PC based simulation program that predicted sound levels at residential receivers from common sources of environmental noise such as automobiles, aircraft, rail operations, and point sources of sound such as HVAC, generators, exhaust ports, etc. Dr. MacDonald has conducted long term environmental sound surveys in 40 National Parks and has developed numerous custom software methods to analyze environmental acoustic data. He is a computer modeling expert, a programmer and has developed custom data acquisition systems for his engineering work.

WYOMING GAME AND FISH DEPARTMENT

5400 Bishop Blvd. Cheyenne, WY 82006
Phone: (307) 777-4600 Fax: (307) 777-4610
Web site: http://gf.state. wy.us

GOVERNOR
DAVE FREUDENTHAL
DIRECTOR
TERRY CLEVELAND
COMMISSIONERS
BILL WILLIAMS, DVM – President
JERRY GALLES – Vice President
CLARK ALLAN
CLIFFORD KIRK
FRED LINDZEY
RON LOVERCHECK
ED MIGNERY

January 29, 2008

MEMORANDUM

TO: Terry Cleveland and John Emmerich

FROM: Tom Christiansen and Joe Bohne

COPY TO: Jay Lawson, Bill Rudd, Reg Rothwell, Bob Oakleaf

SUBJECT: Multi-State Sage-Grouse Coordination and Research-based Recommendations

As assigned by Assistant Director Emmerich, we have been working with other state fish and wildlife agencies in WAFWA Sage-Grouse Management Zones 1 and 2 (MT, CO, UT, SD, ND, WY) in order to coordinate interpretation of recent sage-grouse research related to oil and gas development.

Attached for your review, please find the latest and final document capturing the multi-state interpretation of the recent science related to sage-grouse conservation and oil and gas development. It has been well scrutinized by staff from MT, WY, CO, ND and UT and there is consensus on the content by the participants. South Dakota was unable to attend the initial meeting in Salt Lake City on January 8-9, but they have been provided with meeting notes and the resulting document.

It is our recommendation that WGFD acknowledge this document as the correct interpretation of the recently published sage-grouse research and use this information to update and augment department documents and policies. It should be used in the forthcoming discussions with the BLM regarding their update to their sage-grouse Instruction Memorandum. In addition, we suggest that in order for this document to serve the broadest purpose for sage-grouse conservation four additional actions are needed. First, the document should be shared with Governor Freudenthal's staff. Second, we recommend that the Director's Office enter into discussions with MT FWP Director Jeff Hagener to ensure consistency in the application of these recommendations between our border states, and especially with the WY and MT BLM State Field Offices. Third, we recommend the document be submitted to WAFWA's Sage-Grouse Technical Committee as well as the WAFWA Executive Committee for their consideration and use. Finally, we recommend this document be included with other materials sent to the USFWS for consideration in their review of the status of sage-grouse and measures in place to conserve those populations.

We look forward to your direction on how to proceed.

**Using the Best Available Science to Coordinate Conservation Actions that Benefit Greater Sage-Grouse Across States Affected by Oil & Gas Development in Management Zones I-II (Colorado, Montana, North Dakota, South Dakota, Utah, and Wyoming)**

## Background

Greater Sage-grouse are widely considered in scientific and public policy arenas to be a species of significant conservation concern. Loss, degradation and fragmentation of important sagebrush grassland habitats have negatively impacted sage-grouse populations. Much of this loss of habitat function is occurring in Sage-grouse Management Zones (MZ) 1 and 2 (Stiver et al. 2006) in Colorado, Montana, North Dakota, South Dakota, Utah, and Wyoming as a result of oil and gas development (Connelly et al. 2004). Oil and gas development is rapidly increasing within these areas. In response to those concerns, states and provinces are in various stages of completing or updating management plans in order to provide for long-term sage-grouse conservation. Special emphasis is being placed on oil and gas development as it rapidly spreads across much of the eastern range of sage-grouse.

The recent decision by B. Lynn Winmill, Chief U.S. District Judge (2007), which remands the original 2005 not warranted decision back to the USFWS for reconsideration, has highlighted the need for States to coordinate their application of best available science. Representatives from the state agencies with authority for managing fish and wildlife from the major sage-grouse and energy producing states comprising MZ 1 and 2 and sage-grouse researchers who have published new findings, met on January 8 and 9, 2008 in Salt Lake City. The objectives of the meeting were to better understand the application of most recent peer-reviewed science within the context of oil and gas development and coordinate and compare implementation of conservation actions utilizing that information.

## Review Process

The participants at this meeting represented technical science and management advisors from each of the states. Researchers having the most recently peer reviewed and published articles concerning sage grouse and oil and gas development were invited to present their findings and answer questions. State agency participants agreed that the goal was not to establish state or regional policy or to determine the management actions that will be implemented in any or all states within MZ 1 or 2. Rather, the goal was to reach agreement on the conservation concepts and strategies related to oil and gas development that are supported by current published peer-reviewed and unpublished literature. If implemented, these concepts and strategies likely will not eliminate impacts to sage-grouse populations that result from energy development. However, when used in combination with other conservation measures, these actions may enhance the likelihood that sage-grouse populations will persist at levels that allow historical uses such as grazing and agriculture and maintain their current distribution and abundance, thereby avoiding the need to list sage-grouse under the federal Endangered Species Act.

Each researcher was invited to present their findings and to answer questions posed by the states. Following this, each state provided an overview of their review of the science and their resulting management actions and recommendations. The group then collectively reviewed, debated and agreed on the concepts and strategies supported by that science. The focus of the meeting was on five key issues: core areas, no-surface-occupancy zones, phased development, timing stipulations, well-pad densities, and restoration. Scientific data are available to inform many other issues related to sage-grouse management and conservation that were not reviewed (e.g., BMPs).

**Core Areas**

Identification and protection of core areas, sometimes also referred to as crucial areas, will help maintain or achieve target goals for populations including distribution and abundance.

Full field energy development appears to have severe negative impacts on sage-grouse populations under current lease stipulations (Lyon and Anderson 2003, Holloran 2005, Kaiser 2006, Holloran et al. 2007, Aldridge and Boyce 2007, Walker et al 2007, Doherty et al. 2008). Much of greater sage-grouse habitat in MZ 1 and 2 has already been leased for oil and gas development. These leases carry stipulations that have been shown to be inadequate for protecting breeding and wintering sage-grouse populations during full field development. (Holloran 2005, Walker et. al. 2007, Doherty et al. 2008) New leases continue to be issued utilizing these same stipulations. To ensure long-term persistence of populations and meet goals set by the states for sage-grouse, identifying and implementing greater protection within core areas from impacts of oil and gas development is a high priority.

In order to conserve core areas it is essential that they be identified and delineated. Sage-grouse populations occur over large landscapes comprising a series of leks and lek complexes with associated seasonal habitats. Therefore, core areas should capture the range required by a defined population to maintain itself. This concept is consistent with Crucial Wildlife Habitats recently endorsed by the Western Governor's Association (2007). Criteria that could be used to identify and map core areas include, but are not limited to: (1) lek densities, (2) displaying male densities, (3) sagebrush patch sizes, (4) seasonal habitats (breeding, summering, wintering areas), (5) seasonal linkages, or (6) appropriate buffers around important seasonal habitats.

Research indicates that oil or gas development exceeding approximately 1 well pad per square mile with the associated infrastructure, results in calculable impacts on breeding populations, as measured by the number of male sage-grouse attending leks (Holloran 2005, Naugle et al. 2006). Because breeding, summer, and winter habitats are essential to populations, development within these areas should be avoided. If development cannot be avoided within core areas, infrastructure should be minimized and the area should be managed in a manner that effectively conserves sagebrush habitats within that area.

**No Surface Occupancy (NSO)**

At the scale that NSOs are established, they alone will not conserve sage-grouse populations without being used in combination with core areas. The intent of NSOs is to maintain sage-grouse distribution and a semblance of habitat integrity as an area is developed.

*Breeding Habitat - Leks*

Research in Montana and Wyoming in coal-bed methane natural gas (CBNG) and deep-well fields suggests that impacts to leks from energy development are discernable out to a minimum of 4 miles, and that some leks within this radius have been extirpated as a direct result of energy development (Holloran 2005, Walker et al. 2007). Walker et al. (2007) indicates that the current 0.25-mile buffer lease stipulation is insufficient to adequately conserve breeding sage-grouse populations in areas having full CBNG development. A 0.25-mi. buffer leaves 98% of the landscape within 2 miles open to full-scale energy development. In a typical landscape in the Powder River Basin, 98% CBNG development within 2 miles of leks is projected to reduce the average probability of lek persistence from 87% to 5% (Walker et al. 2007). Only 38% of 26 leks inside of CBNG development remained active compared to 84% of 250 leks outside of development (Walker et al. 2007). Of leks that persisted, the numbers of attending males were reduced by approximately 50% when compared to those outside of CBNG development (Walker et al. 2007).

The impact analyses provided in Walker et al. (2007) are based on a 7-year dataset where probability of lek persistence is strongly related to extent of sagebrush habitat and the extent of energy development within 4 miles of the lek and the extent of agricultural tillage in the surrounding landscape. The estimated probabilities of lek persistence are only reliable for the length of the dataset, and it is not understood how other stressors (e.g., West Nile virus [Naugle et al. 2004], invasive weeds [Bergquist et al. 2007]) will cumulatively impact sage-grouse over longer time periods. While increased NSO buffers alone are unlikely to conserve sage-grouse populations, results from Walker et al. 2007 suggest they will increase the likelihood of maintaining the distribution and abundance of grouse and should increase the likelihood of successful restoration following energy development.

Additional information provided in Walker et al. (2007) allows managers and policy makers to estimate trade-offs associated with allowing development within a range of different distances from leks (Figures 1a and 1b). These probabilities will also need to be applied over larger landscapes in future analyses to better understand projected region- and state-wide population impacts under current and future development scenarios. Walker et al. (2007) studied lek persistence from 1997-2005 in relation to coal bed natural gas (CBNG) development in the Powder River Basin. These models are based on projected impacts of full-field development within (a) 2 miles and (b) 4 miles of the lek. We present results from these models (rather than models with impacts at smaller scales)

because development within 2 and 4 miles of leks are known to decrease breeding populations as measured by the number of displaying males (Holloran et al. 2005, Walker et al. 2007), and 52% and 74-80% of hens are known to nest within 2 and 4 miles of leks, respectively (Holloran and Anderson 2005, Colorado Greater Sage-Grouse Conservation Plan Steering Committee 2008). Sizes of NSO buffers required to protect breeding populations may be underestimated because leks in CBNG fields have fewer males per lek and a time lag occurs (avg. 3-4 years) between development and when leks go inactive. As a result, it is expected that not only will lek persistence decline, the number of males per lek will also decline. In contrast, sizes may be overestimated where high lek densities cause buffers from adjacent leks to overlap. Additional time is required to develop models demonstrating the probabilities of lek persistence at well-pad densities less than full development.

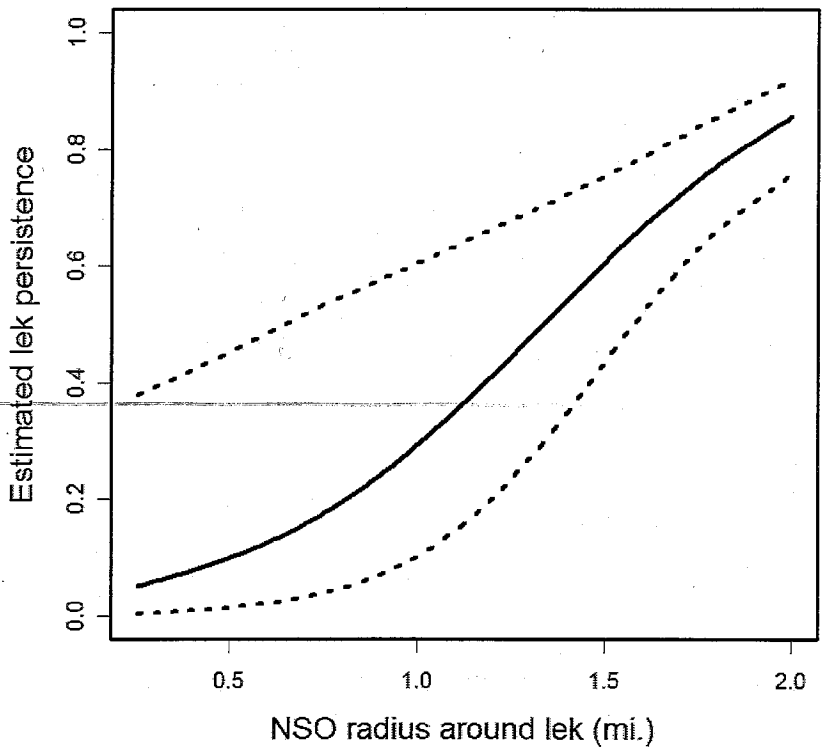



Figure 1a. Estimated probability of lek persistence (dashed lines represent 95% CIs) in fully-developed[1] coal-bed natural gas fields within an average landscape in the Powder River Basin (74% sagebrush habitat, 26% other habitats types) with different sizes of no-surface-occupancy (NSO) buffers around leks, assuming that only CBNG within 2 miles of the lek affects persistence. Buffer sizes of 0.25 mi., 0.5 mi., 0.6 mi., and 1.0 mi. result in estimated lek persistence of 5%, 11%, 14%, and 30%. Lek persistence in the absence of CBNG averages ~85%.

[1] Defined as entire area outside the NSO buffer, but within 2 miles, being within 350 meters of a well.

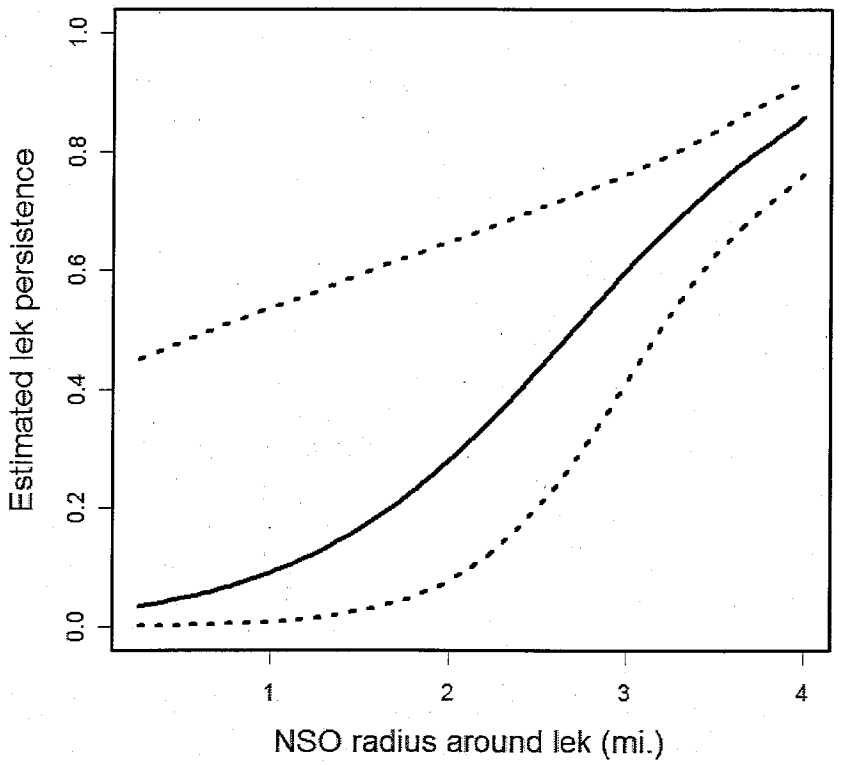



Figure 1b. Estimated probability of lek persistence (dashed lines represent 95% CIs) in fully-developed[2] coal-bed natural gas fields within an average landscape in the Powder River Basin (74% sagebrush habitat, 26% other habitats types) with different sizes of no-surface-occupancy (NSO) buffers around leks, assuming that only CBNG within 4 miles of the lek affects persistence. Buffer sizes of 0.25 mi., 0.5 mi., 0.6 mi., 1.0 mi., and 2.0 mi. result in estimated lek persistence of 4%, 5%, 6%, 10%, and 28%. Lek persistence in the absence of CBNG averages ~85%.

Figures 1a and 1b provide an illustration of the trade-offs between differing NSO buffers in relation to lek persistence in developing CBNG fields. The group does not offer a specific NSO recommendation but provides these graphs to guide decision-making.

*Breeding Habitat - Nesting and Early Brood-rearing*

Yearling female greater sage-grouse avoid nesting in areas within 0.6 miles of producing well pads (Holloran et al. 2007), and brood-rearing females avoid areas within 0.6 miles of producing wells (Aldridge and Boyce 2007). This suggests a 0.6-mile NSO around all suitable nesting and brood-rearing habitats is required to minimize impacts to females during these seasonal periods. In areas where nesting habitats have not been delineated, research suggests that greater sage-grouse nests are not randomly distributed. Rather, they are spatially associated with lek location within 3.1 miles in Wyoming (Holloran and Anderson 2005). However, a 4-mile buffer is needed to encompass 74-80% (Moynahan

[2] Defined as entire area outside the NSO buffer, but within 4 miles, being within 350 meters of a well.

2004, Holloran and Anderson 2005, Colorado Greater Sage-Grouse Conservation Plan Steering Committee 2008). These suggest that all areas within at least 4-miles of a lek should be considered nesting and brood-rearing habitats in the absence of mapping.

*Winter Habitat*

NSO or other protections may also need to be considered for crucial winter range. Survival of juvenile, yearling, and adult females are the three most important vital rates that drive population growth in greater sage-grouse (Holloran 2005, Colorado Greater Sage-Grouse Conservation Plan Steering Committee 2008). Although overwinter survival in sage-grouse is typically high, severe winter conditions can decrease hen survival (Moynahan et al 2006). Crucial wintering habitats can constitute a small part of the overall landscape (Beck 1977, Hupp and Braun 1989). Doherty et al. (2008) demonstrated that sage-grouse avoided otherwise suitable wintering habitats once they have been developed for energy production, even after timing and lek buffer stipulations had been applied (Doherty et al. 2008). For this reason, increased levels of protection may need to be considered in crucial winter habitats.

**Phased Development**

Population-level impacts and avoidance associated with energy development have been documented (Braun et al. 2002, Lyon and Anderson 2003, Holloran 2005, Kaiser 2006, Holloran et al. 2007, Aldridge and Boyce 2007, Walker et al 2007, Doherty et al. 2008). Phased development maximizes the amount of area within a landscape that is not being impacted by development at any one time, and can occur at multiple spatial scales (e.g., phased development of separate fields in a landscape, phased development of infrastructure within a single unit or field, or phased development within a single lease). Unitization, clustering, and geographically staggered development are all forms of phased development. As a tool to minimize impacts to sage-grouse, developing oil and gas resources by employing one of these phased methods may help maintain large, functional blocks of sage-grouse habitat.

**Timing Stipulations**

As with NSOs, at the scale that timing stipulations are established, they alone will not conserve sage-grouse populations without being used in combination with core areas. The intent of timing stipulations is to help maintain sage-grouse distribution and a semblance of habitat integrity as an area is developed. Timing stipulations are of lesser value at the scale of full-field development.

*Breeding Habitat - Leks*

Traffic during the strutting period when males are on a lek results in declines in male attendance when road-related disturbance is within 0.8 miles (Holloran 2005). The distance traveled by males from the lek during the breeding season has been reported in varying ways but generally averages 0.6 miles from a lek (Colorado Greater Sage-Grouse

Conservation Plan Steering Committee 2008 - see Appendix B). Additionally, females breeding on leks within 1.9 miles of natural gas development had lower nest initiation rates and nested farther from the lek compared to non-impacted individuals (Lyon and Anderson 2003), suggesting disturbance to leks influence females as well. Local variations may influence the application of specific dates, which are typically within a window of March 1 and May 31.

*Breeding Habitat - Nesting and Early Brood-rearing*

Often, timing stipulations (periods where no activity that creates disturbance are allowed) for breeding habitat have been applied using a radius around a lek. However, nesting and brood-rearing habitat is not uniformly distributed around the lek. Mapping of habitat would allow for more accurate application of this stipulation. Research on the distribution of nests relative to leks and on the timing of nesting indicates that timing stipulations to protect nesting hens and their habitat should be in place from March through June in mapped breeding habitat or (when nesting habitat has not been mapped) within 4 miles of active lek sites (Moynahan 2004, Holloran et al. 2005, Colorado Greater Sage-Grouse Conservation Plan Steering Committee 2008).

*Winter Habitat*

Research suggests that no surface occupancy should also be applied to important wintering habitats (Doherty et al. 2008), but if development occurs, impacts would be reduced if development activities were avoided between December 1 and March 15.

**Well-Pad Densities**

Leks tend to remain active when well-pad densities within 1.9 miles of leks are less than 1 pad per square mile (Holloran 2005) but leks tend to go inactive at higher pad densities (Holloran 2005, Naugle et al. 2006).

**Restoration**

The purpose of restoration in sage-grouse habitat should be the removal of infrastructure associated with energy development from the land surface and subsequent re-establishment of native grasses, forbs, and shrubs, including sagebrush, to promote natural ecological function. Restoration should reestablish functionality of seasonal habitats for sage-grouse. Thus a field should not be considered restored until sagebrush-grassland habitats have been reestablished.

**Future Needs**

Time did not allow for a detailed discussion of specific Best Management Practices for oil and gas development and restoration, seasonal habitat mapping, or future research. These topics are all recognized as needing action in the immediate future.

**Literature Cited**


Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: a habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508-526.

Beck, T. D. I. 1977. Sage grouse flock characteristics and habitat selection during winter. Journal of Wildlife Management 41:18-26.

Bergquist, E., P. Evangelista, T. J. Stohlgren, and N. Alley. 2007. Invasive species and coal bed methane development in the Powder River Basin, Wyoming. Environmental Monitoring and Assessment. 128:381-394.

Braun, C. E., O. O. Oedekoven, and C. L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage grouse. Transactions North American Wildlife and Natural Resources Conference 67:337-349.

Colorado Greater Sage-Grouse Conservation Plan Steering Committee. 2008. The Colorado Greater Sage-Grouse Conservation Plan. Colorado Division of Wildlife. Denver, CO. Unpublished Report.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Doherty, K.E., D.E. Naugle, B.L. Walker, J.M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management *In Press.*

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation. University of Wyoming, Laramie, USA.

Holloran, M. J. and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742-752.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69: 638-649.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2007. Population response of yearling greater sage-grouse to the infrastructure of natural gas fields in southwestern Wyoming. Completion report. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, WY, USA.

Hupp, J. W. and C. E. Braun. 1989. Topographic distribution of sage grouse foraging in winter. Journal of Wildlife Management 53: 823-829.

Kaiser, R. C. 2006. Recruitment by greater sage-grouse in association with natural gas development in western Wyoming. Thesis. University of Wyoming. Laramie, USA.

Lyon, A. G. and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486-491.

Moynahan B. J. 2004. Landscape-scale factors affecting population dynamics of greater sage-grouse *(Centrocercus urophasianus)* in northcentral Montana, 2001–2004. Dissertation, The University of Montana. Missoula, USA.

Moynahan, B.J., M.S. Lindberg, and J.W. Thomas. 2006. Factors contributing to process variance in annual survival of female greater sage-grouse in north-central Montana. Ecological Applications 16:1529-1538.

Naugle, D. E., C. L. Aldridge, B. L. walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R.T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: pending crisis for greater sage-grouse. Ecology Letters 7:704-713.

Naugle, D. E., B. L. Walker, and K. E. Doherty. 2006. Sage-grouse population response to coal-bed natural gas development in the Powder River Basin: interim progress report on region-wide lek-count analyses. Unpublished Report, University of Montana, Missoula, USA.

Stiver, S.J., A.D. Apa, J.R. Bohne, S.D. Bunnell, P.A. Deibert, S.C. Gardner, M.A. Hilliard, C.W. McCarthy, and M.A. Schroeder. 2006. Greater sage-grouse comprehensive conservation strategy. Western Association of Fish and Wildlife Agencies. Unpublished report. Cheyenne, Wyoming.

Walker, B.L., D. E. Naugle, and K.E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644-2654.

Western Governor's Association. 2007. Wildlife corridors initiative oil and gas working group report. http://www.westgov.org/wga/publicat/OilGas07.pdf. Accessed 15 January 2007.

Appendix 1.

**Participants (Alphabetical)**

Dr. Tony Apa, Colorado Division of Wildlife
Mr. Joe Bohne, Wyoming Game and Fish Department
Mr. Tom Christiansen, Wyoming Game and Fish Department
Mr. Jeff Herbert, Montana Department of Fish, Wildlife and Parks
Mr. Bill James, Utah Division of Wildlife Resources
Mr. Rick Northrup, Montana Department of Fish, Wildlife and Parks
Mr. Dave Olsen, Utah Division of Wildlife Resources
Mr. Aaron Robinson, North Dakota Game and Fish
Ms. Pam Schnurr, Colorado Division of Wildlife
Mr. T.O. Smith, Montana Department of Fish, Wildlife and Parks
Mr. Brett Walker, Colorado Division of Wildlife

**Invited Guests**

Dr. Matt Holloran, Wyoming Wildlife Consultants, LLC
Dr. David Naugle, University of Montana

*Journal of International Wildlife Law & Policy, 13:274–292, 2010*
*Copyright © Taylor & Francis Group, LLC*
*ISSN: 1388-0292 print / 1548-1476 online*
*DOI: 10.1080/13880292.2010.524564*

Routledge
Taylor & Francis Group

# Impacts of Anthropogenic Noise on Wildlife: Research Priorities for the Development of Standards and Mitigation

JESSICA L. BLICKLEY[1]
GAIL L. PATRICELLI[2]

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

## 1. INTRODUCTION

Human development introduces anthropogenic noise sources into the environment across many elements of the modern terrestrial landscape, including roads, airports, military bases, and cities. The impacts of these introduced noise sources on wildlife are less well studied than many of the other effects human activities have on wildlife, the most well known of which are habitat fragmentation and the introduction of invasive species. A growing and substantial body of literature suggests, however, that noise impacts may be more important and widespread than previously imagined.[3] They range in effects from mild to severe. They can impact wildlife species at both the individual and population levels. The types of impacts run the gamut from damage to the auditory system, the masking of sounds important to survival and reproduction, the imposition of chronic stress and associated physiological responses, startling, interference with mating, and population declines.

Anthropogenic noise is a global phenomenon, with the potential to affect wildlife across all continents and habitat types. Despite the widespread

[1] Department of Evolution and Ecology, University of California, Davis, CA 95616, USA. E-mail: jlblickley@ucdavis.edu
[2] Department of Evolution and Ecology and Center for Population Biology, University of California, Davis, CA 95616, USA. E-mail: glpatricelli@ucdavis.edu. For helpful discussion both authors thank Tom Rinkes, Sue Oberlie, Stan Harter, Tom Christiansen, Alan Krakauer, Geoffrey Wandesforde-Smith, Paul Haverkamp, Margaret Swisher, Ed West, Dave Buehler, Fraser Schilling, and the UC Davis Road Ecology Center. Research funding is acknowledged from UC Davis, the U.S. Bureau of Land Management, National Fish & Wildlife Foundation, Wyoming Sage-Grouse Conservation Fund (Wind River/Sweetwater River Basin, Upper Green River, and Northeast Sage-Grouse Local Working Groups), and the Wyoming Community Foundation Tom Thorne Sage Grouse Conservation Fund.
[3] For a review of noise impacts on birds and other wildlife, see P. A. KASELOO & K. O. TYSON, SYNTHESIS OF NOISE EFFECTS ON WILDLIFE POPULATIONS (U.S. Department of Transportation, Federal Highway Administration, 2004); ROBERT J. DOOLING & ARTHUR N. POPPER, THE EFFECTS OF HIGHWAY NOISE ON BIRDS (California Department of Transportation, Division of Environmental Analysis, 2007).

distribution of noise, the bulk of research on the effects of noise on terrestrial wildlife has been limited to European countries and the United States. This geographic bias in research may limit the application of the results from previous studies on a global basis, since the impacts may differ among habitats and species.[4]

Since much human development involves the introduction of noise, separating out and understanding the impacts of noise pollution is a critical step in developing effective wildlife policy, particularly the setting of standards and the use of mitigation measures. The first step typically is to determine the overall impact on the population demography of a species, by measuring population declines and birth rates. Mitigation requires that the mechanisms of this effect then be understood. From an initial determination, for example, that roads decrease songbird population densities, there must next be an estimation of the extent to which noise, dust, chemical pollution, habitat fragmentation, invasive weeds, visual disturbance, or road mortality are partial and contributory causes of that impact before effective mitigation measures aimed at noise can be chosen. Quieter pavements will not help songbirds if the true cause of the problem is visual disturbance. The key challenge, then, is to measure the contribution of noise to observed impacts on animal populations while controlling for other variables.

In this article, we address three questions: what are the common sources of anthropogenic noise; what is known about the mechanisms by which noise impacts wildlife; and how can we use observational and experimental approaches to estimate the impacts of noise on whatever species are of concern?

In answering these questions we deal at length with both observational and experimental methods, the latter including both laboratory and field work. We describe observational field studies on animal abundance and reproduction in impacted areas and a method for estimating the potential of noise sources to mask animal vocalizations. We address both the feasibility and value of laboratory and field experiments and describe a case study based on an ongoing noise-playback experiment we have designed to quantify the impacts of noise from energy development on greater sage-grouse (*Centrocercus urophasianus)* in Wyoming.

[4] The geographic bias in research has lead to a focus on species that live in temperate zones, with little to no study of tropical species. Also of concern, many of the landscapes that have been the focus of research on noise and wildlife in these industrialized nations have already been profoundly influenced by human development such that the species or individuals living in these areas may be more tolerant of disturbance. Application of the results of studies from developed to less developed landscapes would potentially lead to an underestimation of the effects of noise. Anthropogenic changes to the environment are occurring at an unprecedented rate in developing nations in tropical latitudes, however, we do not yet know whether the results from existing research are applicable in these regions.

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

Our focus, then, is on noise impacts on animals in the terrestrial environment,[5,6] especially birds, which are the subjects of most terrestrial studies.[7] We also outline directions for future research and in a final section emphasize the importance of this research for developing flexible wildlife management strategies in landscapes that are increasingly subject to human encroachment.

## 2. SOURCES OF NOISE

Noise is associated with most phases in the cycle of human development activity, from early construction to the daily operation of a completed project. Transportation systems are one of the most pervasive sources of noise across all landscapes, including common sources like roads and their associated vehicular traffic, airports and airplanes, off-road vehicles, trains, and ships. Roads deserve special attention, because they are a widespread and rapidly increasing terrestrial noise source. Although the surface area covered by roads is relatively small, the ecological effects of roads, including noise, extend far beyond the road itself, impacting up to one-fifth of the land area of the United States, for example.[8] Industrial noise sources, such as military bases, factories, mining operations, and wind farms may be more localized in the landscape, but are problematic for wildlife because the noise produced can be very loud.

The characteristics of noise vary substantially among sources. Each source type exhibits variance in amplitude (i.e., loudness), frequency profile

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

[5] Many terrestrial noise sources produce noise that travels through the ground as well as the air. Seismic noise is likely to impact fossorial animals and animals that possess specialized receptors for seismic detection, many of which communicate by seismic signals. We do not address seismic noise in this paper, but it is an issue that warrants further discussion.

[6] For recent treatments of noise in the marine environment, its impacts on marine species, and legal and policy responses, see *Noise Pollution and the Oceans: Legal and Policy Responses Part 1*, 10 J. INT'L WILDLIFE L. & POL'Y (2007) 101–199 and *Noise Pollution and the Oceans: Legal and Policy Responses Part 2*, 10 J. INT'L WILDLIFE L. & POL'Y (2007) 219–288. See also, Committee on Characterizing Biologically Significant Marine Mammal Behavior, Marine Mammal Populations and Ocean Noise, DETERMINING WHEN NOISE CAUSES BIOLOGICALLY SIGNIFICANT EFFECTS 142 (Ocean Studies Board, Division on Earth and Life Studies, National Research Council, The National Academies, 2005).

[7] Birds have often been used in noise research because birds are generally easy to study due to their high detectability, most species use vocal communication (making them likely to be impacted by noise) and they are generally of high conservation importance.

[8] R.T.T. Forman & R.D. Deblinger, *The Ecological Road-Effect Zone of a Massachusetts (U.S.A.) Suburban Highway*, 14 CONS. BIOL. 36–46 (2000); R.T.T. Forman, *Estimate of the Area Affected Ecologically by the Road System in the United States*, 14 CONS. BIOL. 31–35 (2000); R.T.T. Forman, B. Reineking, and A.M. Hersberger, *Road Traffic and Nearby Grassland Bird Patterns in a Suburbanizing Landscape*, 29 ENVT'L. MGMT. 782–800 (2002). Due to its ubiquity, road noise is the most commonly studied type of terrestrial noise. Road noise is, in general, similar to other types of anthropogenic noise and affects a wide range of species and habitat types, so the research techniques and results can be applied to many other types of anthropogenic noise.

(i.e., pitch), and spatial and temporal patterns. The interaction of these characteristics is what determines in a narrow sense the impact of noise on wildlife, setting aside the possibly confounding influence of contextual variables.

Intuitively, loud noise is more disruptive than quiet noise[9] and noise with frequencies similar to animal vocalizations is more likely to interfere with (i.e., mask) communication than noise with different frequencies.[10] Most anthropogenic noise sources have energy concentrated in low frequencies (<250 Hz), which can travel long distances with relatively little energy loss. Such noise is also more difficult to control using traditional noise-abatement structures, such as noise reflecting or absorbing walls along highways or surrounding other fixed noise sources, such as industrial sites.[11] Spatial patterning of noise may also affect the level of disturbance. A highly localized point source, like a drilling rig, will generally impact a smaller area than a linear source, such as a highway, although the area of impact will also depend on the amplitude and frequency structure of the noise. The temporal patterning of noise can also be important, because animal behaviors are often temporally patterned. Rush hour traffic, for example, often coincides with the dawn chorus of bird song,[12] an important time for birds because this is when mates are attracted and territories defended.[13]

Environmental noise is not an entirely new problem for animals, nor is human activity the exclusive cause of it. Natural environments have numerous sources of ambient noise, such as wind, moving water, and sounds produced by other animals. There is also evidence that animals living in naturally noisy areas have made adaptations through the use of signals and signaling behaviors to overcome the masking impacts of noise.[14] However, if anthropogenic noise

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

---

[9] M.E. Weisenberger et al., *Effects of Simulated Jet Aircraft Noise on Heart Rate and Behavior of Desert Ungulates*, 60 J. WILDLIFE MGMT. 52–61 (1996).

[10] Bernard Lohr et al., *Detection and Discrimination of Natural Calls in Masking Noise by Birds: Estimating the Active Space of a Signal*, 66 ANIMAL BEHAV. 703–710 (2003).

[11] S.P. SINGAL, NOISE POLLUTION AND CONTROL STRATEGY (2005).

[12] R.A. Fuller et al., *Daytime Noise Predicts Nocturnal Singing in Urban Robins*, 3 BIOL. LETTERS 368–370 (2007).

[13] C.K. CATCHPOLE & PETER J.B. SLATER, BIRD SONG: THEMES AND VARIATIONS (1995).

[14] For example, the structural and temporal properties of many acoustic signals are adapted—by evolution or through individual plasticity—to maximize the propagation distance and/or minimize interference from natural noise sources. R. Haven Wiley & Douglas G. Richards, *Adaptations for Acoustic Communication in Birds: Sound Transmission and Signal Detection*, *in* 1 ACOUSTIC COMMUNICATION IN BIRDS 131–181 (D. Kroodsma & E.H. Miller eds., 1982); H. Brumm, *Signalling through Acoustic Windows: Nightingales Avoid interspecific Competition by Short-Term Adjustment of Song Timing*, 192 J. COMP. PHYSIOL. A 1279–1285 (2006); Henrik Brumm & Hans Slabbekoorn, *Acoustic Communication in Noise*, 35 ADVANCES STUDY BEHAV. 151–209 (2005); Hans Slabbekoorn & Thomas B. Smith, *Habitat-Dependent Song Divergence in the Little Greenbul: An Analysis of Environmental Selection Pressures on Acoustic Signals*, 56 EVOLUTION 1849–1858 (2002); G.M. Klump, *Bird Communication in the Noisy World*, *in* ECOLOGY AND EVOLUTION OF ACOUSTIC COMMUNICATION IN BIRDS 321–338 (D. Kroodsma & E.H. Miller eds., 1996); Eugene S. Morton, *Ecological Sources of Selection on Avian Sounds*, 109 AM. NATURALIST 17–34 (1975).

differs enough from natural noise in frequency, amplitude, or daily/seasonal patterns, animal adaptations to natural noise can be overwhelmed. Furthermore, the extensive introduction of anthropogenic noise into the environment on a large scale is a relatively recent phenomenon, so that animals have had only a limited opportunity to adapt to widespread and sometimes drastic changes in their acoustic environments.[15]

## 3. THE POTENTIAL IMPACTS OF NOISE ON WILDLIFE

Animals exhibit a variety of responses to noise pollution (also called introduced noise), depending on the characteristics of the noise and the animal's ability to tolerate or adapt to it. Noise impacts on wildlife can be observed at the individual and population levels, which we now consider in turn.

### 3.1 Individual-Level Impacts

Some of the most dramatic impacts of noise on individuals are acute and need to be distinguished from chronic effects. Acute impacts include physiological damage, masking of communication, disruption of behavior, and startling. The most direct physiological impact affects an animal's ability to hear, either by permanently damaging the auditory system, in which case it produces what is called a permanent threshold shift (PTS) in hearing, or by causing temporary decreases in hearing sensitivity, which are called temporary threshold shifts (TTS).[16] The noise levels required for PTS and TTS are quite loud,[17] making hearing damage unlikely in most terrestrial situations. Even extremely loud sound sources will only cause PTS and TTS over a small area, because on land sound attenuates very quickly with distance.[18] This is why most studies

[15] G. Patricelli & J. Blickley, *Avian Communication in Urban Noise: Causes and Consequences of Vocal Adjustment*, 123 THE AUK 639–649 (2006); Paige S. Warren et al., *Urban Bioacoustics: It's Not Just Noise*, 71 ANIMAL BEHAV. 491–502 (2006); Lawrence A. Rabin et al., *Anthropogenic Noise and Its Effects on Animal Communication: An Interface Between Comparative Psychology and Conservation Biology*, 16 INT'L J. COMP. PSYCHOL. 172–192 (2003); Lawrence A. Rabin & Correigh M. Greene, *Changes to Acoustic Communication Systems in Human-Altered Environments*, 116 J. COMP. PSYCHOL. 137–141 (2002); H. Slabbekorn & E.A.P. Ripmeester, *Birdsong and Anthropogenic Noise: Implications and Applications for Conservation*, 17 MOLECULAR ECOLOGY 72–83 (2008).

[16] P. Marler et al., *Effects of Continuous Noise on Avian Hearing and Vocal Development*, 70 PROC. NAT'L ACAD. SCI. 1393–1396 (1973); J. Saunders & R. Dooling, *Noise-Induced Threshold Shift in the Parakeet (*Melopsittacus undulatus), 71 PROC. NAT'L ACAD. SCI. 1962–1965 (1974); Brenda M. Ryals et al., *Avian Species Differences in Susceptibility to Noise Exposure*, 131 HEARING RES. 71–88 (1999).

[17] PTS in birds may result from sound levels of ∼125 dBA SPL for multiple impulsive sounds and ∼140 dBA SPL for a single impulsive sound. TTS can result from continuous noise levels of ∼93 dBA SPL. The term "dBA SPL" refers to the A-weighted decibel, the most common unit for noise measurements. It adjusts for human perception of sound and is scaled relative to the threshold for human hearing.

[18] Sound levels drop by approximately 6 dB (measured using dBA SPL, or any other decibel measure), which represents a halving of loudness, with every doubling in distance from a point source, and 3 dB with every doubling of distance from a linear source, such as a highway.

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

of impacts from highway and urban noise do not directly address PTS and TTS, although they may need to be considered in extremely noisy areas.

Other acute impacts of noise, such as masking and behavioral disruption, occur over a much larger area. Masking occurs when the perception of a sound is affected by the presence of background noise, with high levels of background noise decreasing the perception of a sound.[19] One possible consequence of masking is a decrease in the efficacy of acoustic communication. Many animals use acoustic signals to attract and retain mates, settle territorial disputes, promote social bonding, and alert other individuals to predators. Disruption of communication can, therefore, have dramatic impacts on survival and reproduction.[20] In one laboratory study, high environmental noise reduced the strength of the pair bond in monogamous zebra finches, *Taeniopygia guttata*, likely because females either had increased difficulty identifying mates or pair-bond maintenance calls were masked.[21] The broader consequence of this finding is that females in noisy areas may be more likely to copulate with extra-pair partners, and this in turn can change the social and genetic dynamics of a population.

In other research, birds have been found to change their songs and calls in response to noise in urban areas, which may reduce masking of communication.[22] However, the consequences of this vocal adjustment on reproduction in a species remain unclear. One outcome may be that populations using urban dialects have a better chance to thrive in urban areas. But by the same token they may experience a decrease in mate recognition and/or gene flow with populations in non-urban areas.[23]

Beyond interfering with communication, introduced background noise can also mask the sounds of approaching predators or prey, and increase the perception of risk from predation. Studies have yet to compare predation rates or hunting success in noisy and quiet areas while controlling for other confounding factors. The degree to which noise affects predator/prey relations

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

[19] Lohr et al., *supra* note 5.

[20] M.A. Bee & E.M. Swanson, *Auditory Masking of Anuran Advertisement Calls by Road Traffic Noise*, 74 ANIMAL BEHAV. 1765–1776 (2007); Henrik Brumm, *The Impact of Environmental Noise on Song Amplitude in a Territorial Bird*, 73 J. ANIMAL ECOLOGY 434–440 (2004); L. Habib et al., *Chronic Industrial Noise Affects Pairing Success and Age Structure of Ovenbirds* Seiurus aurocapilla, 44 J. APPLIED ECOLOGY 176–184 (2007); Frank E. Rheindt, *The Impact of Roads on Birds: Does Song Frequency Play a Role in Determining Susceptibility to Noise Pollution?*, 144 J. ORNITHOLOGIE 295–306 (2003).

[21] J.P. Swaddle & L.C. Page, *Increased Amplitude of Environmental White Noise Erodes Pair Preferences in Zebra Finches: Implications for Noise Pollution*, 74 ANIMAL BEHAV. 363–368 (2007).

[22] Slabbekorn & Ripmeester, *supra* note 10; Brumm, *supra* note 15; Hans Slabbekoorn & Margriet Peet, *Birds Sing at a Higher Pitch in Urban Noise*, 424 NATURE 267 (2003); William E. Wood & Stephen M. Yezerinac, *Song Sparrow (*Melozpiza melodia*) Song Varies with Urban Noise*, 123 THE AUK 650–659 (2006).

[23] Patricelli & Blickley, *supra* note 10; Warren et al. *supra* note 10; Slabbekoorn & Peet, *supra* note 17.

in any species, therefore, remains largely unexplored.[24] One study found that birds nesting near noisy natural gas pads had higher nesting success, likely due to reduced presence of the most common nest predator, the western scrub jay.[25] As suggested by these authors, the higher nesting success of birds in noisy areas provides a mechanism by which noise-tolerant species could become more common in a noisy world. Noise also causes short-term disruptions in behavior, such as startling or frightening animals away from food or other resources.[26]

In addition to the acute effects of noise, animals may suffer chronic effects, including elevated stress levels and associated physiological responses. Over the short term, chronic stress can result in elevated heart rate.[27] Longer-term stress can be associated with the ability to resist disease, survive, and successfully reproduce.[28] Good measures of chronic stress come from elevated stress hormones, like corticosterone, in blood or fecal samples.[29] In noise-stressed laboratory rats, elevated corticosterone was linked with reduced food consumption and decreased weight gain,[30] raising the possibility that for some individuals there may be longer-term welfare and survival consequences from the elevated stress associated with noise introduction.

### 3.2 Population Level Impacts

The cumulative impacts of noise on individuals can manifest at the population level in various ways that can potentially range from population declines up to

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

[24] Quinn found that chaffinchs (*Fringilla coelebs*) perceived an increased risk of predation while feeding in noisy conditions, likely due to a reduced ability to detect auditory cues from potential predators. L. Quinn et al., *Noise, Predation Risk Compensation and Vigilance in the Chaffinch* Fringilla coelebs, 37 J. AVIAN BIOL. 601–608 (2006). Research on greater sage-grouse also highlights the potential for noise to contribute to predation. One of the methods for capturing sage-grouse is to mask the sound of researcher footfalls using a noise source such as a stereo or a chain saw. With such masking, the grouse can be easily approached and netted in their night roosts for banding or blood sampling. Presumably, predators would be equally fortunate in noisy areas, though the ability of predators to use acoustic cues for hunting could be diminished by masking as well.

[25] Clinton D. Francis et al., *Noise Pollution Changes Avian Communities and Species Interactions*, 19 CURRENT BIOL. 1–5 (2009).

[26] Dooling & Popper, *supra* note 1; N. Kempf & O. Huppop, *The Effects of Aircraft Noise on Wildlife: A Review and Comment*, 137 J. ORNITHOLOGIE 101–113 (1996); D.K. Delaney et al., *Effects of Helicopter Noise on Mexican Spotted Owls*, 63 J. WILDLIFE MGMT. 60–76 (1999); L.A. Rabin, R.G. Coss, & D.H. Owings, *The Effects of Wind Turbines on Antipredator Behavior in California Ground Squirrels* (Spermophilus beecheyi), 131 BIOL. CONS. 410–420 (2006).

[27] Weisenberger et al., *supra* note 4.

[28] J.C. Wingfield & R.M. Sapolsky, *Reproduction and Resistance to Stress: When and how*, 15 J. NEUROENDOCRINOL, 711 (2003); A. Opplinger et al., *Environmental Stress Increases the Prevalence and Intensity of Blood Parasite Infection in the Common Lizard* Lacerta vivipara, 1 ECOLOGY LETTERS 129–138 (1998).

[29] Wingfield & Sapolsky, *supra* note 23; S.K. Wasser et al., *Noninvasive Physiological Measures of Disturbance in the Northern Spotted Owl*, 11 CONS. BIOL. 1019–1022 (1997); D.M. Powell et al., *Effects of Construction Noise on Behavior and Cortisol Levels in a Pair of Captive Giant Pandas (*Ailuropoda melanoleuca*)*, 25 ZOO BIOL. 391–408 (2006).

[30] P. Alario et al., *Body Weight Gain, Food Intake, and Adrenal Development in Chronic Noise Stressed Rats*, 40 PHYSIOL. BEHAV. 29–32 (1987).

regional extinction. If species already threatened or endangered due to habitat loss avoid noisy areas and abandon otherwise suitable habitat because of a particular sensitivity to noise, their status becomes even more critical. As discussed below, numerous studies have documented reduced habitat use and lower breeding success in noisy areas by a variety of animals.[31]

## 4. MEASURING THE IMPACTS OF NOISE ON SPECIES OF CONCERN

Species vary widely in their ability to tolerate introduced noise and can exhibit very different responses to altered acoustic environments. This variability in response to noise makes generalizations about noise impacts among species and among noise sources difficult. Generalizations relevant to a single species can also be hard to make, because the ability to tolerate noise may vary with reproductive status, prior exposure to noise, and the presence of other stressors in the environment. This is why more measurements of noise impacts and associated variables are needed for a wider range of species.

Measuring the effects of noise at the individual and population levels is, however, extremely challenging. As we noted earlier, noise is typically accompanied by other changes in the environment that may also have physiological, behavioral, and population level effects. For example, habitat fragmentation is a side effect of road development, and fragmentation alone has been shown to cause population declines and changes in communication and other behaviors.[32] So, can we measure the impacts of noise on wildlife in ways that will support biologically relevant noise standards?

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

[31] Affected animals include birds, mammals, reptiles, and amphibians. Forman et al., *supra* note 6; Rheindt, *supra* note 15; Rien Reijnen et al., *The Effects of Car Traffic on Breeding Bird Populations in Woodland. III. Reduction of Density in Relation to the Proximity of Main Roads*, 32 J. APPLIED ECOLOGY 187–202 (1995); Rien Reijnen et al., *The Effects of Traffic on the Density of Breeding Birds in Dutch Agricultural Grasslands*, 75 BIOL. CONS. 255–260 (1996); S.J. Peris & M. Pescador, *Effects of Traffic Noise on Passerine Populations in Mediterranean Wooded Pastures*, 65 APPLIED ACOUSTICS 357–366 (2004); R.T.T. Forman & L.E. Alexander, *Roads and Their Major Ecological Effects*, 29 ANN. REV. ECOLOGY SYSTEMATICS 207–231 (1998); E. Stone, *Separating the Noise from the Noise: A Finding in Support of the "Niche Hypothesis," That Birds Are Influenced by Human-Induced Noise in Natural Habitats*, 13 ANTHROZOOS 225–231 (2000); Ian Spellerberg, *Ecological Effects of Roads and Traffic: A Literature Review*, 7 GLOBAL ECOLOGY BIOGEOG. LETTERS 317–333 (1998); David Lesbarrères et al., *Inbreeding and Road Effect Zone in a Ranidae: The Case of Agile Frog,* Rana dalmatina *Bonaparte 1840*, 326 COMPTES RENDUS BIOLOGIES 68–72 (2003).

[32] See, *e.g.*, Jeffrey A. Stratford & W. Douglas Robinson, *Gulliver Travels to the Fragmented Tropics: Geographic Variation in Mechanisms of Avian Extinction*, 3 FRONTIERS ECOLOGY & ENV'T 91–98 (2005); P. Laiolo & J. L. Tella, *Erosion of Animal Cultures in Fragmented Landscapes*, 5 FRONTIERS ECOLOGY & ENV'T 68–72 (2007).

## 4.1 The Observational Approach

### *4.1.1 Relating wildlife abundance to noise levels*

Much of the evidence for noise impacts on animals comes from field observations of animal density, species diversity, and/or reproductive success in relation to noise sources. Most studies focus on the presence or absence of wildlife near roads, finding lower population densities of many birds,[33] lower overall diversity for birds, reptiles, and amphibians,[34] and road avoidance in large mammals.[35] Most of this work does not separate the impacts of noise from other road effects or measure spatial and temporal variations in noise levels along transects where animals were studied.

One influential series of studies in the Netherlands did find, however, a negative relationship between noise exposure along roadways and both bird diversity and breeding densities.[36] Noise exposure better explained decreased density and diversity than either visual or chemical disturbance. These Dutch studies have been criticized for research design and statistical analysis problems,[37] underscoring the fact that researchers in different countries have different assumptions about how to measure noise and evaluate its impacts.[38] On their own, the Dutch studies are an inadequate basis for establishing internationally standardized noise regulations, but they are among the few analyses that set measurements of noise levels beside data on species presence/absence and diversity.

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

---

[33] Forman & Deblinger, *supra* note 3; Rheindt, *supra* note 15; Peris & Pescador, *supra* note 26; M. Kuitunen et al., *Do Highways Influence Density of Land Birds?* 22 ENVTL. MGMT. 297–302 (1998); A.N. van der Zande et al., *The Impact of Roads on the Densities of Four Bird Species in an Open Field Habitat—Evidence of a Long-Distance Effect*, 18 BIOL. CONS. 299–321 (1980).

[34] C.S. Findlay & J. Houlahan, *Anthropogenic Correlates of Species Richness in Southeastern Ontario Wetlands*, 11 CONS. BIOL. 1000–1009 (1997).

[35] Studies in large mammals typically find road avoidance, but many small mammals are found in higher densities near roads, due to increased dispersal and reduced numbers of predators. Forman & Deblinger, *supra* note 3; F. J. Singer, *Behavior of Mountain Goats in Relation to US Highway 2, Glacier National Park, Montana*, 42 J. WILDLIFE MGMT. 591–597 (1978); G.R. Rost & J.A. Bailey, *Distribution of Mule Deer and Elk in Relation to Roads*, 43 J. WILDLIFE MGMT. 634–641 (1979); L.W. Adams & A.D. Geis, *Effects of Roads on Small Mammals*, 20 J. APPLIED ECOLOGY 403–415 (1983).

[36] Reijnen et al., *supra* note 29; R. Foppen & R. Reijnen, *The Effects of Car Traffic on Breeding Bird Populations in Woodland. II. Breeding Dispersal of Male Willow Warblers (*Phylloscopus trochilus*) in Relation to the Proximity of a Highway*, 31 J. APPLIED ECOLOGY 95–101 (1994).

[37] N. Sarigul-Klign, D.C. Karnoop, & F.A. Bradley, *Environmental Effect of Transportation Noise. A Case Study: Criteria for the Protection of Endangered Passerine Birds, Final Report* (Transportation Noise Control Center (TNCC), Department of Mechanical and Aeronautical Engineering, University of California, Davis, 1977); G. Bieringer & A. Garniel, Straßenalärm und Vögel—eine kurze Übersicht über die Literatur mit einer Kritik einflussreicher Arbeiten. Bundesministerium für Verkehr, Innovation und Technologie. Schriftenreihe Straßenforschung. Unpublished manuscript, Vienna, 2010 (copy on file with the authors).

[38] Noise is commonly measured in dBA SPL, a unit that is measured differently in different countries, making extrapolation difficult. Bieringer & Garniel, *supra* note 32.

The value of observational studies of presence/absence and diversity also needs to be assessed in context. One would not want to use information about reduced occupancy of a noisy area, for example, as the only indication that noise was having population-level impacts. It is conceivable that, if noise results in increased mortality or decreased reproduction, noisy areas could become population sinks,[39] and a detriment to conservation efforts across the range of the species. But this conclusion would be premature unless the presence/absence data are assessed in the context of other measures of impact, such as breeding success, stress response, startling and other behavioral changes.

So, while observational studies can be and have been helpful in identifying noise as a conservation problem, their policy relevance and value is constrained if they are unable to separate the effects of noise from the many other confounding disturbances that can affect animal densities near roads and other human development. When Fahrig et al.[40] documented reduced densities of frogs and toads near high traffic roads compared to low traffic roads, noise was a potential causal factor. After controlling for other variables, however, their evidence suggested that differences in density more likely reflected varying levels of traffic-associated road mortality.

One way to reduce, though not eliminate, the problem of confounding variables is to compare behaviors and other response variables in the presence and absence of noise. Animals can be observed, for example, before and after noise sources are introduced, or when noise is intermittent. This approach has been used to demonstrate the impact (or lack of impact) of noise from aircraft, machinery, and vehicles on animal behavior and reproductive success.[41] Spatial variation in noise may also allow researchers to control for some confounding factors. One study examined ovenbirds (*Seiurus aurocapilla)* along the edges of clearings containing either compressor stations or gas-producing wells.[42] Both clearings had a similar level of surface disturbance and human activity, but compressors produced high-amplitude noise whereas the wells were relatively quiet. Near compressors, the analysis found reduced pairing success and evidence that the habitat was non-preferred.[43]

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

---

[39] Sinks are areas where successful reproduction is insufficient to maintain the population without immigration. H.R. Pulliam, *Sources, Sinks, and Population Regulation*, 132 AM. NATURALIST 652–661 (1988).

[40] L. Fahrig et al., *Effect of Road Traffic on Amphibian Density*, 73 BIOL. CONS. 177–182 (1995).

[41] Delaney et al., *supra* note 24; D. Hunsaker, J. Rice, & J. Kern, *The Effects of Helicopter Noise on the Reproductive Success of the Coastal California Gnatcatcher*, 122 J. ACOUSTICAL SOC. AM. 3058 (2007); Jennifer W. C. Sun & Peter M. Narins, *Anthropogenic Sounds Differentially Affect Amphibian Call Rate*, 121 BIOL. CONS. 419–427 (2005).

[42] L. Habib, E.M. Bayne, & S. Boutin, *Chronic Industrial Noise Affects Pairing Success and Age Structure of Ovenbirds* Seiurus aurocapilla, 44 J. APPLIED ECOLOGY 176–184 (2007).

[43] Habib et al. found an increased proportion of juveniles in noisy areas, suggesting that the area is undesirable for breeding adults. *Id.*

An additional observational approach is to include noise as a factor in habitat-selection models. These spatially explicit models, typically produced in GIS (Geographic Information Systems), relate species distribution data to information about landscape characteristics in order to determine the impact of disturbance or habitat quality on habitat usage by wildlife.[44] Multiple habitat layers can be added to the model to determine what factors best predict habitat usage. While few studies have incorporated noise into these types of models, GIS layers of noise can readily be created using commercially available and freeware programs. These types of models may be the best option for measuring noise impacts on a large scale and can also be useful in predicting future areas of conflict with human activities.

Ideally, future observational studies encompassing a variety of noise sources, habitats, and species will measure noise exposure levels and then relate observed impacts to noise exposure while controlling for confounding variables. When effects cannot properly be controlled for in a single study design, a second-best choice is to use replicated studies and let statistical modeling separate out the impacts of noise. To date, only a handful of studies follow this approach.[45]

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

### *4.1.2 Estimating the masking potential of noise*

There is a relatively simple technique for addressing possible noise impacts on signal detection. It involves estimating the potential of a noise source to mask communication signals and other important sounds, such as the sounds of predators or prey. Masking occurs when background noise is loud relative to the signal, such that it cannot be detected by the receiver.

The estimation of masking requires knowledge of the physiology and behavior of the organism and the nature of the noise. Masking is frequency-specific, so an acoustic signal will only be masked by the portion of the background noise that is in a similar frequency band as the signal.[46] An

[44] J.B. Dunning et al., *Spatially Explicit Population Models: Current Forms and Future Uses*, 5 ECOLOGICAL APPLICATIONS 3–11 (1995).

[45] Forman, Reineking, & Hersberger, *supra* note 6; Reijnen et al. (1995), *supra* note 29; Reijnen et al. (1996), *supra* note 29; Foppen & Reijnen, *supra* note 34; R. Reijnen & R. Foppen, *The Effects of Car Traffic on Breeding Bird Populations in Woodland. I. Evidence of Reduced Habitat Quality for Willow Warblers (*Phylloscopus trochilus*) Breeding Close to a Highway*, 31 J. APPLIED ECOLOGY 95–101 (1994).

[46] Lohr et al., *supra* note 8; E.A. Brenowitz, *The Active Space of Red-Winged Blackbird Song*, 147 J. COMP. PHYSIOLOGY 511–522 (1982); R.J. Dooling & B. Lohr, *The Role of Hearing in Avian Avoidance of Wind Turbines*, *in* PROC. NAT'L AVIAN-WIND PLANNING MEETING IV 115–134 (S.S. Schwartz ed., for the Avian Subcommittee, National Wind Coordinating Committee, 2001).

estimation of masking requires,[47] first, the audiogram of the focal species;[48] second, the absolute amplitude and frequency spectrum of the noise;[49] third, the absolute amplitude and frequency spectrum of the vocalization or sound of interest; and fourth, the critical ratio for the focal species.[50]

With this information, masking is estimated by determining how introduced noise changes the "active space" of the signal, which is the area around the sender where the signal can be detected by receivers.[51] Intuitively, there is less masking when signals have a different frequency profile than noise, when noise is quiet, when signals are loud and/or when animals are close together when communicating. Conversely, masking is most problematic when signal and noise have similar frequency profiles, when noise is loud, when calls are quiet, and/or when calls are used over large distances.[52]

There are, however, limitations to masking estimations. The method described addresses only the potential impacts of masking animal vocalizations or other sounds and cannot estimate other impacts of noise, such as startling or chronic stress. Further, in the absence of specific information about the auditory physiology and behaviors of the focal species, estimates of masking using this method may be either too conservative or too liberal. Estimates can be too conservative, for example, in situations in which the mere detection of a vocalization is an insufficient basis for extracting necessary information from the sound.[53] Estimates can be too liberal if as part of their communication

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

[47] For detailed methods on calculating masking potential, *see* R.J. Dooling & J.C. Saunders, *Hearing in the Parakeet (*Melopsittacus undulatus*): Absolute Thresholds, Critical Ratios, Frequency Difference Limens, and Vocalizations*, 88 J. COMP. PHYSIOL. 1–20 (1975).

[48] A measure of how hearing sensitivity varies with the frequency of the sound. In general, birds do not hear as well as mammals in very low or high frequencies, or use them to communicate. Dooling & Popper, *supra* note 1.

[49] A measure of how much energy is present in each frequency band of the sound.

[50] This is the difference in amplitude between signal and noise necessary for detection of the signal. For a generalized bird, the critical threshold ranges from approximately 26 to 28 dB between 2 and 3 kHz, meaning that a typical bird cannot hear a 2–3 kHz vocalization unless the vocalization exceeds the background noise in that frequency range by 26–28 dB. In general, birds have higher critical ratios than mammals, making them worse at discriminating signals in noise. If measurements for these parameters are not available for the focal species, then information from closely related species may be used as a substitute. However, this may be misleading if the species of interest has particularly strong or poor hearing capabilities relative to the substitute species. Dooling & Popper, *supra* note 1; Lohr et al., *supra* note 8; Dooling & Saunders, *supra* note 45.

[51] Lohr et al., *supra* note 5; Brenowitz, *supra* note 39.

[52] Lohr et al., *supra* note 5; Bee & Swanson, *supra* note 15; G. Ehret & H.C. Gerhardt, *Auditory Masking and Effects of Noise on Responses of the Green Treefrog (*Hyla cinerea*) to Synthetic Mating Calls*, 141 J. COMP. PHYSIOL. A 13–18 (1980); T. Aubin & P. Jouventin, *Cocktail-Party Effect in King Penguin Colonies* 265 PROC. R. SOC. B 1665–1673 (1998).

[53] This would happen when humans can detect human voices, but not discriminate the identity of the speaker or the words being said. *See* Lohr et al., *supra* note 5, for a discussion of the difference between detection and discrimination.

animals use spatial cues,[54] co-modulation of frequencies,[55] or adjust their vocalizations to reduce masking.[56]

Because so many factors affect the degree of masking, there is a critical need for additional field studies to validate estimation techniques. The available work relating the potential for masking to observed individual- and population-level impacts[57] is just not a sufficient basis for knowing whether masking potential is a reliable predictor of how noise will impact wildlife. If the predictive power of measuring masking potential can be shown, researchers will then have a low-cost tool for predicting impacts in species about which little is known. Otherwise, masking analysis is most informative when used in concert with field studies that assess actual noise impacts. If a disruption of communication or decreased rates of prey capture in noisy areas can be demonstrated, then an analysis of the masking potential of a new noise source could be used to determine the area over which individuals are likely to be affected by that new source.[58]

### 4.2 The Experimental Approach

Experimental manipulations of noise in the laboratory and the field are more powerful than observational studies in isolating the effects of noise and identifying the underlying causes of noise impacts because they deal more effectively with the problem of controlling for confounding variables. The following sections discuss their advantages and limitations.

#### *4.2.1. Laboratory experiments*

Laboratory studies introduce noise to captive animals and measure the impacts in a controlled environment. Studies using captive animals are the basis for much of what we know about the hearing range and sensitivity of a number of animal taxa[59] and about the ability of animals to detect and

[54] The ability to hear sounds is improved if they are separated spatially. M. Ebata, T. Sone, & T. Nimura, *Improvement of Hearing Ability by Directional Information*, 43 J. ACOUSTICAL SOC. AM. 289–297 (1968); J.J. Schwartz & H.C. Gerhardt, *Spatially Mediated Release From Auditory Masking in an Anuran Amphibian*, 166 J. COMP. PHYSIOL. A 37–41 (1989).

[55] Masking is reduced when the noise has amplitude modulation patterns that make it distinct from the signal. G.M. Klump & U. Langemann, *Co-Modulation Masking Release in a Songbird*, 87 HEARING RES. 157–164 (1995).

[56] Patricelli & Blickley, *supra* note 10; Rabin & Greene, *supra* note 10; Warren et al., *supra* note 10; Slabbekoorn & Peet, *supra* note 17.

[57] Rheindt, *supra* note 18.

[58] Lohr et al., *supra* note 8.

[59] Dooling & Saunders, *supra* note 45; K. Okanoya & Robert F. Dooling, *Hearing in the Swamp Sparrow,* Melospiza georgiana, *and the Song Sparrow,* Melospiza melodia, 36 ANIMAL BEHAV. 726–732 (1988); H.E. Heffner et al., *Audiogram of the Hooded Norway Rat*, 73 HEARING RES. 244–247 (1994); H.E. Heffner & R.S. Heffner, *Hearing Ranges of Laboratory Animals*, 46 J. AM. ASS'N LABORATORY ANIMAL SCI. 20–22 (2007).

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

discriminate sounds in the presence of background noise.[60] These psychoacoustic studies are critical for assessing masking potential, and provide a physiological and morphological basis for predicting which species are most likely to be impacted by introduced noise.[61] Laboratory studies also provide insight into the physiological and behavioral impacts of noise, and the potential consequences of masking for breeding individuals.[62] As noted earlier, they demonstrate impacts on pair-bonding[63] and the amplitude at which vocalizations are produced.[64] They do not address, however, the long-term consequences of these behavioral changes, which remain unclear and need further study both in the laboratory and in the field.

Traditionally, psychoacoustic studies use white noise or pure tones to measure hearing ability and noise effects.[65] Recent studies also address the effects of anthropogenic noise directly, increasing their relevance to conservation. Lohr and colleagues, for example, measured the masked thresholds of natural contact calls for budgerigars (*Melopsittacus undulates)* and zebra finches, in the lab using simulated traffic noise, allowing them to predict how traffic noise affects the distance at which vocalizations can be detected by receivers.[66]

The environmental control that gives laboratory studies their analytic power can also be a disadvantage, if there is reason to believe that the response of animals to noise in a laboratory setting will be different from that of animals in the wild, where natural variations in the environment and in animal populations can affect the impact of noise. When increased physiological stress from noise is experienced, for example, in combination with habitat loss, synergistic effects on animals will magnify the overall impact of development.

Laboratory studies also must be careful not to extrapolate findings from animals that thrive in captivity to endangered animals, particularly since the

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

---

[60] Lohr et al., *supra* note 8; Dooling & Saunders, *supra* note 45; Klump & Langemann, *supra* note 53; L. Wollerman, *Acoustic Interference Limits Call Detection in a Neotropical frog* Hyla ebraccata, 57 ANIMAL BEHAV. 529–536 (1999).

[61] Dooling & Popper, *supra* note 1.

[62] Marler et al., *supra* note 14; Ryals et al., *supra* note 14; J. Syka & N. Rybalko, *Threshold Shifts and Enhancement of Cortical Evoked Responses After Noise Exposure in Rats*, 139 HEARING RES. 59–68 (2000); D. Robertson & B.M. Johnstone, *Acoustic Trauma in the Guinea Pig Cochlea: Early Changes in Ultrastructure and Neural Threshold*, 3 HEARING RES. 167–179 (1980).

[63] Swaddle & Page, *supra* note 19.

[64] J. Cynx, et al., *Amplitude Regulation of Vocalizations in Noise by a Songbird*, Taeniopygia guttata, 56 ANIMAL BEHAV. 107–113 (1998); Marty L. Leonard & Andrew G. Horn, *Ambient Noise and the Design of Begging Signals*, 272 PROC. R. SOC. B 651–656 (2005). This finding has been corroborated with studies of birds in the field in Brumm, *supra* note 18.

[65] Dooling & Saunders, *supra* note 45; Klump & Langemann, *supra* note 53; Wollerman, *supra* note 53; J.B. Allen & S.T. Neely, *Modeling the Relation between the Intensity Just-Noticeable Difference and Loudness for Pure Tones and Wideband Noise*, 102 J. ACOUSTICAL SOC. AM. 3628–3646 (1997).

[66] Lohr et al., *supra* note 8. For other studies that introduce anthropogenic noise, see Weisenberger et al., *supra* note 7; Bee & Swanson, *supra* note 18.

animals chosen for laboratory study are often domesticated or otherwise show tolerance for human disturbance. Endangered animals, by contrast, are often driven to rarity due to their inability to tolerate environmental change, which may include sensitivity to noise.[67] The use of surrogate species would be unnecessary if the species of concern could be tested in the lab for noise response. But small population sizes and narrow tolerances often make it impossible to bring threatened or endangered species into the lab for such tests.

The use of anthropogenic noise in laboratory studies of noise effects, particularly noise that is likely to be affecting wild animals, increases the conservation applicability of such research and should be a future priority. Laboratory experiments must also be supplemented with field studies and other methods to fully understand the impacts of noise on wildlife.

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

### *4.2.2. Noise introduction experiments in the field*

Field experiments are another method for isolating and quantifying the impacts of noise on animals under natural conditions. The controlled introduction of noise can be accomplished either by creating noise in the field or by playing back the associated noise through speakers. The first approach has been used to investigate the impacts on wildlife of aircraft, machinery, and vehicles.[68] As is the case with observational studies, interpretations of this type of research are complicated by the problem of controlling for confounding variables, such as the visual and other disturbances, in addition to noise, associated with many sorts of environmental change. Compared to observational studies, however, field experiments offer greater opportunities to examine interactions among multiple associated stressors. They are also generally a more efficient use of scarce research resources and provide the ability to control for (or examine) seasonal effects, time-of-day effects, and other factors influencing responses to noise.

The second experimental approach, playing back noise that has been recorded from a source of interest or synthesized to match that source,[69] has the advantage that noise effects can be easily separated from other aspects of disturbance. Because noise introduction on a large spatial and temporal scale is logistically challenging in natural habitats, studies to date have been short-term and relatively small in scale. A short-term experiment may be appropriate

[67] T. Caro, J. Eadie, & A. Sih, *Use of Substitute Species in Conservation Biology*, 19 CONS. BIOL. 1821–1826 (2005).

[68] Delaney, et al., *supra* note 24; P. R. Krausman, et al., *Effects of Jet Aircraft on Mountain Sheep*, 62 J. WILDLIFE MGMT. 1246–1254 (1998); A. Frid, *Dall's Sheep Responses to Overflights by Helicopter and Fixed-Wing Aircraft*, 110 BIOL. CONS. 387–399 (2003).

[69] Sun & Narins, *supra* note 39; A.L. Brown, *Measuring the Effect of Aircraft Noise on Sea Birds*, 16 ENV'T INT'L 587–592 (1990).

for studying dynamic behaviors, such as call rate, startling, or avoidance,[70] but cannot address the longer-term individual- or population-level consequences of noise.

To illustrate study design for a long-term and large-scale noise introduction experiment, we describe our ongoing experiment in Wyoming, addressing the noise impacts of energy development on greater sage-grouse.

#### *4.2.2.1 Noise impacts on sage-grouse: A long-term field experiment*

Populations of this species are declining throughout their range in the interior West of the United States,[71] enough to merit consideration for listing under the federal Endangered Species Act. Coal-bed methane (CBM) and deep natural gas extraction are increasing rapidly in sage-grouse habitats, and recent studies document dramatic declines in sage-grouse populations in areas of energy development.[72] However, incomplete knowledge of the causes of these declines is hampering the creation of effective management strategies.

Among the number of disturbances associated with energy development that impact sage-grouse, noise is particularly problematic in breeding areas downwind of development when it causes declines in male attendance, although attendance was not affected by visual disturbance from development.[73] In addition, the life history of sage-grouse makes them particularly vulnerable to disturbance from noise pollution. In the breeding season, males gather on communal breeding grounds (leks) to perform complex acoustic displays, used by females to locate leks and choose mates. The risk is that anthropogenic noise in sage-grouse habitat masks male vocalizations and interferes with reproduction. While there are rules governing the noise emitted during drilling of natural gas wells, exemptions are often granted and there has been little research demonstrating that stipulated noise levels reduce the impacts of development on sage-grouse, as well as other sensitive species.

Our multi-year, noise-introduction experiment on sage-grouse leks in an otherwise undisturbed area tries to separate the impacts of noise from other potential impacts of energy development. Two types of noise are of

[70] Weisenberger et al., *supra* note 7; Sun & Narins, *supra* note 39; Leonard & Horn, *supra* note 62; Brown, *supra* note 67.

[71] J.W. Connelly et al., Conservation Assessment of Greater Sage-Grouse and Sagebrush Habitats, Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming, 2004. Copy online at http://www.ndow.org/wild/conservation/sg/resources/greate_sg_cons_assessment.pdf

[72] M.J. Holloran, Greater Sage-Grouse (*Centrocercus urophasianus*) Population Response to Natural Gas Field Development in Western Wyoming (2005) (unpublished Ph.D. dissertation, University of Wyoming) (accessible online from http://www.sagebrushsea.org/th_energy_sage_grouse_study2.htm); Brett L. Walker et al., *Greater Sage-Grouse Population Response to Energy Development and Habitat Loss*, 71 J. WILDLIFE MGMT. (2007); Dooling & Popper, *supra* note 1.

[73] Other factors at work include habitat loss, fragmentation, dust, air pollution, and West Nile virus. Connelly et al, *supra* note 64; Holloran, *supra* note 70; D.E. Naugle et al., *West Nile Virus: Pending Crisis for Greater Sage-Grouse*, 7 ECOLOGY LETTERS 704–713 (2004).

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

primary interest, road noise and drilling noise. Both types are dominated by low frequencies, but drilling noise is high intensity, continuous noise, whereas road noise is intermittent with gradual increases and decreases in amplitude. Monitored leks are divided into pairs of control leks and leks with experimentally introduced noise.[74] Ideally, noise would be introduced at different levels on different leks to determine the noise threshold at which an impact can be observed. However, such a "dose-response" experiment would require a large sample of leks and that is logistically infeasible. The experiment, instead, creates a noise gradient across each lek, so that the effect of noise level on microhabitat use and behavior can be measured and noise-tolerance thresholds estimated.

This experimental approach isolates and makes it possible to assess the impacts of noise on lekking sage-grouse at both the individual and population levels. The individual effects are analyzed from audio and video recordings, to determine whether individuals change the rate, frequency structure, and amplitude of their displays in the presence of noise, as has been found in other species.[75] A non-invasive technique compares the relative stress levels of birds on experimental and control leks through analysis of stress hormones in feces.[76] Population-levels effects of noise derive from comparison of lek attendance patterns on experimental and control leks over multiple seasons. This allows detection of noise impacts while controlling for natural variations in behavior, physiology, and larger-scale fluctuations in the population.

Although introducing noise in the wild is a powerful tool for measuring noise impacts on animals, it is only appropriate in certain circumstances. Noise introduction requires access, for example, to a population of animals residing in a relatively undisturbed area. Such a population may be unavailable in some species of concern, or the species may be too sensitive or rare to risk such an experimental manipulation. In addition, animals must be at fairly high densities in order to collect sufficient data for analysis, because it is difficult to create a noise disturbance over a large area using speakers.[77] During the breeding season, noise introduction can rely on battery-powered speakers, because leks are relatively small and have a high density of birds. This same

[74] Paired leks have similar size and location and are visited by researchers for counts on the same days. Noise is introduced at 70 dBF SPL (unweighted decibels) at 16 meters using three to four battery-powered outdoor speakers. This is similar to noise levels measured at $\frac{1}{4}$-mile from drilling rigs and main haul roads in Pinedale, Wyoming. Control leks have dummy speakers and are visited for "battery changes" with the same frequency as experimental leks.

[75] Patricelli & Blickley, *supra* note 13; Warren et al., *supra* note 13; Rabin et al., *supra* note 13; Rabin & Greene, *supra* note 13; Slabbekoorn & Peet, *supra* note 20.

[76] *See, e.g.*, Wasser et al., *supra* note 27.

[77] Most anthropogenic noise sources are very large, and it is extremely difficult to replicate loud noise over a large area from small speakers, since amplitude (and thus propagation) is limited by source size. This challenge is even greater when speakers are powered by batteries in remote field locations.

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

approach is less able, however, to address noise impacts on nesting or overwintering behaviors, when sage-grouse are more dispersed.

In some situations, the use of semi-captive populations reaps some of the benefits of both field and laboratory studies, by increasing animal density in a more natural setting than is afforded by laboratory animal colonies. This approach is outside the scope of our current study. Another limitation of the experimental approach is that it underestimates (or even misses) the impacts of noise that occur in interaction with other forms of disturbance, such as the combination of noise pollution with an increase of raptor perches in energy development areas.[78] The combined effects will be larger than that attributable to either disturbance alone, but they can only be examined in observational studies and noise-source introduction experiments. This highlights, again, the need for multiple research approaches to measuring wildlife noise impacts.

There are very few experimental studies that use either noise-source introductions or noise playbacks, even though these experimental tools, used in a field setting or in naturalistic captive settings, are among the most powerful for understanding noise impacts on wild populations. Large-scale field experiments are expensive and logistically challenging. They do, however, appear to be warranted, particularly when observational studies and measurements of masking potential suggest a likely role for noise in impacting wild animals. Future field research should also focus on validating results and methods from laboratory studies, thus increasing the ability to apply lab studies and estimates of masking potential to the development of effective mitigation measures and predictions about the impacts future development is likely to have on wildlife.

## 5. FUTURE DIRECTIONS AND POLICY RELEVANCE

Even though the rapid spread of human development and associated anthropogenic noise have impacts on wildlife, it is not always logistically, politically, or economically feasible to eliminate or even minimize noise. The more common policy approach is to set noise standards, in the hope of limiting the levels of noise that development produces. The production of noise can then be reduced structurally[79] or operationally[80] to meet these standards. Road noise, for example, can be reduced through the use of certain types of asphalt, although these road surfaces can also have lower durability, lower traction, and higher cost than noisier varieties. Road noise can also be decreased by noise barriers, but these may cut off migration routes and exacerbate rather than

[78] Connelly et al., *supra* note 69.

[79] Noise can be reduced structurally by using alternative materials and architecture, such as noise barriers, to reduce sound production and propagation.

[80] Noise can be reduced operationally through limitations on the timing and frequency of noisy activities, for example, by avoiding shift changes that occur at 7:00 a.m., in the peak lekking hours of sage-grouse.

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

reduce overall road impacts.[81] Regulations necessarily balance the economic and environmental trade-offs involved in allowing development to proceed and as a general rule the more information that can be brought to bear on this balancing process the better.

There can be no doubt that the first priority in the development of most current noise standards is the protection of human welfare. They use human criteria of disturbance, generated primarily in areas where humans are impacted.[82] These standards protect animal species with noise tolerances and distributions similar to those of humans. They are not effective, however, in reducing the impacts of noise on sensitive species of wildlife. So what should be our goal in the development of effective noise standards for the protection of wildlife? Environmental managers typically prefer a single noise standard that covers all situations. But since species differ in their ability to tolerate noise, a single noise standard is bound to be conservative for some species and insufficient for others. [83] Simply erring on the side of more conservative standards could do more harm than good in cases where it diverts money from more appropriate types of mitigation, and when noise mitigation measures introduce other environmental and economic costs, as discussed above. Rather than a single standard, a set of standards is needed, based on the measured sensitivities of indicator species and species of concern in a particular habitat type or location. Recently, a panel of experts developed a set of general and species-specific recommendations for marine mammal noise exposure criteria.[84] The development of such a set of standards for terrestrial species will require information about sensitivity to noise pollution in both abundant and rare species; the research priorities outlined here will help to achieve this goal.

Downloaded By: [CDL Journals Account] At: 02:49 3 February 2011

[81] Forman, Reineking, and Hersberger, *supra* note 6.

[82] Dooling & Popper, *supra* note 1; SINGAL, *supra* note 9.

[83] A single noise standard, for example, might establish a maximum acceptable noise level of 49 dBA at a one quarter mile from a noise source.

[84] B.L. Southall, A.E. Bowles, & W.T. Ellison, *Marine Mammal Noise Exposure Criteria: Initial Scientific Recommendations*, 125 J. ACOUSTICAL SOC. AM. 2517 (2009). There is no equivalent set of recommendations for terrestrial animals.



*Ornithological Monographs*
Volume (2012), No. 74, 23–35
© The American Ornithologists' Union, 2012.
Printed in USA.

# CHAPTER 3
# POTENTIAL ACOUSTIC MASKING OF GREATER SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*) DISPLAY COMPONENTS BY CHRONIC INDUSTRIAL NOISE

Jessica L. Blickley[1] and Gail L. Patricelli

*Department of Evolution and Ecology, University of California-Davis, One Shields Avenue, Davis, California, USA*

Abstract.—Anthropogenic noise can limit the ability of birds to communicate by masking their acoustic signals. Masking, which reduces the distance over which the signal can be perceived by a receiver, is frequency dependent, so the different notes of a single song may be masked to different degrees. We analyzed the individual notes of mating vocalizations produced by Greater Sage-Grouse (*Centrocercus urophasianus*) and noise from natural gas infrastructure to quantify the potential for such noise to mask Greater Sage-Grouse vocalizations over both long and short distances. We found that noise produced by natural gas infrastructure was dominated by low frequencies, with substantial overlap in frequency with Greater Sage-Grouse acoustic displays. Such overlap predicted substantial masking, reducing the active space of detection and discrimination of all vocalization components, and particularly affecting low-frequency and low-amplitude notes. Such masking could increase the difficulty of mate assessment for lekking Greater Sage-Grouse. We discuss these results in relation to current stipulations that limit the proximity of natural gas infrastructure to leks of this species on some federal lands in the United States. Significant impacts to Greater Sage-Grouse populations have been measured at noise levels that predict little or no masking. Thus, masking is not likely to be the only mechanism of noise impact on this species, and masking analyses should therefore be used in combination with other methods to evaluate stipulations and predict the effects of noise exposure.

Key words: acoustic masking, *Centrocercus urophasianus*, Greater Sage-Grouse, industrial noise.

**Enmascaramiento Acústico Potencial de Mayor Sage-Grouse (*Centrocercus urophasianus*) Mostrar Componentes por Ruido Industrial Crónica**

Resumen.— Antropógena ruido puede limitar la capacidad de las aves para comunicarse por enmascarar sus señales acústicas. Enmascaramiento, que reduce la distancia sobre la que se puede percibir la señal por un receptor, es frecuencia dependiente, por lo que las diferentes notas de una canción pueden enmascararse en diferentes grados. Analizamos las notas individuales de apareamiento vocalizaciones producidas por mayor Sage-Grouse (Centrocercus urophasianus) y el ruido de infraestructura de gas natural para cuantificar el potencial de tal ruido a vocalizaciones de mayor Sage-urogallo de máscara en distancias cortas y largas. Hemos encontrado que ruido producido por la infraestructura de gas natural fue dominado por las frecuencias bajas, con considerable superposición en frecuencia con pantallas acústicas de mayor Sage-urogallo. Tal superposición predijo enmascaramiento sustancial, reduciendo el espacio activo de detección y discriminación de todos los componentes de vocalización y que afectan particularmente a notas de baja frecuencia y baja amplitud. Estas máscaras podrían aumentar la dificultad de evaluación de mate para lekking mayor Sage-urogallo. Analizaremos estos resultados en relación con las actuales disposiciones que limitan la proximidad de la infraestructura de gas natural a leks de esta especie en algunas tierras federales en los Estados Unidos. Impactos

[1]E-mail: jlblickley@ucdavis.edu

*Ornithological Monographs,* Number 74, pages 23–35. ISBN: 978-0-943610-93-1. © 2012 by The American Ornithologists' Union. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp. DOI: 10.1525/om.2011.74.1.23.

significativos a las poblaciones de mayor Sage-urogallo han sido medidos en los niveles de ruido que predicen el enmascaramiento de poca o ninguna. Así, enmascaramiento no es probable que sea el único mecanismo de impacto de ruido en esta especie, y enmascaramiento análisis debe por lo tanto, utilizarse en combinación con otros métodos para evaluar las estipulaciones y predecir los efectos de la exposición al ruido. Así, enmascaramiento no es probable que sea el único mecanismo de impacto de ruido en esta especie, y enmascaramiento análisis debe por lo tanto, utilizarse en combinación con otros métodos para evaluar las estipulaciones y predecir los efectos de la exposición al ruido.

Birds use acoustic signals to communicate with conspecifics for a host of biologically important functions, including mate attraction, territory defense, parent–offspring communication, and predator avoidance. In order for this communication to be successful, the signal must travel from the signaler to the receiver through the local environment. The local physical and acoustic environment, therefore, plays an important role in determining the active space of a signal, the area in which a receiver can successfully perceive it (Brenowitz 1982, Dooling et al. 2009). Background noise, a conspicuous feature of most natural environments, can result in acoustic masking if this noise is loud in relation to the signal of interest. Animals have numerous acoustic and behavioral adaptations to maximize the active space of their signals in the presence of natural background noise. For example, the structural and temporal properties of many acoustic signals appear to be adapted to maximize the propagation distance and minimize masking from abiotic and biotic noise sources in the environment (Marten and Marler 1977, Wiley and Richards 1982, Ryan and Brenowitz 1985, Brumm 2006). However, the spread of humans into natural landscapes has resulted in the proliferation of anthropogenic noise sources, with the potential to affect many of the animal species that live and communicate in these environments (Barber et al. 2010). Acoustic signals that are adapted to deal with natural noise sources may still be susceptible to masking from anthropogenic noise sources if the anthropogenic noise differs enough from natural noise sources in frequency, duration, or daily or seasonal pattern.

Effective communication requires that a receiver be able to detect a given signal, discriminate that signal from other possible signals, and recognize features that may convey information about the specific signaler. The active space of a signal may be different for each of these receiver tasks (Lohr et al. 2003). Detection provides the receiver with the lowest level of information—simply that a signal is present—and requires the lowest contrast between the signal and background noise. For a signal to be successfully detected in a noisy environment requires that the ratio of the signal to the background noise (i.e., signal-to-noise ratio [SNR], the difference between signal and noise amplitudes measured in decibels) within a frequency band exceed a critical detection threshold (Klump 1996). The critical detection threshold for a "typical bird" ranges from 18 dB to 37 dB across frequency bands. Discrimination of the signal from other signals, as would be required to identify the species of the sender or the functional category of the signal, requires a higher SNR than detection. In a laboratory study of two bird species, Lohr et al. (2003) found that discrimination of conspecific song required an SNR approximately 3 dB higher than the levels required for detection. An even more challenging task for a receiver is signal recognition, discerning variation among signals within a category, such as information about individual identity or reproductive quality. For example, receivers may use the acoustic features of the signal such as frequency structure, relative amplitude of notes, and note duration to recognize the identity of the signaling individual. Signal recognition may require an even higher SNR (Dooling and Popper 2007); however, we do not yet know how much higher the signal must be for recognition to occur.

The fitness consequences of being able to detect a signal versus discriminate or recognize a signal is likely to be signal specific. For example, a predator alert call, which functions to alert a conspecific to danger, may be effective so long as it exceeds the critical ratio for detection. However, a mate-attraction call that is used by females to assess the quality of a potential mate may need to exceed the critical recognition threshold in order to be effective. For example, the ability to recognize individual signals is critical to mate choice in the Swamp Sparrow (*Melospiza georgiana*): females use song features such as trill rate and frequency bandwidth to assess the quality of potential mates (Ballentine et al. 2004). Introduced

noise has been demonstrated to weaken pair bonds in captive Zebra Finches (*Taeniopygia guttata*; Swaddle and Page 2007), which suggests that reduced recognition can have fitness consequences.

Active space can vary within a given signal as well as among signals. Many bird vocalizations are highly complex and are composed of multiple acoustic components (bouts, phrases, syllables, or notes). Some multicomponent signals may encode either distinct ("multiple messages hypothesis") or redundant ("redundancy hypothesis") information about the signaler (Møller and Pomiankowski 1993, Hebets and Papaj 2005). For example, the trill note and note complex of White-crowned Sparrow (*Zonotrichia leucophrys*) song each convey distinct information about dialect and individual identity, respectively (Nelson and Poesel 2007). Each component can vary in frequency structure, duration, and relative amplitude; these factors interact with the local physical and acoustic environment to determine the active space of the signal component (Patricelli et al. 2008). The result of this variation is that each component of a complex vocalization may have a different active space and be uniquely susceptible to masking by a given noise source.

Anthropogenic noise is typically dominated by low frequencies, so low-frequency signal components and features are most susceptible to masking (Brumm and Slabbekoorn 2005, Slabbekoorn and Ripmeester 2008). Even if a signal is not completely masked, low-frequency background noise could distort a signal, resulting in a higher-frequency note being perceived as having higher relative amplitude than a masked lower-frequency note. Such distortion could result in increased difficulty in assessment or identification.

Our focal species, the Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-gouse"), is a medium-bodied gallinaceous bird that has long been used as a model system for studies of sexual selection and communication (Wiley 1973; Gibson 1989, 1996). During the breeding season, males gather on strutting grounds (leks) where they establish small display territories that are visited by females for courtship. Males produce a complex visual and acoustic display. Sound is critical to the breeding system on both large and small spatial scales because females use the acoustic component of the display to locate strutting males and, once on a lek, to select a male (Gibson 1989, 1996; Patricelli and Krakauer 2010).

The sage-grouse vocal display is composed of three major note types: a series of low-frequency "coo" notes, two broadband "pops," and a frequency-modulated "whistle" (Fig. 1). The rate of display (strut rate) is positively correlated with male success in mating (Gibson and Bradbury 1985, Gibson 1996, Patricelli and Krakauer 2010). In addition, the time interval between the two pop notes during which the whistle note occurs, the inter-pop interval (IPI), is positively correlated with mating success (Gibson et al. 1991, Gibson 1996). This suggests that assessment of the two pop notes might be particularly critical in female mating decisions. Whistles may also be important in female choice. Gibson and Bradbury (1985) found that the time interval from the first pop to the whistle peak as well as the maximum frequency of the whistle at the apex are related to male mating success. Female sage-grouse also may assess amplitude of the whistle; unpublished results suggest that whistle amplitude may be positively correlated with mating success (J. W. Bradbury pers. comm.), and males orient during courtship so that the highly directional whistle is beamed toward females (Dantzker et al. 1999). This female preference for male-display quantity

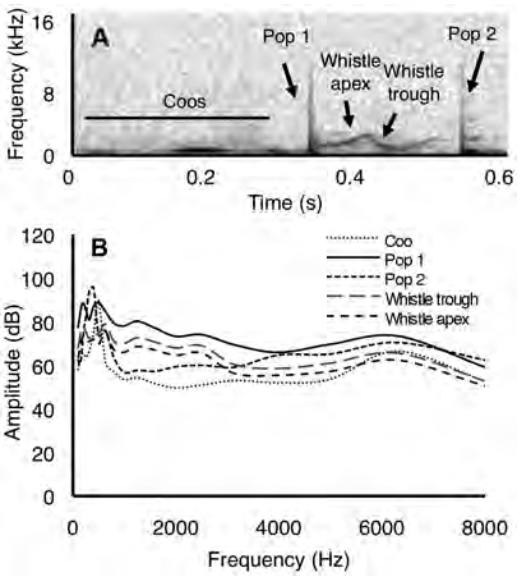



Fig. 1. Spectrogram and (B) power spectra of a male Greater Sage-Grouse strut display with distinct display components labeled. Low-frequency coos are followed by a broadband pop (pop 1), a frequency-modulated whistle with an apex of ~2,500 Hz (whistle apex) and a minimum of ~630 Hz (whistle trough), and another broadband pop (pop 2).

and quality suggests that masking of one or all of these notes by background noise may negatively affect a female's ability to assess males on the lek.

Sage-grouse populations are declining across their range (Connelly et al. 2004, Garton et al. 2011), leading sage-grouse to be listed as endangered under Canada's Species at Risk Act and designated as a candidate species for listing in the United States under the federal Endangered Species Act. Natural gas development has expanded rapidly over the past decade and has been implicated in contributing to population declines (Holloran 2005, Walker et al. 2007, Copeland et al. 2009, Holloran et al. 2010). In particular, noise associated with energy development has been demonstrated to result in reduced attendance on leks (Blickley et al. 2012) and is associated with increased stress hormones in males on noisy leks (J. L. Blickley and G. L. Patricelli unpubl. data). Masked communication has been suggested as a mechanism of this impact, so understanding the potential for introduced noise sources to mask signals used in mating could lead to improved management of vulnerable sage-grouse populations.

The present study addresses the potential for noise pollution from natural gas development to mask or distort acoustic signals that are used in breeding by sage-grouse. We analyzed the individual acoustic components of sage-grouse vocalizations (Fig. 1) and noise from natural gas infrastructure (a compressor station, generator, and drilling rig; Fig. 2) to quantify the potential for such noise to mask sage-grouse vocalizations over both long and short distances. We compared the effect of such noise on the level of both detection and discrimination and discuss the utility of this approach for predicting the impacts of noise on this and other species. For the masking analysis, we focused primarily on noise measurements at 75 m and 400 m (~1/4 mile), which represent a typical distance to the edge of surface disturbance (the pad) from a compressor station or drilling rig and the distance stipulated as the minimum surface-disturbance buffer around leks in our study region, respectively (Bureau of Land Management 2008).

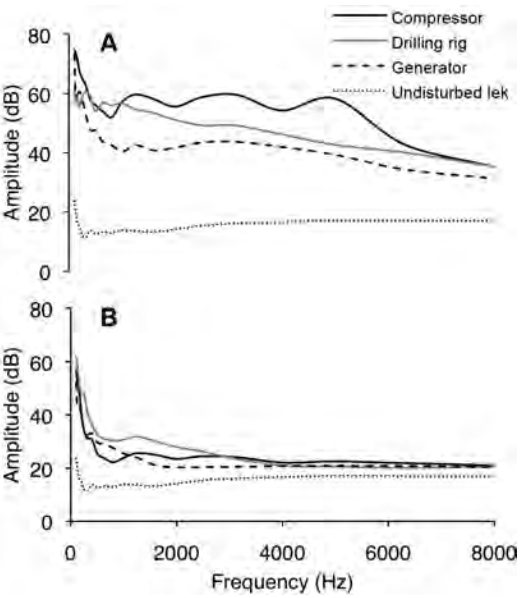



FIG. 2. Power spectra of ambient noise levels at (A) 75 m and (B) 400 m from a natural gas compressor station, natural gas drilling rig, and generator in Sublette County, Wyoming, and on an undisturbed lek (quiet) in Fremont County, Wyoming. Values were interpolated if a measurement for that distance was not available. Noise was dominated by low frequencies at both short and medium distances from the source.

## METHODS

*Field recordings and measurements*.—Between 1 and 5 May 2010, we collected field recordings and vocal amplitude measurements from adult male sage-grouse on Preacher Reservoir lek (42°53.597′N, 108°28.417′W) in Fremont County, Wyoming. Recordings and amplitude measurements were collected simultaneously from a blind on the lek using a handheld Larson Davis 824 sound level meter (software version 3.12) using the logging function with a time-history resolution of 1/32 s and an amplitude resolution of 0.1 dB. A Marantz PMD670 portable solid-state recorder continuously recorded the audio stream from the SPL meter (through the AC/DC output) at 16-bit linear PCM format at 44.1 kHz. Each sound level measurement started prior to the initiation of a display by an individual male. The SPL meter measured and logged the average and peak amplitude in unweighted decibels (dB) at each time interval (0.03 s). Immediately after the vocalization was recorded, the distance between the vocalizing bird and the microphone was measured with a range finder (Leupold RX750). Sage-grouse strut displays are highly directional (Dantzker et al. 1999), so the orientation of the bird and distance to the microphone were also noted for each display measured. We used only high-quality and comparable measurements

in the analysis, including only vocalizations that we recorded from individuals in a small range of orientations and at similar distances in relation to the microphone. All vocalizations included in the analysis were from individuals with side-facing orientations ranging from 30 to 90 degrees (if zero degrees reflects an orientation with the bird directly facing the observer). We did not use recordings if there was temporal overlap with other strutting males or background noises, such as songbirds. Because of the difficulty of obtaining such recordings, a total of only 6 vocalizations, collected from 2 individuals (2 from one male, 4 from the other), were used in the final analysis.

Ambient noise levels were measured on Chugwater Reservoir lek (42°47.192′N, 108°26.292′W), a lek with little human disturbance in Fremont County, Wyoming. Noise was quantified as a 2-min $L_{eq}$ (equivalent sound pressure level); this is a type of average, defined as the equivalent steady sound level that would produce the energetic equivalent of the actual fluctuating sound levels over the defined 2-min period. The sound level meter calculated an overall $L_{eq}$ for the noise level as well as the 2-min $L_{eq}$ for each 1/3-octave band frequency, which was used for SNR analysis (see below). Ambient measurements were made after lekking in the morning. Ambient noise levels tend to be slightly higher during this time than during the lekking hours (J. L. Blickley and G. L. Patricelli unpubl. data), so this measure is a slight overestimate of ambient levels on an undisturbed lek, leading to a slight underestimate of masking on disturbed leks.

Sound level measurements were made on a large compressor station (Falcon Compressor, which consisted of two Ariel JGC-4 compressors driven by 3,500-HP engines; 42°31.319′N, 109°40.271′W) and a deep natural-gas drilling rig (Questar Drilling Rig no. 232; 42°43.501′N, 109°50.876′W) on the Pinedale Anticline Project Area in Sublette County, Wyoming, and at a generator (East Litton Generator, a 300-kW MQ Power diesel generator powered by a Volvo engine; 43°31.501′N, 105°25.573′W) in the Powder River Basin, Campbell County, Wyoming. These noise sources are all commonly found in areas of natural gas development and typically operate 24 h day–1, year round. Noise was measured along one transect extending from each noise source. Noise measurements were taken at points 75, 200, 300, and 400 m from the Falcon Compressor; at points 8, 16, 32, 64, 128, 256, and 512 m from the East Litton Generator; and at points 75 and 400 m from the Questar Drilling Rig. At each point, distance from the source was measured with a laser range finder (Bushnell Yardage Pro). Noise levels were measured using a Larson Davis 824 sound level meter. During measurements, the sound level meter was held 25 cm from the ground, similar to the height of a grouse. The sound level meter calculated an overall $L_{eq}$ for the noise level as well as the 2-min $L_{eq}$ for each 1/3-octave band frequency. Noise levels are reported in unweighted decibels (reported as dB) re 20 μPa because an unweighted measure of amplitude is required for the estimation of masking potential; A-weighted values (dB[A]) are also presented for comparison. All noise measurements were made in the early morning, before the wind rose to detectable levels. Because of the similarity of noise from each of these sources (see Fig. 2), only noise measurements from the Falcon Compressor were used in the masking analysis; results from other noise sources should be very similar. Noise levels were estimated at distances >400 m from Falcon Compressor using NMSIM software (Wyle Laboratories, Arlington, Virginia). NMSIM generates spatially explicit estimates of noise propagation utilizing input topography, ground impedance, and source spectra. We developed a custom source spectrum for Falcon Compressor using noise measurements from transect data and modeled propagation from the source across flat and open ground using a topographic layer from a location at similar elevation to our study site at 200 rayls ground impedance and –1.1°C air temperature. We used NMSim to estimate the noise spectra at receiver points placed along a transect extending from the source.

*Sound analysis*.—Individual vocalizations were identified from a spectrogram of the field recording using RAVEN, version 1.3 beta (Cornell Lab of Ornithology, Ithaca, New York; Hann window function, FFT = 512 with 50% overlap). Audio recordings were synchronized with SPL measurements by identifying distinctive high-frequency device noise produced by the SPL meter with the initiation of the measurement; this allowed us to identify the 1/32-s sample(s) in the SPL-meter output that corresponds to each note on the spectrogram and measure the overall amplitude of that note. Each vocalization was then extracted and low-pass filtered at 8.0 KHz to exclude this device noise. For each vocalization, the amplitude of the 1/3-octave band frequencies was

measured at intervals of 0.004 s using SPECTRAPLUS (Pioneer Hill Software, Poulsbo, Washington). Call components were identified in the audio recordings in RAVEN and matched with the corresponding overall amplitude measurement from synchronized SPL measurement data. The absolute amplitude of each component was calibrated using the equation

$$\text{Peak dB} = \sum 10^{(aX/10)}$$

where a represents a scaling factor and *X* represents the average amplitude for each 1/3-octave band frequency. By adjusting the value of the scaling factor, we could adjust the overall average amplitude (dB) of the vocalization while maintaining the same relative power at each frequency band. The scaling factor was adjusted to yield different overall average amplitudes (dB) for each vocalization for analysis of masking potential at different source levels. Frequency-specific amplitudes for each call component were averaged across vocalizations.

In order to determine the masking potential of the noise sources at different distances from the vocalizing bird and the noise source, SNRs were calculated for each vocalization by subtracting the average amplitude (dB) for 1/3-octave band frequencies of noise sources (taken from 2-min $L_{eq}$ measurements; see above) from the average amplitude (dB) for 1/3-octave band frequencies of vocalizations as measured in SPECTRAPLUS. Each note of the sage-grouse vocalizations was calibrated to absolute amplitude measures made using the SPL meter (see above). We calculated the expected amplitude of the vocalization at distances 2, 4, 8, 16, 32, 64, and 128 m from the vocalizing bird, based on a 6-dB decrease in amplitude for every doubling of distance due to spherical spreading and frequency-specific rate of excess attenuation. Excess attenuation is attenuation caused by propagation of sound through the environment and is determined by habitat characteristics (e.g., groundcover, temperature) and distance of the vocalizing bird from the ground. To model propagation of vocalizations, we estimated frequency-specific rates of excess attenuation by comparing the overall rate of sound attenuation measured along noise transects with predicted amplitude loss due to spherical spreading alone. These estimated amplitudes were used to scale the vocalizations (see scaling equation above), in order to calculate the SNR for the maximum SNR frequency at different distances from the bird and from the noise source. Vocalizations were defined as "masked" if the SNR of the peak SNR frequency did not exceed the minimum threshold (critical ratio) for detection or discrimination (Dooling 2002, Lohr et al. 2003). Minimum masked distance was used to estimate the maximum detection or discrimination distance (active space). Estimates of sage-grouse critical ratios for detection were drawn from the average critical ratios for detection of 15 bird species, the only ones that have been measured to date (Dooling 2002), and ranged from 22 dB at 400–630 Hz to 27 dB at 2,500 Hz. The critical ratios for discrimination at each frequency band were estimated to be 3 dB higher than the critical ratio for detection in that band (Lohr et al. 2003). The critical ratios for detection and discrimination have not been measured specifically for sage-grouse, but there is relatively little variation in hearing abilities among bird species tested thus far, so estimates of the critical ratio are likely to be accurate to within 5 dB (Dooling 2002). All results are presented ± SE unless otherwise noted.

## Results

*Noise measurements*.—Noise produced by Falcon Compressor was 48.9 dB louder than ambient levels at an undisturbed lek at a distance of 75 m from the source and 34.2 dB louder than ambient at a distance of 400 m (Table 1). Noise produced by the Questar Drilling Rig was 43.5 dB louder than ambient levels at a distance of 75 m from the source and 31.8 dB louder than ambient at a distance of 400 m. Noise produced by East Litton Generator was 24.9 dB louder than ambient levels at a distance of 75 m from the source and 18.4 dB louder than ambient at a distance of 400 m (Table 1). The noise produced by all noise sources was dominated by low frequencies (Fig. 2).

*Vocalization measurements*.—Individual components of the sage-grouse vocal display varied in amplitude and peak frequency (the frequency at which amplitude was the highest; Table 2). The pop 1 and pop 2 components had the highest peak amplitudes, with measures of 96 ± 2.1 and 98 ± 1.6 dB at 1 m, respectively. The coo components had an overall peak amplitude of 94 ± 1.3 dB at 1 m. The whistle component, by far the quietest component, had a peak amplitude of 84 ± 0.9 dB for the whistle trough (lowest frequency of the whistle component) and 82 ± 1.5 dB for the

TABLE 1. Overall noise levels (2-min $L_{eq}$ measurements) measured along a transect extending from Falcon Compressor in Sublette County, Wyoming. For comparison, values from an undisturbed lek of Greater Sage-Grouse after the birds departed in late morning are also included (Chugwater Reservoir lek in Fremont County, Wyoming).

| Distance | Amplitude (dB[F]) | Amplitude (dB[A]) |
|---|---|---|
| 75 m | 89.4 | 70.4 |
| 200 m | 82.8 | 58.1 |
| 300 m | 77.9 | 52.9 |
| 400 m | 74.7 | 47.7 |
| Undisturbed lek (quiet) | 40.5 | 30.5 |

whistle apex (highest frequency of the whistle component) at 1 m. All vocal components had peak frequencies (400–630 Hz) overlapping with noise produced by natural gas infrastructure, except the apex of the frequency-modulated whistle, which had a peak frequency (2,500 Hz) above most of the noise.

*Masking analysis*.—We estimated the masking potential of compressor noise for five components of the sage-grouse vocalization: the coos, pop 1, pop 2, whistle trough, and whistle apex. Across all conditions modeled, the maximum detection and discrimination distance (i.e., the active space) for the highest-amplitude frequency band was greatest for the pop 2 component, the loudest note of the display. Overall amplitude of the note was not necessarily an indicator of greater active space—the coo component had a greater maximum detection distance than the pop 1 component (Fig. 3) despite lower overall amplitude, due to the higher amplitude of the maximum frequency. Active space of detection and discrimination for all components was substantially reduced at the noise levels found within 400 m of the compressor station in relation to the ambient conditions on an undisturbed lek (Fig. 3). At 75 m from the noise source, the maximum detection distance and maximum discrimination distance were reduced by 97% and 98%, respectively, for the coo; by 98% and 98% for pop 1; by 97% and 97% for pop 2; by 98% and 98% for the whistle trough; and by 100% and 100% for the whistle apex, in relation to the maximum distances on an undisturbed lek. At 400 m from the noise source, the maximum detection distance and maximum discrimination distance were reduced by 59% and 65%, respectively, for the coo; by 48% and 47% for pop 1; by 59% and 63% for pop 2; by 54% and 57% for the whistle trough; and by 64% and 58% for the whistle apex, in relation to the maximum distances on an undisturbed lek.

The distance from the source at which the active space for detection and discrimination were equal to that in ambient conditions (i.e., the maximum active space) varied for each component. The whistle apex reached maximum active space at 600 m from the noise source. The whistle trough reached maximum active space at 700 m from the source, whereas the coo and pop 1 required a minimum of 700 m from the source before they reached maximum active space. Pop 2 did not reach maximum active space until a minimum of 1,000 m from the noise source.

The SNR varied across frequencies for each component. Peak frequencies for coos, pops, and the whistle trough were relatively low (<1,000 Hz), leading to high overlap with the low-frequency noise produced by the Falcon Compressor and other natural gas infrastructure (Figs. 2 and 4). The SNR was substantially reduced at low frequencies at both short and medium distances to the compressor in relation to quiet lek conditions for all components (Fig. 4). For the whistle, coo, and pop 2 components, the frequency with the peak SNR remained the same under all noise conditions, indicating that no signal distortion would be expected. For the pop 1 component, the frequency with the peak SNR differed under different noise conditions, shifting from 400 Hz under quiet

TABLE 2. Amplitude and frequency characteristics of Greater Sage-Grouse vocalizations recorded in Fremont County, Wyoming. Measurements are normalized to 1 m from the source.

| Note | Peak amplitude (dB) | Peak amplitude range (dB) | Frequency range (Hz) | Peak frequency (Hz, ⅓-octave band) |
|---|---|---|---|---|
| Coo | 94 ± 1.3 | 89–98 | 100–800 | 500 |
| Pop 1 | 96 ± 2.1 | 87–99 | 100–10,500 | 500 |
| Pop 2 | 98 ± 1.6 | 90–100 | 100–11,500 | 400 |
| Whistle apex | 82 ± 1.3 | 76–87 | 2,200–2,600 | 2,500 |
| Whistle trough | 84 ± 0.9 | 81–87 | 450–800 | 630 |

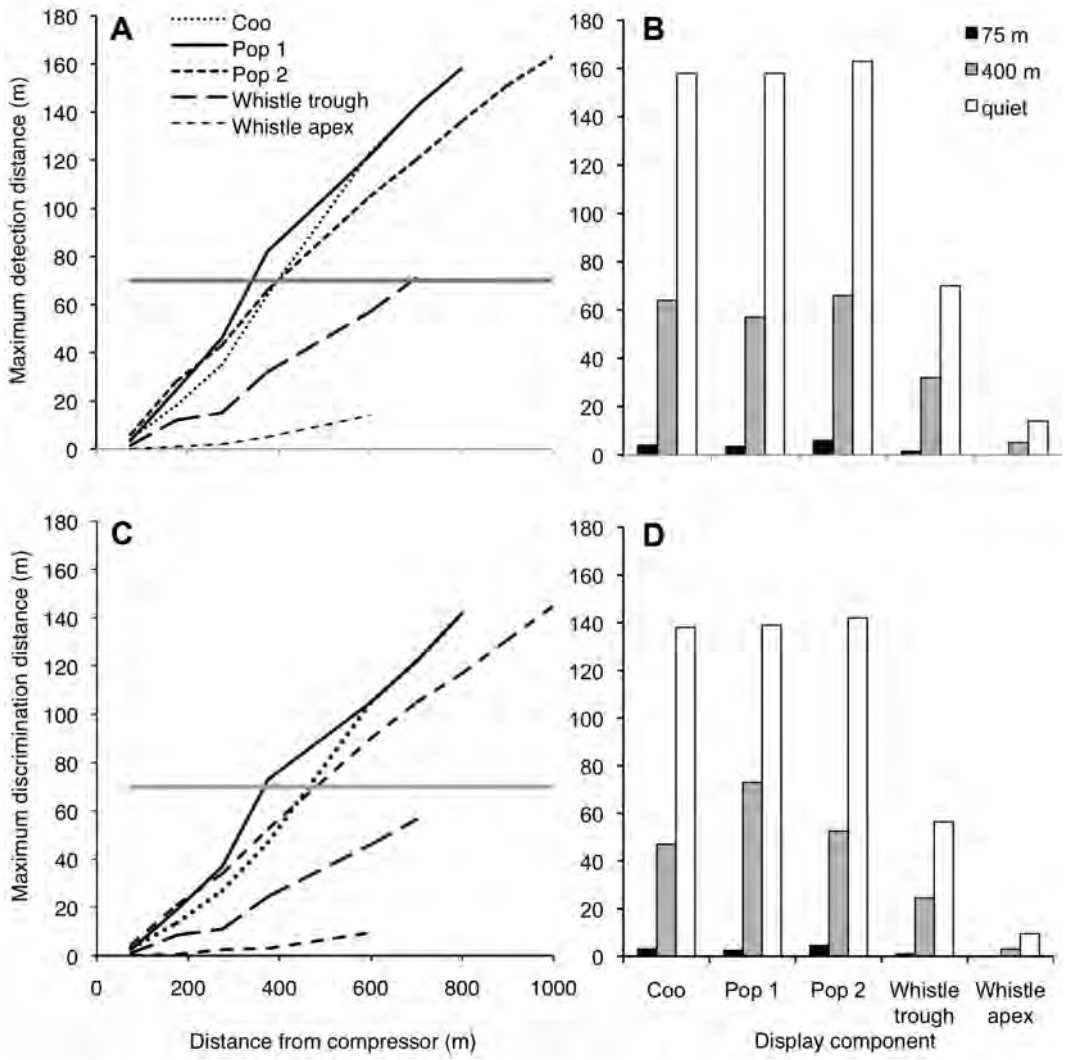



FIG. 3. Maximum (A) detection and (C) discrimination distance of Greater Sage-Grouse strut display components at varying distances from a natural gas compressor station. Gray solid line represents half the length of a typical lek in Fremont County, Wyoming. Lines end at the point where the active space is equal to that under quiet ambient conditions. Maximum (B) detection and (D) discrimination distance of vocalization components at points 75 and 400 m from a natural gas compressor station and under quiet ambient conditions.

conditions to 500 Hz in noisy conditions (Fig. 4B), potentially causing distortion of the signal.

## DISCUSSION

We assessed the potential impact of anthropogenic noise on the transmission of sage-grouse vocalizations used for mate attraction (Wiley 1973; Gibson 1989, 1996; Patricelli and Krakauer 2010). Our results indicate that there are marked differences in the active space of individual notes of the sage-grouse acoustic display, both in noisy and quiet conditions. These differences in active space are primarily determined by the frequency structure and amplitude of the different notes of the sage-grouse vocalization, and by differences in the amplitude of the background noise. These factors and their effects on the active space for detection and discrimination are discussed below.

*Frequency structure*.—The active space of a vocalization is determined, in part, by the frequency structure—including peak frequency and

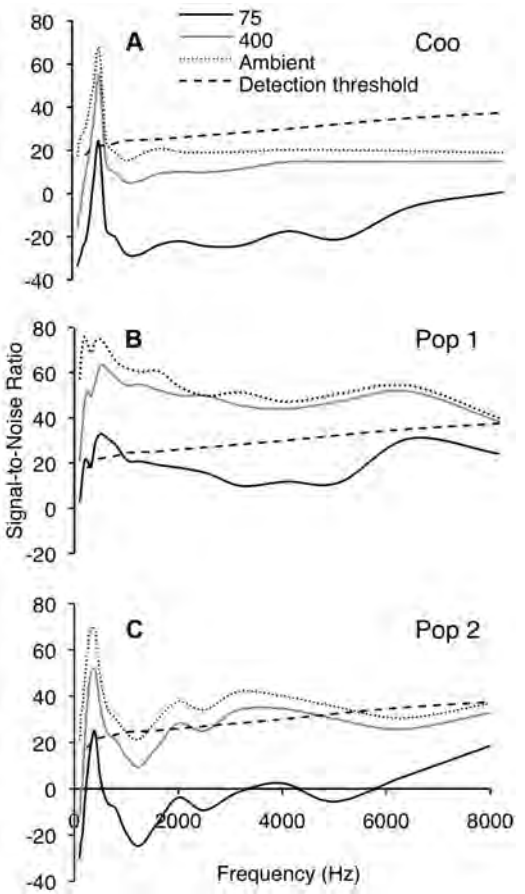



FIG. 4. Signal-to-noise ratio (SNR) of Greater Sage-Grouse acoustic display components (A) coo, (B) pop 1, and (C) pop 2 at a distance of 5 m from the vocalizing male (average close courtship distance) in ambient noise conditions measured 75 and 400 m from a natural gas compressor and on an undisturbed lek. Frequencies with an SNR that exceed the critical ratio for detection (dashed line) can be detected by a receiver. For pop 1, the frequency with the highest SNR is different in noisy and quiet environments, potentially leading to distortion of the vocalization.

frequency range—of both the acoustic signal and the background noise (Lohr et al. 2003). Both of these measures of frequency structure differed among the notes of the sage-grouse display vocalization. Notes with low peak frequencies (the coos, pops, and whistle trough) had high overlap with the noise produced by the Falcon Compressor and other natural gas infrastructure (Figs. 2 and 4), leading to predictions of a substantial reduction in active space of detection and discrimination for these notes in noisy conditions (Fig. 2). The whistle apex had a peak frequency above most of the compressor noise energy, but was still masked because of its lower source amplitude, as discussed below.

The frequency range of a note is also important in determining the degree of overlap with background noise. The coo note of the sage-grouse display is tonal and has a very small frequency range, so the entire note is likely to be masked by low-frequency noise (Fig. 4A). For notes with a broad frequency range, like the broadband pops and the frequency-modulated whistle, some of the higher-frequency energy of the signal is likely to be detectable above background noise that is predominantly low frequency. However, higher frequencies suffer greater attenuation over distance than lower frequencies (Marten and Marler 1977), which reduces the advantage of high-frequency signals in maximizing active space. Because most anthropogenic noise is dominated by low frequencies, species that have low-frequency vocalizations, such as the sage-grouse, will disproportionately experience masking. Indeed, several studies have found that anthropogenic noise more severely affects species with lower-frequency vocalizations (Rheindt 2003; Francis et al. 2009, 2011; Goodwin and Shriver 2011).

*Amplitude*.—The amplitude of each note is also important in determining the active space, such that quieter notes suffer increased masking at a given distance from the noise source and vocalizing individual. Pops and coos could be detected at greater distances than the whistle apex and whistle trough, despite greater overlap with the background noise, because of greater source amplitudes. The whistle apex, which had the lowest source amplitude, had the smallest active space in noise despite the low overlap with the noise frequencies.

The acoustic directionality of a vocalization may also affect the degree to which masking reduces the overall active space. Many vocalizations radiate from the signaler in a directional pattern, such that the amplitude varies with the orientation of the vocalizing individual. Because of our small sample size, we did not include the effects of directionality on active space in our analysis, but instead assessed the impact of noise on the average active space of the signal across multiple orientations. The whistle is highly directional, with differences of up to 22 dB depending on the relative orientation of the individual (Dantzker et al. 1999). We used values from the loudest orientations of those that we measured;

therefore, masking in the quieter orientations may be much greater than described here. Given that the loudest orientation can vary for different strut components (Dantzker et al. 1999), it is possible that using this small range and averaging across vocalizations may have underestimated the maximum active space for some components. Males that adjust their orientation to beam a highly directional vocalization toward a female may gain an advantage over other males, even under quiet conditions (Brumm 2002, Brumm and Todt 2003, Patricelli and Krakauer 2010); this advantage may be even more pronounced in a noisy environment.

*Potential consequences of masking*.—Reductions in the active space of detection and discrimination, as predicted by our analysis, could have significant effects on the fitness of individuals in noisy landscapes. Female sage-grouse use acoustic signals to locate lekking males (Bradbury et al. 1989); thus, their ability to find leks could be compromised in noisy environments because of the reduced active space of detection. Once on the lek, females can detect males visually, making detection using acoustic signals less critical. Discrimination and recognition are likely to be more critical on this smaller spatial scale. Female sage-grouse use the acoustic components of the display to select a mate (Gibson et al. 1991, Gibson 1996). In particular, acoustic features such as the IPI, and possibly the whistle, are thought to play a role in attracting females from across the lek (Gibson 1996). Thus, noise that reduces the maximum distance of discrimination to less than half the length of leks in our study population (half average lek length = ~70 m; J. L. Blickley unpubl. data) could negatively affect a male's ability to attract females. Further, background noise could make active comparison of males difficult for females if the maximum discrimination distance is reduced to less than the average distance between males (Forrest and Raspet 1994).

If the interfering noise only overlaps partially with a vocalization, the frequency with the maximum active space may be different under noisy conditions than under normal ambient conditions, leading to the reception of a signal that is distorted. For example, in the pop 1 component of the sage-grouse display, we found that the frequency with the maximum active space was different in noisy compared with quiet conditions. Therefore, a receiver hearing pop 1 under noisy conditions would hear a call dominated by frequencies in the 500 Hz 1/3-octave band; but under quiet conditions, the receiver would hear a call dominated by frequencies in the 200 Hz 1/3-octave band. Depending on which characteristics of the vocalization are assessed by females or competing males, this distortion may lead to difficulty in discrimination or recognition. Previous studies have suggested that female sage-grouse do not assess natural variation among males in peak frequency during mate choice (Gibson et al. 1991), but further behavioral studies would be needed to determine what, if any, effect such distortion might have on female response to male sage-grouse vocalizations. Distortion may have more significant effects on species in which mate choice is based on the frequency of the signal. For example, in species in which females prefer males with low-frequency song (Halfwerk et al. 2011) or assess the fundamental frequency of song as an indicator of male body size, (Ryan and Brenowitz 1985), distortion may lead to increased difficulty in comparing potential mates.

Ultimately, increased difficulty in finding leks or assessing males on the leks may lead to lower female attendance on noisy leks compared with quieter locations. Males may also avoid leks with high levels of noise if they perceive that their vocalizations are masked. Blickley et al. (2012) found lower male and female attendance on leks with experimentally introduced noise from roads and drilling rigs, both of which produce primarily low-frequency sounds similar to the compressor station modeled here. These declines may be due in part to masking, which would be predicted given the substantial overlap in the frequency range of the introduced noise and the sage-grouse strut display. However, the average level of introduced noise across leks in this experiment was relatively low, especially on leks with intermittent road noise, so masking is not likely the only cause of the observed declines. As discussed below, masking is only one possible effect of noise, and other effects may have a larger impact.

*Masking in the context of noise regulations*.—Are current noise regulations predicted to limit the impact of masking on sage-grouse? Outside of the breeding season, energy development activities are limited within 400 m (1/4 mile) of active sage-grouse leks on federal lands at our study site (Bureau of Land Management 2008). Our analysis indicates that a compressor station, or a similar noise source such as a drilling rig, placed at

or inside this stipulated minimum surface-disturbance buffer would have a substantial effect on the ability of sage-grouse to detect a nearby lek and, potentially, to discriminate among individuals on the lek.

Regulations also institute a 2-mile (3.2-km) buffer around leks for permanent infrastructure and lekking-season drilling activities on federal lands in this region (Bureau of Land Management 2008). Our results suggest that the masking footprint of a single compressor station or drilling rig is unlikely to exceed this buffer. Within the range of the peak frequencies for sage-grouse vocalizations (400–2,500 Hz), the noise produced by the compressor station was estimated to drop to ambient levels ≤1,000 m. Even if noise travels farther during temperature inversions common in the early morning, when sage-grouse are actively lekking (Sutherland and Daigle 1998), masking on the lek is likely to be negligible for sources outside the 2-mile (3.2-km) buffer. However, off-lek communication, such as parent–offspring communication, occurs well beyond the boundaries of a lek (Lyon and Anderson 2003) and may still be susceptible to masking. Further, our analysis considered the masking impact of only a single, stationary noise source, but many developed areas contain a network of such sources connected by roads; this will lead to a much greater area of total impact.

*Mechanisms to reduce masking*.—Features of sound perception and flexibility in signal production may improve the ability of animals to detect signals in noise beyond the active-space predictions calculated by this method. Animals may use directional cues to separate a sound from background noise if the two sound sources are spatially separated (Schwartz and Gerhardt 1989, Dent et al. 1997). Amplitude fluctuations across the spectrum of a sound, or comodulation, may also increase the detectability of the sound against background noise, especially if the noise is relatively constant (Klump and Langemann 1995) like the noise sources investigated here. Animals in noisy areas may adjust their vocalizations to compensate for the increased background noise (Patricelli and Blickley 2006), increasing the amplitude (Brumm 2004) or redundancy (Brumm and Slater 2006) or shifting the peak or minimum frequencies to reduce overlap with background noise frequencies (e.g., Slabbekoorn and Peet 2003, Wood and Yezerinac 2006, Potvin et al. 2011). The potential for these forms of compensation is species specific; the degree to which hearing ability and vocal adjustment affect the active space of sage-grouse vocalizations is unknown.

*Noise impacts beyond masking*.—Masking is one potential effect of noise on wildlife, but it is certainly not the only one (Barber et al. 2010, Blickley and Patricelli 2010, Kight and Swaddle 2011). Blickley et al. (2012) found strong evidence that sage-grouse leks with experimentally introduced intermittent road noise experienced much greater declines in male attendance than those with more continuous drilling noise, despite the lower masking potential of road noise. Even light vehicular traffic (1–12 vehicles $day^{-1}$) has been found to substantially reduce nest initiation rates and increase the distance of nests from lek sites in sage-grouse (Lyon and Anderson 2003), despite minimal opportunity for masking. Together, these studies suggest that masking is not the only potential effect of noise or noisy infrastructure on sage-grouse. So, although a masking analysis can be powerful in making predictions about the effects of noise on lek communication in sage-grouse, this type of analysis may not provide sufficient predictive power for estimating the overall impact of the noise on this species.

Noise pollution has been found to induce stress, disrupt physiological processes and behaviors, cause physical trauma to the auditory system, or mask other natural sounds important to survival and reproduction, such as the sound of predator approach, in a variety of species (Marler et al. 1973, Bowles 1995, Kight and Swaddle 2011). For sage-grouse, these effects may extend beyond the area in which masking of the strut display is an issue, particularly for time spent off lek. Wildlife managers that seek to reduce the overall impact of anthropogenic noise on sage-grouse and other species affected by human encroachment must address all the potential effects of noise, including masking potential.

## Acknowledgments

We thank A. Krakauer, S. Hooper, D. Blackwood, N. Losin, S. Piecuch, T. Rinkes, S. Oberlie, S. Harter, T. Christiansen, B. Ostheimer, and our many excellent field assistants. Funding was provided by the University of California-Davis, U.S. Bureau of Land Management, National Fish and Wildlife Foundation, Wyoming Sage-Grouse Conservation Fund, and Wyoming Community Foundation Tom Thorne Sage-Grouse Conservation Fund.

## Literature Cited


Ballentine, B., J. Hyman, and S. Nowicki. 2004. Vocal performance influences female response to male bird song: An experimental test. Behavioral Ecology 15:163–168.

Barber, J. R., K. R. Crooks, and K. M. Fristrup. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends in Ecology & Evolution 25:180–189.

Blickley, J. L., D. Blackwood, and G. L. Patricelli. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of Greater Sage-Grouse at leks. Conservation Biology 26: in press.

Blickley, J. L., and G. L. Patricelli. 2010. Impacts of anthropogenic noise on wildlife: Research priorities for the development of standards and mitigation. Journal of International Wildlife Law and Policy 13:274–292.

Bowles, A. E. 1995. Responses of wildlife to noise. Pages 109–156 *in* Wildlife and Recreationists: Coexistence through Management and Research (R. L. Knight and K. J. Gutzwiller, Eds.). Island Press, Washington, D.C.

Bradbury, J. W., R. M. Gibson, C. E. McCarthy, and S. L. Vehrencamp. 1989. Dispersion of displaying male sage grouse. II. The role of female dispersion. Behavioral Ecology and Sociobiology 24:15–24.

Brenowitz, E. A. 1982. The active space of Red-winged Blackbird song. Journal of Comparative Physiology 147:511–522.

Brumm, H. 2002. Sound radiation patterns in nightingale (*Luscinia megarhynchos*) songs. Journal für Ornithologie 143:468–471.

Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. Journal of Animal Ecology 73:434–440.

Brumm, H. 2006. Signalling through acoustic windows: Nightingales avoid interspecific competition by short-term adjustment of song timing. Journal of Comparative Physiology A 192:1279–1285.

Brumm, H., and H. Slabbekoorn. 2005. Acoustic communication in noise. Advances in the Study of Behavior 35:151–209.

Brumm, H., and P. J. B. Slater. 2006. Ambient noise, motor fatigue, and serial redundancy in chaffinch song. Behavioral Ecology and Sociobiology 60:475–481.

Brumm, H., and D. Todt. 2003. Facing the rival: Directional singing behaviour in nightingales. Behaviour 140:43–53.

Bureau of Land Management. 2008. Pinedale Anticline Project Area Supplemental Environmental Impact Statement Record of Decision. U.S. Department of Interior, Bureau of Land Management, Pinedale Field Office, Wyoming.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming. [Online.] Available at www.ndow.org/wild/conservation/sg/resources/greate_sg_cons_assessment.pdf.

Copeland, H. E., K. E. Doherty, D. E. Naugle, A. Pocewicz, and J. M. Kiesecker. 2009. Mapping oil and gas development potential in the US intermountain west and estimating impacts to species. PLoS One 4:e7400.

Dantzker, M. S., G. B. Deane, and J. W. Bradbury. 1999. Directional acoustic radiation in the strut display of male sage grouse *Centrocercus urophasianus*. Journal of Experimental Biology 202:2893–2909.

Dent, M. L., O. N. Larsen, and R. J. Dooling. 1997. Free-field binaural unmasking in Budgerigars (*Melopsittacus undulatus*). Behavioral Neuroscience 111:590–598.

Dooling, R. [J.] 2002. Avian hearing and the avoidance of wind turbines. Technical Report NREL/TP-500-30844. National Renewable Energy Lab, Golden, Colorado.

Dooling, R. J., M. Leek, and E. West. 2009. Predicting the effects of masking noise on communication distance in birds. Journal of the Acoustical Society of America 125:2517.

Dooling, R. J., and A. N. Popper. 2007. The Effects of Highway Noise on Birds. [Report prepared for the California Department of Transportation, Sacramento; Jones and Stokes Associates.] [Online.] Available at www.dot.ca.gov/hq/env/bio/files/caltrans_birds_10-7-2007b.pdf.

Forrest, T. G., and R. Raspet. 1994. Models of female choice in acoustic communication. Behavioral Ecology 5:293–303.

Francis, C. D., C. P. Ortega, and A. Cruz. 2009. Noise pollution changes avian communities and species interactions. Current Biology 19:1415–1419.

Francis, C. D., C. P. Ortega, and A. Cruz. 2011. Noise pollution filters bird communities based on vocal frequency. PLoS One 6:e27052.

Garton, E. O., J. W. Connelly, J. S. Horne, C. A. Hagen, A. Moser, and M. A. Schroeder. 2011. Greater Sage-Grouse population dynamics and probablity of persistence. Pages 293–382 *in* Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and Its Habitats (S. T. Knick and J. W. Connelly, Eds.). Studies in Avian Biology, no. 38.

Gibson, R. M. 1989. Field playback of male display attracts females in lek breeding sage grouse. Behavioral Ecology and Sociobiology 24:439–443.

Gibson, R. M. 1996. Female choice in sage grouse: The roles of attraction and active comparison. Behavioral Ecology and Sociobiology 39:55–59.

Gibson, R. M., and J. W. Bradbury. 1985. Sexual selection in lekking grouse: Phenotypic correlates of male strutting success. Behavioral Ecology and Sociobiology 18:117–123.

Gibson, R. M., J. W. Bradbury, and S. L. Vehrencamp. 1991. Mate choice in lekking sage grouse revisited: The roles of vocal diplay, female site fidelity, and copying. Behavioral Ecology 2:165–180.

Goodwin, S. E., and W. G. Shriver. 2011. Effects of traffic noise on occupancy patterns of forest birds. Conservation Biology 25:406–411.

Halfwerk, W., S. Bot, J. Buikx, M. van der Velde, J. Komdeur, C. ten Cate, and H. Slabbekoorn. 2011. Low-frequency songs lose their potency in noisy urban conditions. Proceedings of the National Academy of Sciences USA 108:14549–14554.

Hebets, E. A., and D. R. Papaj. 2005. Complex signal function: Developing a framework of testable hypotheses. Behavioral Ecology and Sociobiology 57:197–214.

Holloran, M. J. 2005. Greater Sage-Grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Ph.D. dissertation, University of Wyoming, Laramie.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling Greater Sage-Grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Kight, C. R., and J. P. Swaddle. 2011. How and why environmental noise impacts animals: An integrative, mechanistic review. Ecology Letters 14:1052–1061.

Klump, G. M. 1996. Bird communication in the noisy world. Pages 321–338 *in* Ecology and Evolution of Acoustic Communication in Birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.

Klump, G. M., and U. Langemann. 1995. Comodulation masking release in a songbird. Hearing Research 87:157–164.

Lohr, B., T. F. Wright, and R. J. Dooling. 2003. Detection and discrimination of natural calls in masking noise by birds: Estimating the active space of a signal. Animal Behaviour 65:763–777.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486–491.

Marler, P., M. Konishi, A. Lutjen, and M. S. Waser. 1973. Effects of continuous noise on avian hearing and vocal development. Proceedings of the National Academy of Sciences USA 70:1393–1396.

Marten, K., and P. Marler. 1977. Sound transmission and its significance for animal vocalization. I. Temperate habitats. Behavioral Ecology and Sociobiology 2:271–290.

Møller, A. P., and A. Pomiankowski. 1993. Why have birds got multiple sexual ornaments? Behavioral Ecology and Sociobiology 32:167–176.

Nelson, D. A., and A. Poesel. 2007. Segregation of information in a complex acoustic signal: Individual and dialect identity in White-crowned Sparrow song. Animal Behaviour 74:1073–1084.

Patricelli, G. L., and J. L. Blickley. 2006. Avian communication in urban noise: Causes and consequences of vocal adjustment. Auk 123:639–649.

Patricelli, G. L., M. S. Dantzker, and J. W. Bradbury. 2008. Acoustic directionality of Red-winged Blackbird (*Agelaius phoeniceus*) song relates to amplitude and singing behaviours. Animal Behaviour 76:1389–1401.

Patricelli, G. L., and A. H. Krakauer. 2010. Tactical allocation of effort among multiple signals in sage grouse: An experiment with a robotic female. Behavioral Ecology 21:97–106.

Potvin, D. A., K. M. Parris, and R. A. Mulder. 2011. Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in Silvereyes (*Zosterops lateralis*). Proceedings of the Royal Society of London, Series B 278:2464–2469.

Rheindt, F. E. 2003. The impact of roads on birds: Does song frequency play a role in determining susceptibility to noise pollution? Journal für Ornithologie 144:295–306.

Ryan, M. J., and E. A. Brenowitz. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. American Naturalist:87–100.

Schwartz, J. J., and H. C. Gerhardt. 1989. Spatially mediated release from auditory masking in an anuran amphibian. Journal of Comparative Physiology A 166:37–41.

Slabbekoorn, H., and M. Peet. 2003. Birds sing at a higher pitch in urban noise—Great Tits hit the high notes to ensure that their mating calls are heard above the city's din. Nature 424:267.

Slabbekoorn, H., and E. A. Ripmeester. 2008. Birdsong and anthropogenic noise: Implications and applications for conservation. Molecular Ecology 17:72–83.

Sutherland, L. C., and G. A. Daigle. 1998. Atmospheric Sound Propagation. Wiley, New York.

Swaddle, J. P., and L. C. Page. 2007. High levels of environmental noise erode pair preferences in Zebra Finches: Implications for noise pollution. Animal Behaviour 74:363–368.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater Sage-Grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

Wiley, R. H. 1973. Territoriality and non-random mating in sage grouse (*Centrocercus urophasianus*). Animal Behaviour Monographs 6:85–169.

Wiley, R. H., and D. G. Richards. 1982. Adaptations for acoustic communication in birds: Sound transmission and signal detection. Pages 131–181 *in* Acoustic Communication in Birds (D. E. Kroodsma, E. H. Miller, and H. Ouellet, Eds.). Academic Press, New York.

Wood, W. E., and S. M. Yezerinac. 2006. Song Sparrow (*Melospiza melodia*) song varies with urban noise. Auk 123:650–659.

Conservation Biology

*Contributed Paper*

# Experimental Evidence for the Effects of Chronic Anthropogenic Noise on Abundance of Greater Sage-Grouse at Leks

JESSICA L. BLICKLEY,*† DIANE BLACKWOOD,*‡ AND GAIL L. PATRICELLI*

*Department of Evolution and Ecology and Graduate Group in Ecology, 2320 Storer Hall, One Shields Avenue, University of California, Davis, CA 95616, U.S.A.

‡Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, FL, U.S.A.

**Abstract:** *Increasing evidence suggests that chronic noise from human activities negatively affects wild animals, but most studies have failed to separate the effects of chronic noise from confounding factors, such as habitat fragmentation. We played back recorded continuous and intermittent anthropogenic sounds associated with natural gas drilling and roads at leks of Greater Sage-Grouse (*Centrocercus urophasianus*). For 3 breeding seasons, we monitored sage grouse abundance at leks with and without noise. Peak male attendance (i.e., abundance) at leks experimentally treated with noise from natural gas drilling and roads decreased 29% and 73%, respectively, relative to paired controls. Decreases in abundance at leks treated with noise occurred in the first year of the study and continued throughout the experiment. Noise playback did not have a cumulative effect over time on peak male attendance. There was limited evidence for an effect of noise playback on peak female attendance at leks or male attendance the year after the experiment ended. Our results suggest that sage-grouse avoid leks with anthropogenic noise and that intermittent noise has a greater effect on attendance than continuous noise. Our results highlight the threat of anthropogenic noise to population viability for this and other sensitive species.*

**Keywords:** chronic noise, energy development, *Centrocercus urophasianus*, roads

Evidencia Experimental de los Efectos de Ruido Antropogénico Crónico sobre la Abundancia de *Centrocercus urophasianus* en Leks

**Resumen:** *El incremento de evidencias sugiere que el ruido crónico de actividades humanas afecta negativamente a los animales silvestres, pero la mayoría de los estudios no separan los efectos del ruido crónico de los factores de confusión, como la fragmentación del hábitat. Reprodujimos sonidos antropogénicos intermitentes y continuos asociados con la perforación de pozos de gas natural y caminos en leks de* Centrocercus urophasianus. *Durante 3 épocas reproductivas, monitoreamos la abundancia de* C. urophasianus e *leks con y sin ruido. La abundancia máxima de machos (i.e., abundancia) en leks tratados con ruido de la perforación de pozos de gas natural y caminos decreció 29% y 73% respectivamente en relación con los controles pareados. La disminución en abundancia en leks tratados con ruido ocurrió en el primer año del estudio y continuó a lo largo del experimento. La reproducción de ruido no tuvo efecto acumulativo en el tiempo sobre la abundancia máxima de machos. Hubo evidencia limitada para un efecto de la reproducción de ruido sobre la abundancia máxima de hembras en los leks o sobre la asistencia de machos el año después de que concluyó el experimento. Nuestros resultados sugieren que* C. urophasianus *evita leks con ruido anropogénico y que el ruido intermitente tiene un mayor efecto sobre la asistencia que el ruido continuo. Nuestros*

†*Address for correspondence: J. Blickley, Department of Evolution and Ecology, 2320 Storer Hall, One Shields Ave, Davis, CA 95616, USA, email jlblickley@ucdavis.edu*

*Paper submitted October 19, 2010; revised manuscript accepted November 20, 2011.*



©2012 Society for Conservation Biology

DOI: 10.1111/j.1523-1739.2012.01840.x

*resultados resaltan amenaza del ruido antropogénico para la viabilidad poblacional de esta y otras especies sensibles.*

**Palabras Clave:** *Centrocercus urophasianus*, desarrollo energético, ruido crónico, caminos

## Introduction

Noise associated with human activity is widespread and expanding rapidly in aquatic and terrestrial environments, even across areas that are otherwise relatively unaffected by humans, but there is still much to learn about its effects on animals (Barber et al. 2009). Effects of noise on behavior of some marine organisms are well-documented (Richardson 1995). In terrestrial systems, the effects of noise have been studied less, but include behavioral change, physiological stress, and the masking of communication signals and predator sounds (Slabbekoorn & Ripmeester 2008; Barber et al. 2009). These effects of noise on individual animals may lead to population decreases if survival and reproduction of individuals in noisy habitats are lower than survival and reproduction of individuals in similar but quiet habitats (Patricelli & Blickley 2006; Warren et al. 2006; Slabbekoorn & Ripmeester 2008). Population declines may also result if animals avoid noisy areas, which may cause a decrease in the area available for foraging and reproduction.

There is evidence of variation among species in their sensitivity to noise. Noise sensitivity may also differ with the type of noise, which varies in amplitude, frequency, temporal pattern, and duration (Barber et al. 2009). Duration may be particularly critical; most anthropogenic noise is chronic and the effects of chronic noise may differ substantially from those of short-term noise in both severity and response type. For example, brief noise exposure may cause elevated heart rate and a startle response, whereas chronic noise may induce physiological stress and alter social interactions. Therefore, when assessing habitat quality for a given species, it is critical to understand the potential effects of the full spectrum of anthropogenic noise present in the species' range.

The effects of noise on wild animals are difficult to study because noise is typically accompanied by other environmental changes. Infrastructure that produces noise may be associated with fragmentation of land cover, visual disturbance, discharge of chemicals, or increased human activity. Each of these factors may affect the physiology, behavior, and spatial distribution of animals, which increases the difficulty of isolating the effects of the noise.

Controlled studies of noise effects on wild animals in terrestrial systems thus far have focused largely on birds. Recent studies have compared avian species richness, occupancy, and nesting success near natural gas wells operating with and without noise-producing compressors. In these studies, spatial variation in noise was used to control for confounding visual changes due to infrastructure (Habib et al. 2007; Bayne et al. 2008; Francis et al. 2009). Results of these studies show that continuous noise affects density and occupancy of a range of bird species and leads to decreases or increases in abundance of some species and has no effect on other species (Bayne et al. 2008; Francis et al. 2009; Francis et al. 2011). Results of these studies also show that noise affects demographic processes, such as reproduction, by reducing the pairing or nesting success of individuals (Habib et al. 2007; Francis et al. 2009).

Although these studies in areas near natural gas wells controlled for the effects of most types of disturbance besides noise, they could not address the effect of noise on naïve individuals in areas without natural gas wells and compressors. Furthermore, there have been no controlled experiments that address the effects of chronic but intermittent noise, such as traffic, which may be more difficult for species to habituate. Road noise may have large negative effects because it is widespread (affecting an estimated 20% of the United States) (Forman 2000) and observational studies indicate that noise may contribute to decreases in abundance of many species near roads (e.g., Forman & Deblinger 2000).

Noise playback experiments offer a way to isolate noise effects on populations from effects of other disturbances and to compare directly the effects of noise from different sources. Playback experiments have been used to study short-term behavioral responses to noise, such as effects of noise on calling rate of amphibians (Sun & Narins 2005; Lengagne 2008), heart rate of ungulates (Weisenberger et al. 1996), diving and foraging behavior of cetaceans (Tyack et al. 2011), and song structure of birds (Leonard & Horn 2008), but have not been used to study effects of chronic noise on wild animals because producing long-term noise over extensive areas is challenging. We conducted a playback experiment intended to isolate and quantify the effects of chronic noise on wild animals. We focused on the effects of noise from natural gas drilling on Greater Sage-Grouse (*Centrocercus urophasianus*).

Greater Sage-Grouse occur in the western United States and Canada and have long been a focus of sexual selection studies (Wiley 1973; Gibson 1989; Gibson 1996). Greater Sage-Grouse populations are decreasing in density and number across the species' range, largely due to extensive habitat loss (Connelly et al. 2004; Garton et al. 2010). The species is listed as endangered under Canada's

Species at Risk Act and is a candidate species for listing under the U.S. Endangered Species Act. Deep natural gas and coal-bed methane development have been expanded rapidly across the species' range since 2000 and substantial evidence suggests that these processes may contribute to observed decreases in the number of Greater Sage-Grouse (Holloran 2005; Walker et al. 2007; Holloran et al. 2010). Many factors associated with deep natural gas and coal-bed methane development are thought to lead to these decreases, including habitat loss, increased occurrence of West Nile Virus, and altered fire regimes due to the expansion of nonnative invasive species (Naugle et al. 2004; Walker et al. 2007; Copeland et al. 2009).

The noise created by energy development may also affect sage grouse by disrupting behavior, causing physiological stress, or masking biologically important sounds. During the breeding season (February–May), male sage grouse gather on communal breeding grounds called leks. Male attendance (number of male birds on the lek) at sage grouse leks downwind of deep natural gas development decreases up to 50% per year compared with attendance at other leks, which suggests noise or aerial spread of chemical pollution as factors contributing to these decreases (Holloran 2005).

We sought to test the hypothesis that lek attendance by male and female sage grouse is negatively affected by both chronic intermittent and continuous noise from energy development. To do so, we conducted a noise playback experiment in a population that is relatively unaffected by human activity. Over 3 breeding seasons (late February to early May), we played noise recorded from natural gas drilling rigs and traffic on gas-field access roads at sage grouse leks and compared attendance patterns on these leks to those on nearby control leks.

We conducted our experiment at leks because lekking sage grouse are highly concentrated in a predictable area, which makes them good subjects for a playback experiment. More importantly, sage grouse may be particularly responsive to noise during the breeding season, when energetic demands and predation risk are high (Vehrencamp et al. 1989; Boyko et al. 2004). Additionally, noise may mask sexual communication on the lek. Lekking males produce a complex visual and acoustic display (Supporting Information) and females use the acoustic component of the display to find lekking males and select a mate (Gibson 1989; Gibson 1996; Patricelli & Krakauer 2010). Furthermore, lek attendance is commonly used as a metric of relative abundance of sage grouse at the local and population level (Connelly et al. 2003; Holloran 2005; Walker et al. 2007). We used counts of lek attendance (lek counts) to assess local abundance relative to noise versus control treatments.

## Methods

### Study Site and Lek Monitoring

Our study area included 16 leks (Table 1 & Supporting Information) on public land in Fremont County, Wyoming, U.S.A. (42° 50′, 108° 29′). Dominant vegetation in this region is big sagebrush (*Artemisia tridentata wyomingensis*) with a grass and forb understory. The primary land use is cattle ranching, and there are low levels of recreation and natural gas development.

We paired leks on the basis of similarity in previous male attendance and geographic location (Table 2 & Supporting Information). Within a pair, one lek was

**Table 1. Pairing, treatment type, location, and baseline attendance for leks used in noise playback experiment.**

| *Lek* | *Pair* | *Pair noise type* | *Noise or control* | *Years of playback* | *Baseline attendance** |
|---|---|---|---|---|---|
| Gustin | A | drilling | control | 3 | 26 |
| Preacher Reservoir | A | drilling | noise | 3 | 49 |
| North Sand Gulch | B | road | control | 3 | 32 |
| Lander Valley | B | road | noise | 3 | 67 |
| East Twin Creek | C | drilling | control | 3 | 44 |
| Coal Mine Gulch | C | drilling | noise | 3 | 83 |
| East Carr Springs | D | road | control | 3 | 67 |
| Carr Springs | D | road | noise | 3 | 92 |
| Powerline | E | drilling | control | 2 | 49 |
| Conant Creek North | E | drilling | noise | 2 | 44 |
| Monument | F | road | control | 2 | 53 |
| Government Slide Draw | F | road | noise | 2 | 55 |
| Nebo | G | drilling | control | 2 | 18 |
| Arrowhead West | G | drilling | noise | 2 | 24 |
| Onion Flats 1 | H | road | control | 2 | 41 |
| Ballenger Draw | H | road | noise | 2 | 38 |

**Baseline attendance is the average peak male attendance value (annual maximum number of males observed averaged across years) for that lek from 2002 to 2005.*

**Table 2. Mixed-effect candidate models used to assess change in peak attendance of male Greater Sage-Grouse at leks from pre-experiment baseline attendance during the natural gas drilling noise playback (2006–2008) and after the experiment (2009).**

| *Model (year)*[a] | K[b] | $\Delta AIC_c$[c] | $w_i$[d] |
|---|---|---|---|
| Male experiment (2006–2008) | | | |
| treatment×type+season[e] | 9 | 0 | 0.64 |
| treatment×type[e] | 7 | 1.8 | 0.26 |
| treatment+experiment year | 6 | 6.1 | 0.03 |
| treatment+season | 7 | 6.8 | 0.02 |
| treatment | 5 | 7.3 | 0.02 |
| treatment×experiment year | 7 | 8.0 | 0.01 |
| treatment×type+treatment×season+experiment year | 12 | 8.6 | <0.01 |
| treatment×type+treatment×season | 11 | 9.9 | <0.01 |
| treatment×type+treatment×season+treatment×experiment year | 13 | 10.0 | <0.01 |
| treatment+type | 6 | 10.4 | <0.01 |
| treatment×season | 9 | 16.2 | <0.01 |
| null- random effects only | 4 | 57.0 | <0.01 |
| Male after experiment (2009) | | | |
| null, random effects only[e] | 3 | 0.0 | 0.84 |
| treatment | 4 | 3.3 | 0.16 |

[a] *All models contain pair as a random effect, and experiment (2006–2008) models also include year as a random effect. Covariates: treatment, lek treatment (noise or control) assigned to individual leks within a pair; type, pair noise treatment type (road or drilling assigned to pair); season, time of year (early [late February to 1 week prior to peak female attendance for that lek; female peak ranged from 15 March to 6 April], mid [1 week before and after female peak], and late [starting 1 week after female peak]); experiment year, years of experimental noise exposure.*
[b] *Number of parameters in the model.*
[c] *Difference in $AIC_c$ (Akaike's information criterion for small sample size) values from the model with lowest $AIC_c$.*
[d] *Akaike weight.*
[e] *Model with substantial support ($\Delta AIC_c < 2$).*

randomly assigned to receive experimental noise treatment and the other lek was designated a control. We randomly assigned the experimental leks to receive playback of either drilling or road noise. In 2006, we counted attendance at 8 leks (2 treated with drilling noise, 2 treated with road noise, and 4 control). In both 2007 and 2008, we included an additional 8 leks for a total of 16 leks (4 treated with drilling noise, 4 treated with road noise, and 8 controls).

Throughout the breeding season, we counted males and females on leks with a spotting scope from a nearby point selected to maximize our visibility of the lek. We visited paired leks sequentially on the same days between 05:00 and 09:00, alternating the order in which each member of the pair was visited. We visited lek pairs every day during the breeding season in 2006 and, after expanding our sample size in 2007, every 2–4 days in 2007 and 2008. Peak estimates of male attendance from >4 visits are a highly repeatable measure of abundance at individual leks (Garton et al. 2010), so the lower frequency of visits in 2007 and 2008 was unlikely to have a substantial effect on estimates of peak male attendance. At a minimum, we conducted 2 counts per visit at 10- to 15-min intervals. The annual peak attendance was the highest daily attendance value at each lek for the season for males or females. For males we also calculated the peak attendance in 3 nonoverlapping date ranges: early (late February to 1 week prior to peak female attendance for that lek; female peak ranged from 15 March to 6 April), mid (1 week before and after female peak), and late (starting 1 week after female peak).

### Noise Introduction

We recorded noise used for playback near natural gas drilling sites and gas-field access roads in a region of extensive deep natural gas development in Sublette County, Wyoming (Pinedale Anticline Gas Field and Jonah Gas Field). We recorded drilling noise in 2006 within 50 m of the source on a digital recorder (model PMD670, 44.1 kHz/16 bit; Marantz, Mahwah, New Jersey) with a shotgun microphone (model K6 with an ME60 capsule; Sennheiser, Old Lyme, Connecticut). We recorded road noise in 2005 with a handheld computer (iPAQ h5550 Pocket PC, 44.1 KHz/16 bit; Hewlett Packard, Palo Alto, California) and omnidirectional microphone (model K6 with an ME62 capsule; Sennheiser). Drilling noise is relatively continuous and road noise is intermittent (Supporting Information). Both types of noise are predominantly low frequency (<2 kHz).

We played noise on experimental leks from 2 to 4 rock-shaped outdoor speakers (300 W Outdoor Rock Speakers; TIC Corporation, City of Industry, California) hooked to a car amplifier (Xtant1.1; Xtant Technologies, Phoenix, Arizona) and an MP3 player (Sansa m240; SanDisk, Milpitas, California). The playback system was powered with 12 V batteries that we changed every 1–3 days when no birds were present. We placed the speakers

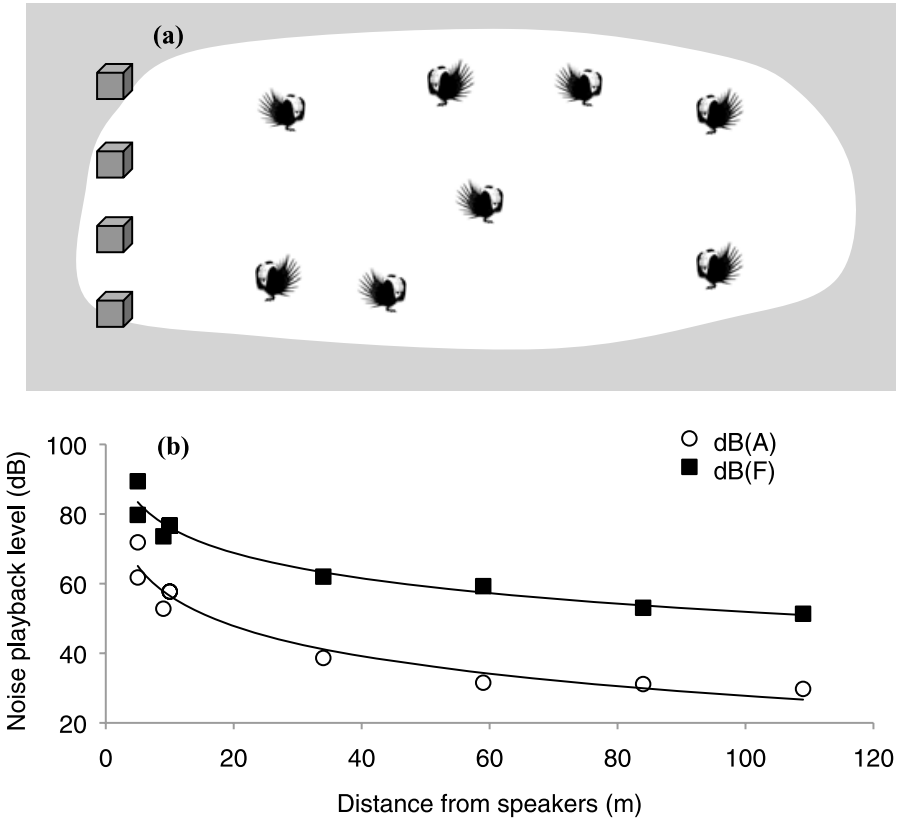



*Figure 1. (a) Placement of speakers (on noise-treated leks) or dummy speakers (on control leks) (boxes) at Greater Sage-Grouse leks. (b) Mean maximum noise level (unweighted decibels, dB[F], and A-weighted decibels, dB[A], measured in Lmax [highest root-mean-square sound pressure level within the measurement period]) at Greater Sage-Grouse leks measured on transects at 25-m intervals from the line of speakers on a typical lek treated with road noise. Playback levels of natural gas drilling noise (measured in Leq) followed the same pattern. Ambient levels of noise at control leks ranged from 30 to 35 dB(A).*

in a straight line across one end of the lek (Fig. 1a). In 2006 we placed 3 speakers at leks treated with drilling noise and 2 speakers at leks treated with road noise. In 2007 and 2008, we increased the number of speakers, placing 4 at each noise-treated lek to increase the area in which noise was present on the lek. At control leks, we placed dummy speakers of similar size and color to playback speakers (68-L plastic tubs). Within each lek pair, dummy and real speakers were placed in similar configurations. To control for playback-related disturbance, the leks in each pair were visited an equal number of times during the morning for counts of birds and in the afternoon for battery changes.

We played drilling noise and road noise on leks at 70 dB(F) sound pressure level (unweighted decibels) measured 16 m directly in front of the speakers (Fig. 1 & Supporting Information). This is similar to noise levels measured approximately 400 m from drilling rigs and main access roads in Pinedale (J. L. Blickley and G. L. Patricelli, unpublished data). Four hundred meters (0.25 miles) is the minimum surface disturbance buffer around leks at this location (BLM 2008). We calibrated and measured noise playback levels with a hand-held meter that provides sound-pressure levels (System 824; Larson-Davis, Depew, New York) when wind was <9.65 k/h. On drilling-noise-treated leks, where noise was continuous, we calibrated the noise playback level by measuring the average sound level (Leq [equivalent continuous sound level]) over 30 s. On leks treated with road noise, where the amplitude of the noise varied during playback to simulate the passing of vehicles, we calibrated the playback level by measuring the maximum sound level (Lmax [highest root-mean-square sound pressure level within the measurement period]).

For leks treated with drilling noise, recordings from 3 drilling sites were spliced into a 13-min mp3 file that played on continuous repeat. On leks treated with road noise, we randomly interspersed mp3 recordings of 56 semitrailers and 61 light trucks with 170 thirty-second silent files to simulate average levels of traffic on an access road (Holloran 2005). Noise playback on experimental leks continued throughout April in 2006, from mid February or early March through late April in 2007, and from late February through late April in 2008. We played back noise on leks 24 hours/day because noise from deep natural gas drilling and vehicular traffic is present at all times. This experimental protocol was reviewed and approved by the Animal Care and Use Committee at University of California, Davis (protocol 16435).

To measure noise levels across experimental leks, we measured the average amplitude (15 s Leq) of white-noise played at 1–5 points along transects that extended across the lek at 25-m intervals roughly parallel to the line of speakers. We calibrated white-noise measurements by measuring the noise level of both the white noise and either a representative clip of drilling noise or a semitrailer

10 m directly in front of each speaker. To minimize disturbance, we took propagation measurements during the day. Daytime ambient noise levels are typically 5–10 dBA higher than those in the early morning (J. L. Blickley and G. L. Patricelli, unpublished data) and are likely higher than those heard by birds at a lek.

After the experiment, we counted individuals on all leks 2–6 times from 1 March through 30 April 2009. In 2009 we continued to play noise on 2 experimental leks as part of a related experiment, so we did not include these lek pairs in our analysis of postexperiment male attendance at a lek.

### Response Variables and Baseline Attendance Levels

Sage grouse leks are highly variable in size and, even within pairs, our leks varied up to 50% in size. To facilitate comparison of changes in attendance on leks of different sizes, we calculated the attendance relative to attendance levels before treatment (i.e., baseline attendance levels). We obtained male baseline abundance from the Wyoming Game and Fish Department. We used the standard lek-count protocol (Connelly et al. 2003) to count birds at leks approximately 3 times/breeding season. Due to the small number of counts in pre-experiment years, we calculated male baseline attendance by averaging the annual peak male attendance at each individual lek over 4 years (2002–2005). We assessed changes in early-, mid-, and late-season peak male attendance from this 4-year baseline attendance. Female attendance was highly variable throughout the season with a short (1–3 day) peak in attendance at each lek. Due to the limited number of annual counts, female counts from 2002 to 2005 were not reliable estimates of peak female attendance and could not be used as baseline attendance levels. Because we introduced noise to experimental leks after the peak in female attendance in 2006, we used maximum female counts from 2006 as a baseline for each of the 8 leks monitored that year. We assessed changes in annual peak female attendance from this 1-year baseline attendance. The 8 leks added to the experiment in 2007 were not included in statistical analyses of female attendance due to the lack of a baseline.

### Statistical Analyses

We used an information-theoretic approach to evaluate the support for alternative candidate models (Table 2). All candidate models were linear mixed-effect models that assessed the relation between covariates and the proportional difference in annual and within-season peak attendance and baseline attendance (both males and female) (Tables 2 & 3). We ranked models on the basis of differences in Akaike's information criterion for small sample sizes ($\Delta AIC_c$) (Burnham & Anderson 2002). Akaike weights ($w_i$) were computed for each model on the basis of $\Delta AIC_c$ scores. We calculated model-averaged variable coefficients, unconditional 95% CI, and variable importance (weight across models) for variables contained in models that were strongly supported ($\Delta AIC_c < 2$). All statistical analyses were performed in R (version 2.12.1) (R Development Team 2010).

**Table 3. Mixed-effect candidate models used to assess change in peak annual attendance of female Greater Sage-Grouse at leks from pre-experiment baseline attendance in 2006 during noise playback.**

| *Model*[a] | K[b] | $\Delta AIC_c$[c] | $w_i$[d] |
|---|---|---|---|
| Null, random effects only[e] | 4 | 0 | 0.71 |
| Treatment[e] | 5 | 1.9 | 0.27 |
| Treatment+experiment year | 6 | 8 | 0.01 |
| Treatment×experiment year | 7 | 14 | <0.001 |

[a]*All models contained pair and year as random effects. Due to the small sample size (4 pairs), pair type variable (road versus drilling) was not included in the model set. Covariates: treatment, lek treatment (noise or control assigned to individual leks within a pair); experiment year, years of experimental noise exposure.*
[b]*Number of parameters in the model.*
[c]*Difference in $AIC_c$ (Akaike's information criterion for small sample size) values from the most strongly supported (lowest AICc) model.*
[d]*Akaike weight.*
[e]*Model with substantial support ($\Delta AIC_c < 2$).*

The detection probability for males and females is likely to vary across a season and among leks (Walsh et al. 2004). We sought to minimize sources of error and maximize detection by conducting frequent counts from locations with a clear view of the lek and by implementing a paired treatment design (each noise lek is compared with a similar control lek, monitored by the same observer on the same days). To ensure that detection probability did not differ among noise and control leks, we corrected our data for detection probability. First, we used detection error rates, estimated as difference between the maximum count and the count immediately before or after the maximum count within a day (for both males and females), and then we applied the bounded-count method (for males only; Walsh et al. 2004). With the multiple-count estimator, estimates of detection between noise and control leks did not differ (males: $t = 1.02$, $df = 6$, $p = 0.35$; females: $t = 0.21$, $df = 3$, $p = 0.84$). We analyzed both corrected and uncorrected counts and found that neither correction qualitatively changed our results; therefore, results are presented for uncorrected counts.

## Results

### Male Attendance

Peak male attendance at both types of noise leks decreased more than attendance at paired control leks, but the decreases varied by noise type. In the most strongly supported models of the candidate set ($w_i = 0.90$, all

**Table 4. Model-averaged parameter direction and effect sizes and variable importance for all variables present in strongly supported models ($\Delta AIC_c < 2$ in Table 2) of changes in peak attendance of male greater sage-grouse at leks from baseline attendance during experimental noise playback.**

| *Variable* | *Percent effect size (SE)* | *Variable importance** |
|---|---|---|
| Intercept | 31 (22) | 1.0 |
| Treatment, noise | −29 (7) | 0.91 |
| Type, road | 33 (22) | 0.91 |
| Treatment, noise∗type, road | −40 (10) | 0.91 |
| Season, mid | 18 (6) | 0.66 |
| Season, late | 23 (6) | |

**Variable importance is the summed weight of all models containing that variable.*

other models $\Delta AIC_c > 6.1$) (Table 2), there was an interaction of the effects of experimental treatment (control versus noise) and noise type (drilling versus road) on annual peak male attendance. At leks treated with road noise, decreases in annual peak male attendance were greater (73%), relative to paired controls, than at drilling noise leks (29%). As indicated by the effect size for the main effect of pair type, attendance at control leks paired with road noise leks was 33% greater relative to the baseline than control leks paired with drilling noise leks (Table 4). However, changes in attendance were compared within a pair to control for such differences. Male attendance increased over the course of a season, with 18% and 23% increases in peak male attendance in mid and late season from the early-season peaks, but seasonal increases were similar across noise and control leks (Table 4 & Fig. 2b).

There was no evidence that the effect of noise on attendance changed as years of exposure to noise increased. The models with substantial support did not contain a main effect of years of exposure or an interaction of years of exposure and treatment type (control versus noise) (Table 2). In spite of decreases in attendance throughout the experiment, peak male attendance exceeded baseline attendance on all leks in 2006, 13 leks in 2007, and 11 leks in 2008 (Table 4 & Fig. 2c). There was an increase in sage grouse abundance regionally in 2006 (Fig. 3).

After the experiment (2009), attendance at leks we experimentally exposed to drilling and road noise was lower relative to paired controls (Table 2). The model that included the treatment variable showed an effect size of −30% (across road and drilling noise leks) but had only moderate support ($\Delta AIC_c = 3.3$) relative to the null model.

### Female Attendance

Peak female attendance at leks treated with noise in 2007 and 2008 decreased from the 2006 baseline, relative to control leks (Table 3). The most strongly supported model in the set was the null model; however, the model that included noise treatment was highly supported ($\Delta AIC_c < 2$). The effect size of noise treatment on female attendance was −48% (10% SE), which is similar to the effect of noise on male attendance averaged across both noise types (51%).

## Discussion

Results of previous studies show abundance of Greater Sage-Grouse decreases when natural gas and coal-bed methane fields are developed (Holloran 2005; Walker et al. 2007; Doherty et al. 2008). Our results suggest that chronic noise may contribute to these decreases. Peak male attendance relative to the baseline was lower on noise leks than paired control leks, and the decrease was larger at road noise leks (73% decrease in abundance compared with paired controls) than drilling noise leks (29%; Fig. 3). These decreases were immediate and sustained. The effects of noise occurred in the first year of the study and were observed throughout the experiment, although patterns of male attendance within a season were similar at noise and control leks. Differences in male attendance between noise and control leks in the year after the experiment were not supported in the top models, which suggests attendance rebounded after noise ceased. However, the sample size for this analysis was small, and the effect size (30% average decreases in male attendance for both noise types) suggests a residual effect of noise.

There are 2 mechanisms by which noise may reduce male attendance. First, males on noise leks may have had higher mortality than males on control leks. Noise playback was not loud enough to cause direct injury to individuals, but mortality could be increased indirectly by noise playback if the sounds of predators (coyotes [*Canis latrans*] or Golden Eagles [*Aquila chrysaetos*]) were masked by noise. However, on-lek predation events were rare. We observed ≤1 predation event per lek per season during the experiment (observations of sage-grouse carcasses or feathers at a lek [J. L. Blickley, personal observation]). The cumulative effect of rare predation events would lead to a gradual decrease in attendance, rather than the rapid and sustained decrease we observed. Furthermore, experimental noise was likely too localized to substantially affect off-lek predation because noise levels decreased exponentially as distance to the speakers increased (Fig. 1b). To date, increased predation risk of adults due to anthropogenic noise has not been demonstrated in any species, but some species increase vigilance when exposed to noise, leaving less time for feeding, displaying, and other important behaviors (Quinn et al. 2006; Rabin et al. 2006). Noise may also affect off-lek mortality indirectly. For example, noise-stressed males may be more susceptible to disease due to a suppressed

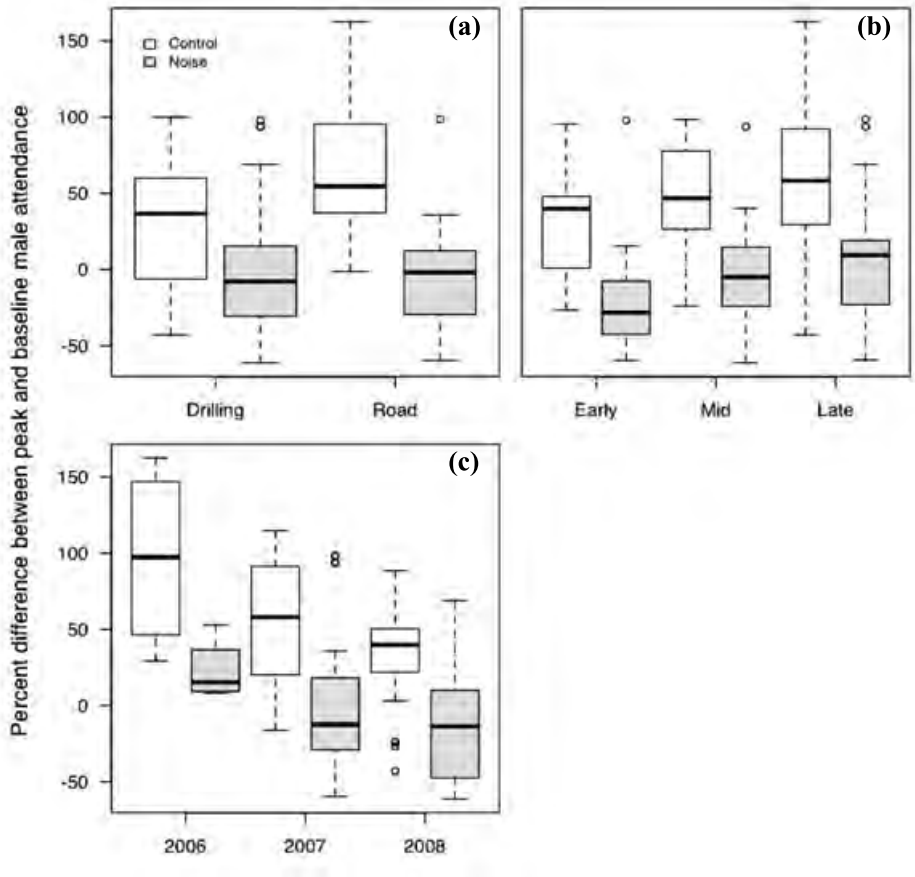



*Figure 2. Percent difference between baseline attendance (i.e., abundance before experiments) of male Greater Sage-Grouse and (a) peak male attendance on control leks and leks treated with noise from natural gas drilling and road noise, (b) peak male attendance in the early (late February to 1 week prior to peak female attendance for that lek), mid (1 week before and after female peak [female peak ranged from 15 March to 6 April]), and late (starting 1 week after female peak) breeding season; on control leks and leks treated with noise, and (c) peak male attendance at control leks and leks treated with noise in experimental years 2006, 2007, and 2008 in Fremont County, Wyoming (U.S.A.) (horizontal lines, median value; box ends, upper and lower quartiles, whiskers, maximum and minimum values). Data are observed values, not model output.*

immune response (Jankowski et al. 2010). Although long-term stress from noise is unlikely to be the primary cause of the rapid decreases in attendance we observed here, it may have been a contributing factor over the course of the experiment. Furthermore, in areas of dense industrial development, where noise is widespread, noise effects on mortality may be more likely.

Alternatively, noise may lower male attendance through displacement, which would occur if adult or juvenile males avoid leks with anthropogenic noise. Such behavioral shifts are consistent with the rapid decreases in attendance we observed. Adult male sage grouse typically exhibit high lek fidelity (Schroeder & Robb 2003) and visit leks regularly throughout the season, whereas juvenile males visit multiple leks and their attendance peaks late in the season (Kaiser 2006). If juveniles or adults avoid noise by visiting noisy leks less frequently or moving to quieter leks, overall attendance on noisy leks could be reduced. We could not reliably differentiate between juveniles and adults, so we do not know the relative proportion of adults and juveniles observed. Consistent with displacement due to noise avoidance, radio-collared juvenile males avoid leks near deep natural gas developments in Pinedale, Wyoming, which has resulted in decreases in attendance at leks in close proximity to development and increased attendance at nearby leks with less human activity (Kaiser 2006; Holloran et al. 2010). Reduced recruitment of juvenile males is unlikely to be the only driver of the patterns we observed because we did not observe larger decreases in lek attendance on noise-treated leks later in the season, when juvenile attendance peaks. Rather, we found immediate decreases in attendance early in the season when playback began (Fig. 2b), at which time there are few juveniles on the lek. This

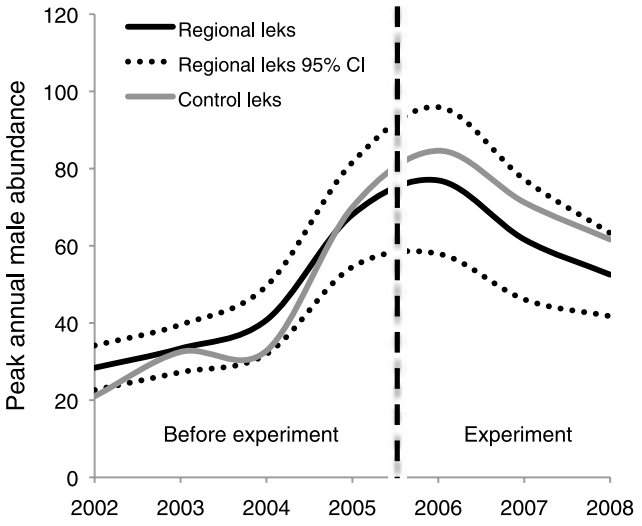



*Figure 3. Maximum abundance of male Greater Sage-Grouse from 2002 to 2008 at control leks (*n = *8) (no anthropogenic sound played) and other leks in the region that were not part of the experiment (regional leks) (*n = *38).*

is consistent with both adult and juvenile noise avoidance. We did not find evidence for a cumulative negative effect of noise on lek attendance, although cumulative effects may have been masked by regional population declines after 2006, a year of unusually high abundance (Fig. 3).

Female attendance at leks treated with noise was lower than that on control leks; however, the null model and the model that included noise treatment were both highly supported, providing only moderate support for the effects on noise on attendance. For this model, the overall estimated effect of noise on female attendance (−48%) was similar to that of the effect of noise on male attendance. Due to the high variability of female daily maximum attendance throughout the season and small sample size for this analysis (female attendance data available for only 4 of the 8 lek pairs), our statistical power to detect differences in female attendance was limited and effect sizes may not be representative of actual noise effects.

Our results suggest that males and possibly females avoid leks exposed to anthropogenic noise. A potential cause of avoidance is the masking of communication. Masked communication is hypothesized to cause decreases in abundance of some animal species in urban and other noisy areas. For example, bird species with low-frequency vocalizations are more likely to have low abundance or be absent from natural gas developments, roads, and urban areas than species with high-frequency vocalizations, which suggests that masking is the mechanism associated with differences in abundance (Rheindt 2003; Francis et al. 2009; Hu & Cardoso 2010). Sage-grouse may be particularly vulnerable to masked communication because their low-frequency vocalizations are likely to be masked by most sources of anthropogenic noise, including the noises we played in our experiment (Supporting Information). This may be particularly important for females if they cannot use acoustic cues to find leks or assess displaying males in noisy areas.

Alternatively, individuals may avoid noisy sites if noise is annoying or stressful, particularly if this noise is associated with danger (Wright et al. 2007). Intermittent road noise was associated with lower relative lek attendance than continuous drilling noise, in spite of the overall higher mean noise levels and greater masking potential at leks treated with drilling noise (Supporting Information). Due to the presence of roads in our study area, sage grouse may have associated road noise with potentially dangerous vehicular traffic and thus avoided traffic-noise leks more than drilling-noise leks. Alternatively, the pattern of decrease may indicate that an irregular noise is more disturbing to sage grouse than a relatively continuous noise. Regardless, our results suggest that average noise level alone is not a good predictor of the effects of noise (Slabbekoorn & Ripmeester 2008) and that species can respond differently to different types of noise.

Our results cannot be used to estimate the quantitative contribution of noise alone to observed decreases in Greater Sage-Grouse abundance at energy development sites because our experimental design may have led us to underestimate or overestimate the magnitude of these effects. Decreases in abundance due to noise could be overestimated in our study if adults and juveniles are displaced from noise leks and move to nearby control leks, which would have increased the difference in abundance between paired leks. Similar displacement occurs in areas of energy development, but over a much larger extent than is likely to have occurred in response to localized playbacks in our experiment (Holloran et al. 2010).

In contrast, we could have underestimated noise effects if there were synergistic effects of noise and other disturbances associated with energy development. For example, birds with increased stress levels due to poor forage quality may have lower tolerance for noise-induced stress, or vice versa. Noise in our experiment was localized to the immediate lek area and only played during the breeding season, so we cannot quantify the effects of noise on wintering, nesting, or foraging birds. Noise at energy development sites is less seasonal and more widespread than noise introduced in this study and may thus affect birds at all life stages and have a potentially greater effect on lek attendance. Leks do not represent discrete populations; therefore, local decreases in lek attendance do not necessarily reflect population-level decreases in abundance. However, at large energy development sites, similar displacement of Greater Sage-Grouse away from the ubiquitous noise may result in population-level declines due to spatially exten-

sive changes in land use or increases in dispersal-related and density-dependent sources of mortality (Aldridge & Boyce 2007). Enforcement and refinement of existing seasonal restrictions on human activity could potentially reduce these effects.

We focused on the effect of noise associated with deep natural gas and coal-bed methane development on sage grouse, but our results may increase broader understanding of the effects of noise on animals. Both intermittent and constant noise from energy development affected sage grouse. Other noise sources with similar frequency range and temporal pattern, such as wind turbines, oil-drilling rigs, and mines, may have comparable effects. Similar effects may also be associated with highways, off-road vehicles, and urbanization so that the potential for noise to have an effect is large.

We believe that noise should be investigated as one potential cause of population declines in other lekking North American grouse species that are exposed to similar anthropogenic development. Populations of many bird (van der Zande et al. 1980; Rheindt 2003; Ingelfinger & Anderson 2004) and mammal (Forman & Deblinger 2000; Sawyer et al. 2009) species have been shown to decrease in abundance in response to road, urban, and energy development, and noise produced by these activities may contribute to these decreases. Our results also demonstrate that wild animals may respond differently to chronic intermittent and continuous noise, a comparison that should be expanded to other species. Additionally, we think these results highlight that experimental noise playbacks may be useful in assessing the response of wild animals to chronic noise (Blickley & Patricelli 2010).

## Acknowledgments

We thank A. Krakauer, T. Rinkes, S. Oberlie, S. Harter, T. Christiansen, W. Elsberry, our many excellent field assistants, and reviewers. Funding was provided by the University of California, Davis, U.S. Bureau of Land Management, U.S. National Fish & Wildlife Foundation, Wyoming Sage-Grouse Conservation Fund, and the Wyoming Community Foundation Tom Thorne Sage-Grouse Conservation Fund.

## Supporting Information

Spectrograms and power spectrums of drilling noise, road noise and male sage-grouse vocal display (Appendix S1), map of experimental and control leks (Appendix S2), and noise playback levels on experimental leks (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

## Literature Cited

Aldridge, C., and M. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications **17:**508–526.

Barber, J. R., K. R. Crooks, and K. M. Fristrup. 2009. The costs of chronic noise exposure for terrestrial organisms. Trends in Ecology & Evolution **25:**180–189.

Bayne, E., L. Habib, and S. Boutin. 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. Conservation Biology **22:**1186–1193.

Blickley, J. L., and G. L. Patricelli. 2010. Impacts of anthropogenic noise on wildlife: research priorities for the development of standards and mitigation. Journal of International Wildlife Law & Policy **13:**274–292.

BLM (Bureau of Land Management). 2008. Pinedale Anticline Project area. Supplemental environmental impact statement record of decision. Appendix A. BLM, Pinedale, Wyoming.

Boyko, A. R., R. M. Gibson, and J. R. Lucas. 2004. How predation risk affects the temporal dynamics of avian leks: greater sage grouse versus golden eagles. The American Naturalist **163:**154–165.

Burnham, K. P., and D. R. Anderson 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station, University of Idaho, Moscow.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming.

Copeland, H. E., K. E. Doherty, D. E. Naugle, A. Pocewicz, and J. M. Kiesecker. 2009. Mapping oil and gas development potential in the US intermountain west and estimating impacts to species. Public Library of Science One **4:**e7400. DOI: 10.1371.

Doherty, K., D. Naugle, B. Walker, and J. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management **72:**187–195.

Forman, R. T. T. 2000. Estimate of the area affected ecologically by the road system in the United States. Conservation Biology **14:**31–35.

Forman, R. T. T., and R. D. Deblinger. 2000. The ecological road-effect zone of a Massachusetts(U. S. A.) suburban highway. Conservation Biology **14:**36–46.

Francis, C. D., C. P. Ortega, and A. Cruz. 2009. Noise pollution changes avian communities and species interactions. Current Biology **19:**415–419.

Francis, C., C. Ortega, and A. Cruz. 2011. Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. Proceedings of the Royal Society B: Biological Sciences **278:**2025–2031.

Garton, E. O., J. W. Connelly, J. S. Horne, C. A. Hagen, A. Moser, and M. A. Schroeder. 2010. Greater sage-grouse population dynamics and probablity of persistence. Pages 293–382. Studies in avian biology. University of California Press, Berkeley.

Gibson, R. M. 1989. Field playback of male display attracts females in lek breeding sage grouse. Behavioral Ecology and Sociobiology **24:**439–443.

Gibson, R. M. 1996. Female choice in sage grouse: the roles of attraction and active comparison. Behavioral Ecology and Sociobiology **39:**55–59.

Habib, L., E. M. Bayne, and S. Boutin. 2007. Chronic industrial noise affects pairing success and age structure of ovenbirds Seiurus aurocapilla. Journal of Applied Ecology **44:**176–184.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western

Wyoming. Department of Zoology and Physiology, University of Wyoming, Laramie.
Holloran, M., R. Kaiser, and W. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management **74:**65–72.
Hu, Y., and G. C. Cardoso. 2010. Which birds adjust the frequency of vocalizations in urban noise? Animal Behaviour **79:**863–867.
Ingelfinger, F., and S. Anderson. 2004. Passerine response to roads associated with natural gas extraction in a sagebrush steppe habitat. Western North American Naturalist **64:**385–395.
Jankowski, M. D., J. C. Franson, E. Möstl, W. P. Porter, and E. K. Hofmeister. 2010. Testing independent and interactive effects of corticosterone and synergized resmethrin on the immune response to West Nile virus in chickens. Toxicology **269:**81–88.
Kaiser, R. 2006. Recruitment by greater sage-grouse in association with natural gas development in western Wyoming. Department of Zoology and Physiology, University of Wyoming, Laramie.
Lengagne, T. 2008. Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. Biological Conservation **141:**2023–2031.
Leonard, M., and A. Horn. 2008. Does ambient noise affect growth and begging call structure in nestling birds? Behavioral Ecology **19:**502–507.
Naugle, D. E., et al. 2004. West Nile virus: pending crisis for greater sage-grouse. Ecology Letters **7:**704–713.
Patricelli, G., and J. Blickley. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. The Auk **123:**639–649.
Patricelli, G., and A. Krakauer. 2010. Tactical allocation of effort among multiple signals in sage grouse: an experiment with a robotic female. Behavioral Ecology **21:**97–106.
Quinn, L., J. Whittingham, J. Butler, and W. Cresswell. 2006. Noise, predation risk compensation and vigilance in the chaffinch Fringilla coelebs. Journal of Avian Biology **37:**601–608.
Rabin, L. A., R. G. Coss, and D. H. Owings. 2006. The effects of wind turbines on antipredator behavior in California ground squirrels (*Spermophilus beecheyi*). Biological Conservation **131:**410–420.
Rheindt, F. E. 2003. The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution? Journal of Ornithology **144:**295–306.
Richardson, W. J. 1995. Marine mammals and noise. Academic Press, San Diego, California.
Sawyer, H., M. Kauffman, and R. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management **73:**1052–1061.
Schroeder, M., and L. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildlife Biology **9:**291–299.
Slabbekoorn, H., and E. A. P. Ripmeester. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Molecular Ecology **17:**72–83.
Sun, J. W. C., and P. M. Narins. 2005. Anthropogenic sounds differentially affect amphibian call rate. Biological Conservation **121:**419–427.
Tyack, P. L., et al. 2011. Beaked whales respond to simulated and actual navy sonar. Public Library of Science One **6:**e17009. DOI: 10.1371.
van der Zande, A. N., W. J. ter Keurs, and W. J. van der Weijden. 1980. The impact of roads on the densities of four bird species in an open field habitat—evidence of a long-distance effect. Biological Conservation **18:**299–321.
Vehrencamp, S., J. Bradbury, and R. Gibson. 1989. The energetic cost of display in male sage grouse. Animal Behaviour **38:**885–896.
Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management **71:**2644–2654.
Walsh, D. P., G. C. White, T. E. Remington, and D. C. Bowden. 2004. Evaluation of the lek-count index for greater sage-grouse. Wildlife Society Bulletin **32:**56–68.
Warren, P. S., M. Katti, M. Ermann, and A. Brazel. 2006. Urban bioacoustics: it's not just noise. Animal Behaviour **71:**491–502.
Weisenberger, M. E., P. R. Krausman, M. C. Wallace, D. W. D. Young, and O. E. Maughan. 1996. Effects of simulated jet aircraft noise on heart rate and behavior of desert ungulates. The Journal of Wildlife Management **60:**52–61.
Wiley, R. H. 1973. Territoriality and non-random mating in sage grouse (*Centrocercus urophasianus*). Animal Behaviour Monographs **6:**85–169.
Wright, A., et al. 2007. Anthropogenic noise as a stressor in animals: a multidisciplinary perspective. International Journal of Comparative Psychology **20:**250–273.



OPEN ACCESS Freely available online

PLOS ONE

# Experimental Chronic Noise Is Related to Elevated Fecal Corticosteroid Metabolites in Lekking Male Greater Sage-Grouse (*Centrocercus urophasianus*)

**Jessica L. Blickley[1], Karen R. Word[2], Alan H. Krakauer[1], Jennifer L. Phillips[1], Sarah N. Sells[3], Conor C. Taff[1], John C. Wingfield[2], Gail L. Patricelli[1]***

**1** Dept of Evolution and Ecology, University of California Davis, Davis, California, United States of America, **2** Dept of Neurobiology, Physiology and Behavior, University of California Davis, Davis, California, United States of America, **3** University of Montana, Wildlife Biology Program, Missoula, Montana, United States of America

## Abstract

There is increasing evidence that individuals in many species avoid areas exposed to chronic anthropogenic noise, but the impact of noise on those who remain in these habitats is unclear. One potential impact is chronic physiological stress, which can affect disease resistance, survival and reproductive success. Previous studies have found evidence of elevated stress-related hormones (glucocorticoids) in wildlife exposed to human activities, but the impacts of noise alone are difficult to separate from confounding factors. Here we used an experimental playback study to isolate the impacts of noise from industrial activity (natural gas drilling and road noise) on glucocorticoid levels in greater sage-grouse (*Centrocercus urophasianus*), a species of conservation concern. We non-invasively measured immunoreactive corticosterone metabolites from fecal samples (FCMs) of males on both noise-treated and control leks (display grounds) in two breeding seasons. We found strong support for an impact of noise playback on stress levels, with 16.7% higher mean FCM levels in samples from noise leks compared with samples from paired control leks. Taken together with results from a previous study finding declines in male lek attendance in response to noise playbacks, these results suggest that chronic noise pollution can cause greater sage-grouse to avoid otherwise suitable habitat, and can cause elevated stress levels in the birds who remain in noisy areas.

**Citation:** Blickley JL, Word KR, Krakauer AH, Phillips JL, Sells SN, et al. (2012) Experimental Chronic Noise Is Related to Elevated Fecal Corticosteroid Metabolites in Lekking Male Greater Sage-Grouse (*Centrocercus urophasianus*). PLoS ONE 7(11): e50462. doi:10.1371/journal.pone.0050462

**Editor:** Nicola Saino, University of Milan, Italy

**Received** July 18, 2012; **Accepted** October 22, 2012; **Published** November 20, 2012

**Copyright:** © 2012 Blickley et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Funding:** Funding was provided by the National Parks Service, US Bureau of Land Management, Wyoming Sage-Grouse Conservation Fund (State of Wyoming), National Fish and Wildlife Foundation, the Wyoming Community Foundation Tom Thorne Sage-Grouse Conservation Fund, UC Davis, and the National Science Foundation (IOS-0925038). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing Interests:** The authors have declared that no competing interests exist.

* E-mail: GPatricelli@ucdavis.edu

## Introduction

Anthropogenic noise is becoming ubiquitous as natural landscapes are increasingly dominated by humans, but we still have much to learn about the impacts of chronic noise exposure on wildlife [1–3]. Recent studies have shown that some species avoid developed areas with high noise levels, reducing available habitat and potentially leading to reduced populations [4–6]. However, there is variation among species and individuals in the tendency to avoid noise [4,5,7], which raises the question of whether animals that remain suffer detrimental effects, or if these individuals are better able to habituate to noise or are less susceptible to its effects. It has been suggested that animals remaining in (or unable to leave) noisy areas may have lower survival and reproductive success [8–10]; indeed, recent studies have demonstrated complex effects of noise on community structure and on breeding and pairing success [4–6,11]. Given the ubiquity of noise in the environment, it is critical that we understand noise impacts on animals whether they remain in or avoid disturbed areas.

One possible impact of introduced noise on animals is the induction of stress, which may be defined broadly as nonspecific adverse effects in vertebrates but is most often characterized by its influence on neuroendocrine physiology. The duration of noise exposure affects the stress response of animals exposed to it [12]. Exposure to a brief but loud noise event, such as a single sonic boom, will result in an acute stress response. An acute stress response is characterized by a rapid release of epinephrine and norepinephrine (the "fight or flight" response) followed by a hypothalamic-pituitary-adrenal (HPA) cascade. The HPA cascade results in increased secretion of glucocorticoid hormones, cortisol or corticosterone, in the blood. Long-term exposure to a chronic noise stressor, such as a high-traffic freeway, can lead to chronic stress, defined as long-term overstimulation of coping mechanisms. This in turn can lead to less predictable changes in the HPA axis. Acclimation or exhaustion may result in reduced glucocorticoid release to the same or novel stressors; facilitation, conversely, can lead to elevated glucocorticoid release in response to novel stressors, and even in cases of reduced peak glucocorticoid response, deficits in negative feedback may develop that result in greater overall exposure to glucocorticoids due to prolonged elevation [12,13].

Glucocorticoid hormones and their metabolites are commonly used to measure a stress response [14–16]. Glucocorticoid hormones can be measured from blood samples or their metabolites may be measured non-invasively from fecal samples

as an index of the relative physiological stress of animals [17–19]. Glucocorticoid hormones play a major role in allocating energy, and prolonged exposure due to chronic stress can affect fitness by inhibiting resource allocation to reproductive or immune activities, a condition known as allostatic overload [12,20–24].

Studies in captive animals have found that noise can increase HPA activity and glucocorticoid levels [25,26]; indeed studies of stress physiology often use noise exposure as a method to induce a stress response [27,28]. Previous observational and experimental studies on the impacts of anthropogenic noise on glucocorticoid levels in wild animals have yielded mixed results. Snowmobile and wheeled-vehicle traffic was associated with elevated fecal glucocorticoid metabolites in wolves and elk [14]. Noise is one potential mechanism of this impact, but visual and other types of disturbance may also contribute to these responses; indeed, the quieter activity of Nordic skiing also correlates with FCMs in capercaillie (*Tetrao urogallus*) [29]. Delaney et al. [30] found behavioral responses in spotted owls to loud noise from visually hidden chainsaws and helicopters, but subsequent studies found no evidence of change in FCMs with exposure to quieter chainsaw noise (below behavioral response threshold) or road proximity to nesting sites [31]. Results from chronic noise studies on humans have also been mixed [32]. Studies of children in areas with high road noise have found increased overnight glucocorticoid levels in urine, as well as impaired circadian rhythms, sleep, memory and concentration, [33] and increased heart-rate responsiveness to acute stressors [34]. However, a study in children living in communities near airports found increases in some measures of stress (blood pressure, epinephrine and norepinephrine) but no similar elevation in overnight urinary cortisol [35]. These results indicate that noise may have a significant effect on glucocorticoids and other stress-related variables in many species, but that further study is needed to determine the degree and extent of these effects and how the effects may vary with different types of noise.

In this study, we test the hypothesis that chronic noise causes an increase in stress levels of lekking greater sage-grouse. We used fecal levels of immunoreactive corticosteroid metabolites (FCMs) as an index of physiological stress and compared FCMs for breeding males on display grounds (leks) with and without experimentally introduced noise. The greater sage-grouse, an iconic species once widespread in western North America, is now declining throughout its range, leading to its listing as an endangered species in Canada and its recent designation as "warranted but precluded" for listing under the Endangered Species Act in the USA [36,37]. Over the last decade, natural gas development has expanded rapidly across much of the sage-grouse range and has been implicated in reduced lek attendance and abandonment of long-occupied (often for decades) lek sites by males [e.g. 38,39–41]. Males typically gather on lekking grounds for several hours in the early morning when conditions are quiet and still, a time when they may be particularly vulnerable to disturbance from noise pollution from natural gas development and other sources [42]. To investigate whether noise exposure may have contributed to declines in lek attendance, Blickley et al. [43] experimentally introduced noise from natural gas development activities (drilling and road noise) on leks over three breeding seasons (2006–2008). This noise playback caused immediate and sustained declines in sage-grouse lek attendance. Further, different types of noise had different degrees of impact, with drilling noise and road noise causing an average 29% and 73% decline in lek attendance, respectively, compared to their paired controls. That study provides evidence that anthropogenic noise from energy development causes some males to avoid attending leks with introduced noise, but we do not yet know whether noise also has a negative impact on the individuals that remain on noisy leks. The lekking season is a time of high metabolic demand [44] and stress [45] for males, so exposure to noise during this period may have a greater fitness cost.

Here we compare the FCM levels of male sage-grouse on control leks and leks with experimentally introduced noise in the second and third seasons of experimental noise playback (2007 and 2008) [43]. We predict that if noise exposure leads to chronic stress, male sage-grouse on experimental leks will have higher FCMs than males on control leks. Such differences in observed FCM levels may also be observed if males with low glucocorticoid levels are more likely to disperse from noise-treated leks, so we compared the variance in FCM levels on noise and control leks. We also investigated whether elevated FCM levels were associated with declines in peak male attendance on leks to determine the value of this metric as a tool for predicting lek declines.

## Materials and Methods

### Study Area & Experimental Design

Study sites were located on federal land relatively undisturbed by human development in Fremont County, Wyoming (42° 50′, 108° 29′30). We monitored a total of 16 leks that were divided into 8 pairs, with the leks of a pair matched according to size and location (6 pairs near the town of Hudson and 2 pairs near the town of Riverton) (Figure 1). Of the 8 lek pairs, 4 pairs were randomly assigned to each noise type, such that there were 4 "drilling pairs", each including one lek exposed to drilling noise and a similar lek as its control, and 4 "road pairs," each with one road noise and a matched control. For 3 of the pairs, one lek within a pair was randomly assigned to the treatment (noise) group and the other assigned as control. For the fourth pair, the treatment and control leks were deliberately assigned due to another study that was in progress. During sample collection periods, both leks in a pair were normally visited on the same day.

Noise and playback methods have been previously described [43] and are summarized here. Noise was played beginning in mid-February to early March and continuing through the end of April of each year. Noise was recorded from drilling and main road sites at the Pinedale Anticline natural gas fields and played back using a commercial car amplifier and 3–4 rock-shaped outdoor speakers placed along one edge of the lek. On leks with road-noise playback, recordings of semi-trailer trucks and pickup trucks were combined with 30- and 60-second files of silence at a ratio reflecting the average number of each truck type found on a main energy field access road; these files were then played using the "random shuffle" feature on an MP3 player. Most shift changes occur at 8 am, so our playback may underestimate actual traffic levels during the lekking time. On leks with drilling noise, a 14-minute recording of a drilling rig was played on continuous loop. Natural gas development activities occur 24 hours a day, so noise was broadcast continuously day and night at playback levels that approximate the noise level at 0.25 mile (402 m) from a typical drilling site (JLB and GLP unpublished data). Drilling-noise recordings were broadcast on experimental leks at an equivalent sound level ($L_{eq}$) of 71.4±1.7 dBF (unweighted decibels) SPL re 20 μPa (56.1±0.5 dBA [A-weighted decibels]) as measured at 16 meters; on road-noise leks, where the amplitude of the noise varied with the simulated passing of vehicles, noise was broadcast at an $L_{max}$ (maximum RMS amplitude) of 67.6±2.0 dBF SPL (51.7±0.8 dBA) (see Blickley, et al. [43], for detailed noise-exposure measurements). Noise from playback was localized to each lek due to the small size of our speakers. To control for visual disturbance of the speaker system and researcher presence, control

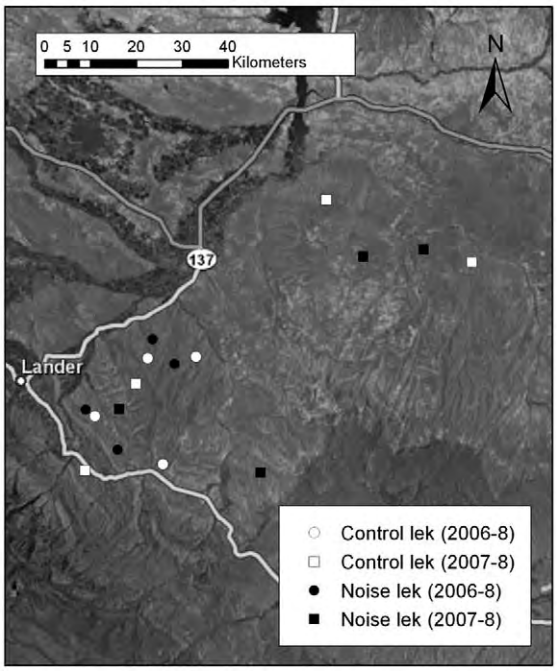



**Figure 1. Noise playback study area in Fremont County, Wyoming, USA, 2006–2009.** Experimental and control leks were paired on the basis of size and geographic location (the four leks in the upper right are part of the Riverton region, whereas the rest of the leks are in the Lander region).
doi:10.1371/journal.pone.0050462.g001

leks had dummy speakers placed in the same arrangement and were also visited to simulate the periodic battery changes on noise leks. This experimental protocol was reviewed and approved by the Animal Care and Use Committee at UC Davis (Protocol # 16435) and the Wyoming Game and Fish Department (Permit # 33–405).

In the first year of the experiment (2006), we played noise on only 4 of the 8 lek pairs (2 experimental leks with introduced drilling noise, 2 with introduced road noise). Therefore, some leks had been exposed to noise the breeding season prior to the first year of FCM measurement; however, we detected no significant impact of duration of noise exposure on lek attendance [43], so years of noise exposure was not included as a potential explanatory variable in candidate model sets.

## Collection of Fecal Samples

Fecal samples were collected from leks soon after all sage-grouse had left the lek for the morning. Samples were collected twice per year from each lek (once during the mid season [April 4–6 in 2007, April 6–8 in 2008] and once during the late season [April 23–26 in 2007, April 22–24 in 2008]) and were collected from paired leks on the same day. Samples were collected using a sweep-search method in which the entire lek was systematically searched and fresh fecal samples were collected individually in Whirl-Pak bags and labeled with a location on the lek relative to the speakers (or dummy speakers). To minimize the chance of collecting multiple fecal samples from the same individual, we collected samples that were a minimum of 5 meters apart, roughly the minimum territory size of a male sage-grouse. Jankowski [45] found lower FCM levels in female sage-grouse than in breeding male sage-grouse. Therefore to avoid collecting samples from females, we collected samples on dates when female visitation is rare; if there were more than 1–2 females on the lek on a potential collection day, sampling for that lek pair was postponed until the next day. Time to collect samples varied among leks from 20–80 minutes. Samples were frozen at $-20^{\circ}$C within a few hours of collection until processing. Jankowski et al. [45] found no difference in FCM levels for greater sage-grouse samples held for variable times up to 16 hours prior to freezing.

## Extraction & Radioimmunoassay of Cort

We used extraction and assay procedures, with minor modifications, that were previously validated for application to greater sage-grouse by Jankowski et al. [46]. Individual fecal pellets were kept on ice while uric acid (often present in a discrete cap on the pellet) was removed and discarded. Samples were then lyophilized and returned to storage at $-20^{\circ}$C. On the day of extraction, individual fecal pellets were weighed to the nearest 0.0001 g, then manually homogenized, vortexed, and shaken in 5 mL of 80% methanol for at least 30 minutes. Longer incubation in methanol often occurred due to the large number of tubes in each assay, but experimentation with overnight extraction produced no substantial change in detected metabolites. Samples were centrifuged at 5000 rpm for 30 minutes, then 1.5mL of supernatant was drawn off, placed in a separate tube, dried under streaming air in a $70^{\circ}$C water bath and reconstituted in 1.0 mL of steroid diluent provided in the RIA kit (see below). For some very large samples, it was not possible to remove 1.5 mL; in these cases, 500 μL of supernatant was drawn off and reconstitution volume was adjusted accordingly after drying. Extracts were covered with Parafilm and stored at $4^{\circ}$C until assayed.

A pooled sample was made by homogenizing a collection of multiple samples from one control lek (Monument lek) in a blender prior to lyophilization. From this pooled sample, 0.5 g was assayed initially to determine parallelism with the RIA standard curve, and one or more pooled samples were included in each extraction and assay.

Radioimmunoassays were conducted according to the manufacturer's instructions (catalog # 07-120103, MP Biomedicals, Costa Mesa, CA) using 1:16 dilution of reconstituted extract. This RIA kit utilizes a rabbit-produced BSA IgG polyclonal antibody against corticosterone-3-carboxymethyloxime. This antibody has been widely used for fecal assays due to its ability to bind a broad spectrum of corticosteroid metabolites [47]. Samples were randomly distributed among assays with respect to year and treatment to minimize any impacts of inter-assay variation.

FCM measures were adjusted for the mass of the fecal sample (ng ICM/g sample) to account for differences among leks in fecal pellet mass. In dividing ICM by sample mass, we effectively assume that the relationship between sample mass and fecal transit time (during which corticosteroid metabolites are secreted into the lumen of the gut) is positive and linear. To guard against faults in this assumption, we ran the same statistical analyses using "per sample" FCM data and found no difference in the main effects as reported.

## Statistical Analysis

Fecal glucocorticoid metabolites levels were natural log-transformed to meet assumptions of normality and homoscedasticity prior to analysis. We used an information theoretic approach to evaluate the support for alternative candidate models using Akaike's Information Criterion for small sample sizes ($AIC_c$) [48]. Candidate models for the overall effect of noise (Noise effect models) were linear mixed-effect models that assessed the relationship between explanatory variables and the concentration of FCMs collected from experimental and control leks. Potential

explanatory variables included pair type (NoiseType, drilling or road noise), control status (Treatment, noise or control), pellet/collection distance from speakers (SpeakerDist), maximum lek size for that year (MaxSize), location (Hudson or Riverton), season (early or late April), and relevant interactions (see Table 1 for full set of candidate models). All models contained lek pair ID, and year (2007 or 2008) as random effects.

We also evaluated a set of candidate models that assessed the relationship between the concentration of FCMs on experimental leks and the declines in peak male attendance from the previous year (attendance models). Models contained lek ID and year (2007 or 2008) as random effects. Models were ranked on the basis of differences in AICc scores (ΔAICc) and were assigned Akaike weights ($w_i$) corresponding to the degree of support. We calculated model-averaged coefficients and variable importance (sum of variable weights for all models in which the variable was included) for variables contained in all models that received strong support (ΔAICc <2). We also compared the variance in FCM concentrations measured on noise and control leks using a Levene's test. All statistical analyses were performed in R (version 2.12.1, R Development Team 2010).

## Results

We measured baseline fecal immunoreactive corticosterone metabolites of 103.2 and 119.9 ng/g for control and treatment groups, respectively (Table 2). These values are lower than baseline measures of approximately 149 ng/g obtained previously for breeding male greater sage-grouse in Nevada, from which fecal samples were collected after capture [45].

Males on leks exposed to noise had higher (16.7% on average) FCM levels compared with controls ($w_i = 0.96$, Table 1, 2; Figure 2). While models that included the effect of Treatment (noise versus control) were highly supported by the data, there was little support for an interaction of Treatment with NoiseType variable ($w_i = 0.01$, Table 1), indicating that while noise exposure was associated with increased cort, there was little difference in FCM levels between leks with drilling versus road-noise playback. Candidate models containing other possible explanatory variables, including distance from the nearest speaker (SpeakerDist), maximum size of the lek (MaxSize), the regional location of the lek in the Hudson area or Riverton area (Location) and time of the season (Season), received little support relative to the null model (Table 1, Figure 2B), indicating that none of these factors had a strong influence on FCM levels.

To determine whether noise-playback leks with a higher stress response were associated with larger declines in lek attendance, we compared candidate models for the relationship between FCM level and change in lek attendance from the previous year. Only the null model received support (Table 3), indicating that fecal FCM level was not associated with the magnitude of changes in lek attendance on noise leks.

Finally, we examined whether there was a difference in variance among samples on noise leks and control leks. We found no significant differences in variance between treatment types in 2007 (variance on noise leks = 7729.94, control leks = 6168.28, Levene's

**Table 1.** Mixed-effect candidate models for the effect of noise playback on mass-dependent FCM concentrations (natural log-transformed).

| Model[a,b] | $K$[c] | $\Delta AIC_c$[d] | $w_i$[e] |
|---|---|---|---|
| Treatment[f] | 5 | 0 | 0.66 |
| Treatment + Location | 6 | 2.4 | 0.20 |
| Treatment + Location + Treatment:Location | 7 | 4.7 | 0.06 |
| Null- random effects only | 4 | 5.5 | 0.04 |
| Treatment + Season | 6 | 6.5 | 0.03 |
| Treatment + Season + Treatment:Season | 7 | 10.0 | <0.01 |
| Treatment + NoiseType + Treatment:NoiseType | 7 | 10.8 | <0.01 |
| Treatment + Location + NoiseType + Treatment:Location + Treatment:NoiseType | 9 | 11.2 | <0.01 |
| Treatment + NoiseType + Season + Treatment:Season + Treatment:NoiseType | 9 | 20.7 | <0.01 |
| Treatment + MaxSize + Treatment:MaxSize | 7 | 25.3 | <0.01 |
| Treatment + NoiseType + Season + Treatment:NoiseType + Treatment:Season + Treatment:NoiseType:Season | 11 | 27.3 | <0.01 |
| Treatment + SpeakerDistance + Treatment:SpeakerDistance | 7 | 27.5 | <0.01 |
| Treatment + NoiseType + MaxSize + Treatment:NoiseType + Treatment:MaxSize | 10 | 35.4 | <0.01 |
| Treatment + NoiseType + SpeakerDistance + Treatment:NoiseType + Treatment:SpeakerDistance | 9 | 38.2 | <0.01 |
| Treatment + NoiseType + MaxSize + Treatment:NoiseType + Treatment:MaxSize + Treatment:NoiseType:MaxSize | 12 | 45.1 | <0.01 |
| Treatment + NoiseType + SpeakerDistance + Treatment:NoiseType + Treatment:SpeakerDistance + Treatment:NoiseType:SpeakerDistance | 11 | 60.4 | <0.01 |

[a]Abbreviations of predictor variables in methods.
[b]All models contain lek pairing and year as a random effect.
[c]Number of parameters in the model.
[d]Difference in $AIC_c$ (Akaike's Information criteria for small sample size) values from the top ranking model.
[e]Akaike weight (Probability that the model is the best fit model giving the data and model candidate set).
[f]Model with substantial support ($\Delta AIC_c$ <2).
doi:10.1371/journal.pone.0050462.t001

**Table 2.** Parameter estimates (± SE) and relative variable importance for variables in highly supported models ($\Delta AIC_c < 3$).

| Variable | Parameter estimates[a] | Parameter estimates (back-transformed)[b] | Relative variable importance[c] |
|---|---|---|---|
| Intercept | 4.63 (.06) | 103.2[d] | - |
| Treatment:Noise | .15 (.04) | 16.7[d] | 0.96 |
| Location: Hudson | 0.02(.01) | 2.9[d] | 0.26 |

[a]Parameter estimates are natural-log transformed.
[b]SE not included due to back-transformation.
[c]Relative variable importance is the summed total of the model weights for models containing that variable.
[d]Intercept value was added to parameter estimates prior to back-transformation and then subtracted.
doi:10.1371/journal.pone.0050462.t002

W = 0.6327, p = 0.427). Variance on noise leks was significantly higher than on control leks in 2008 (variance on noise leks = 4462.28, control leks = 2758.69, Levene's W = 6.6064, p = 0.01).

## Discussion

We found higher (16.7%) FCM levels on noise-treated leks compared to controls, supporting the hypothesis that chronic noise pollution increases stress levels in male greater sage-grouse. Combined with results from monitoring of lek attendance in the same experiment [43], these results suggest that noise from natural gas development activities can dramatically decrease male attendance on leks and cause physiological impacts on males that remain on noisy leks. The mean level of FCMs in remaining birds was not a good predictor of the degree of decline in peak male attendance on a lek compared with the previous year, indicating that the FCM level measured on a lek is not diagnostic of an effect of noise on peak male attendance (Table 3). Further, we did not find support for an effect of distance from the speakers on FCM levels. Male sage-grouse typically maintain a fixed territory on a lek throughout the season. Within a noise-treated lek, each individual's exposure to noise varied, depending on the location of their territory relative to the speakers. Since noise levels decline exponentially with distance from the speakers, the lack of a distance effect suggests that stress is not exclusively dependent on the noise exposure of individuals. Instead, noise impacted FCM levels on a lek-wide basis.

Blickley et al. [43] found a decline in lek attendance on road-noise leks more than twofold larger than the decline in lek attendance on drilling-noise leks, yet we found no difference in FCM levels between noise-playback types (Table 1, Figure 1). Both noise sources have most of their sound energy ≤2 kHz, but road noise is less predictable than drilling noise and more intermittent,

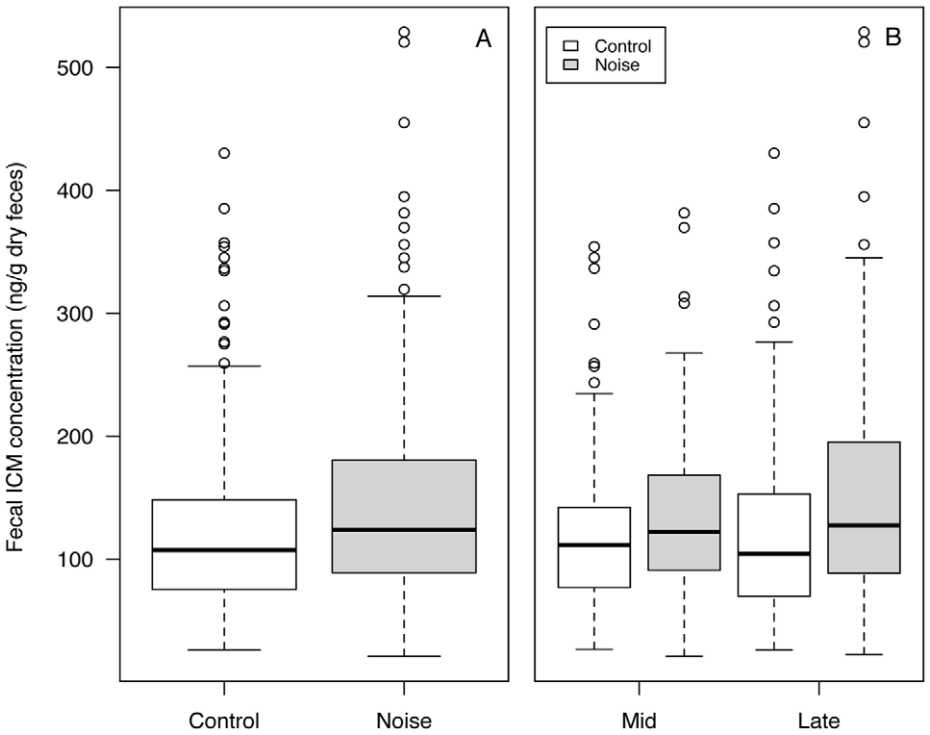



**Figure 2. FCM concentrations from control and noise-treated groups.** Data shown (A) pooled by season and (B) for mid and late season samples. Horizontal line represents the median value, box ends represent upper and lower quartiles, whiskers represent maximum and minimum values and open circles represent outliers. Plots present measured FCM values, not model output, which is presented in Table 2.
doi:10.1371/journal.pone.0050462.g002

**Table 3.** Mixed-effect candidate models assessing the relationship of FCM concentrations and changes in lek attendance from the previous year on noise-playback leks.

| Model[a,b] | $K$[c] | $\Delta AIC_c$[d] | $w_i$[e] |
|---|---|---|---|
| Null- random effects only[f] | 5 | 0 | 0.90 |
| Fecal cort | 6 | 4.6 | 0.10 |

[a]Abbreviations of predictor variables in methods.
[b]All models contain lek pairing and year as a random effect.
[c]Number of parameters in the model.
[d]Difference in $AIC_c$ (Akaike's Information criteria for small sample size) values from the top ranking model.
[e]Akaike weight.
[f]Model with substantial support ($\Delta AIC_c < 3$).
doi:10.1371/journal.pone.0050462.t003

leading to a lower average noise exposure across road-noise leks ($43.2 \pm 0.89$ dBA $L_{eq}$) than drilling-noise leks ($56.1 \pm 0.45$ dBA $L_{eq}$) [43]. Studies on physiological stress in rodents indicate that stressors administered at unpredictable intervals result in greater elevations in plasma corticosterone [49]. Since cort levels may also be implicated in decisions to escape from deleterious conditions [50], we cannot say with certainty that noise type has no differential impact on FCM levels, only that there was no difference observed among males that chose to remain. If road noise did result in a greater cort response in some birds, but the most susceptible birds were also the most likely to disperse, differences would not necessarily be expected among remaining birds. In this scenario, it is likely that variance would be reduced in leks with high losses, reflecting disappearance of individuals with higher FCM levels. Levene's tests did not identify any such difference in variance (indeed, there was a significant difference in one year of the study, but in the opposite direction to predictions). However, the possibility that dispersal is linked to FCM levels cannot be ruled out. Regardless of whether the stress levels of birds on noise leks increased, or whether only high-stress-level individuals remained on noisy leks, these results indicate that chronic noise at leks creates less desirable habitat for greater sage-grouse.

The unknown status of dispersed grouse – and their unknown destinations – leaves several other possible scenarios that should be considered. It is possible that the individuals most likely to disperse could have had different cort profiles at the outset compared with those more prone to remain. If noise playback caused individuals with lower integrated cort to disperse away from noisy leks, that coupled with the possible addition of those birds to control leks could cause trends similar to those observed here. Two possible sources of variation in pre-experiment cort levels among individuals are age and social status [51–53]. Reduced juvenile recruitment may have contributed to the observed declines in lek attendance on noise leks, potentially leading to a difference in age structure on noise and control leks [43]; however, this is unlikely to explain the results of this study. Studies of altricial and semi-altricial birds have found lower stress responsiveness shortly after hatching, but responses resemble those of adults by the age of fledging or first molt [54–57]. Since young male sage-grouse attending leks are likely to be at least 10 months old and after their first molt, it is unlikely that they would have lower stress response than adults. Social status can also be related to corticosteroid levels [58], therefore social upheaval caused by dispersal between noise and control leks may have contributed to observed FCM levels. Further studies are needed determine whether age-class- and social-status-dependent dispersal in response to noise contributed to the observed results.

Unlike noise sources in most energy development sites, our noise introduction in this study was localized to the immediate lek area, so birds were exposed to noise for only a few hours a day, and only during the breeding season. Therefore, we cannot quantify the effects of noise on FCMs for wintering, nesting or foraging males. Noise at energy development sites is less seasonal and more widespread and may thus affect birds at all life stages, with a potentially greater impact on stress levels. In addition, we looked only at male stress levels in this study, but males and females may respond differently to stress. For example, Jankowski et al. [45] measured FCM levels in sage-grouse in habitats with and without cattle grazing; they found no difference in male FCM levels in response to grazing regime, however, breeding females showed elevated stress response in grazed areas. This suggests that females may be more vulnerable to some types of disturbance; further studies are needed to assess whether female stress levels are influenced by noise.

## Why might noise be stressful?

Increased adrenocortical activity occurs in response to circumstances perceived as threatening by an animal. Although we cannot determine from this study the extent to which noise itself is a threat to sage-grouse, noise may affect social dynamics and increase the perception of threat. Noise may have social impacts on sage-grouse by masking acoustic communication on the lekking grounds [42]. Masking occurs when the perception of a sound is decreased by the presence of background noise, which may reduce the efficacy of acoustic communication. Acoustic signals play an important role in many social interactions, including mate attraction and assessment, territorial interactions, recognition of conspecifics and alarm calling in response to environmental threats [9,10,59]. Masking of these acoustic signals may alter or interfere with social interactions and mate choice behaviors [60,61].

For prey species such as sage-grouse, noise may also increase stress levels by masking the sounds of approaching predators and increasing the perception of risk from predation [62,63]. The degree to which noise directly affects mortality through changes in predation is largely unknown, as few studies have compared predation rates or hunting success in noisy and quiet areas while controlling for other confounding factors. Francis et al. [4] did so and found that nest predation rates in some songbirds decline in noise-impacted areas, as the dominant nest predator avoided noise. This suggests that noise may cause complicated changes in predator-prey dynamics. Noise may also cause stress due to short-term disruptions in behavior, such as startling or frightening animals away from food or other resources [2,64]. Further, if individuals associate a particular type of noise, such as road noise, with a danger, such as vehicular traffic, this may provoke a stress response [43].

## The impacts of chronic stress

Glucocorticoid release under challenging conditions is an adaptation to life in an unpredictable and threatening world [20]; individuals benefit from curtailing reproduction, altering behavioral patterns, and redirecting metabolic substrates to maximize glucose availability for action in response to genuine threats. Glucocorticoid levels alone are not directly or inversely correlated with fitness measures under all conditions [65], however, chronic adrenal activation has many known trade-offs that result in vulnerability to disease and death [22]. Unlike threats from predators, food shortages and inclement weather, noise typically does not directly threaten the survival of an individual or

its offspring (though there may be exceptions, as discussed below). Therefore, the cost of chronic adrenal activation in response to noise pollution is unlikely to be outweighed by the benefits in most cases, and thus the net result may be adverse.

One important trade-off is the effect of corticosterone on immune response. Chickens infected with West Nile Virus (WNV) and administered corticosterone had increased oral shedding and lengthened duration of viremia compared to those without elevated cort [66]. For sage-grouse, which are highly susceptible to WNV [67,68], reduced immune response due to elevated glucocorticoid levels could have a significant effect on survival in areas where they are exposed to WNV. Therefore, despite the adaptive nature of the stress response under natural conditions, elevated glucocorticoid levels due to human disturbance may have detrimental long-term impacts on welfare and survival of sage-grouse and other wildlife.

### Stress as an indicator of human impacts on sage-grouse

Measurement of FCMs may provide a non-invasive monitoring tool to assess the impact of human development (e.g. oil and gas drilling, wind farms, highways, off-road vehicle traffic) on stress levels of greater sage-grouse and other species. However comparisons between disturbed and undisturbed areas would need to account for differences in age, sex, and breeding condition of individuals sampled as well as for differences in the environmental conditions between sites in order to isolate stress as the likely cause of change [15,18,69]. We controlled for such differences by using an experimental presentation of noise that minimized effect on other habitat variables, limiting our collection to lekking birds, collecting only on days with limited female attendance and collecting samples from all leks within a short 2–3 day window. We did not find support for differences in FCM levels from samples collected in early versus late April within each season (~20 days apart in a 2–3 month breeding season), and only limited evidence for an effect of location (Hudson vs. Riverton, ~32 kilometers apart), suggesting that these temporal and spatial differences did not affect FCM levels in our study. However with a larger sample of leks or in another region or time period, it is possible that such differences might emerge.

### Conclusions

Taken together, results from Blickley et al. [43] and this study suggest that noise alone can cause greater sage-grouse to avoid otherwise suitable habitat and increase the stress responses of birds that remain in noisy areas. Thus, noise mitigation may be a fruitful conservation measure for this species of concern. In this study, we focused on the effects of noise from roads and drilling rigs in natural gas development areas; other natural gas development infrastructure, including compressor stations and generators, produces noise similar to drilling rigs, with the potential for similar effects on FCM levels. Likewise, other types of energy development produce noise similar in frequency, timing, and amplitude to the noise sources used here, including shale gas, coal-bed methane, oil, and geothermal development. The noise sources used in this study also share some characteristics with other anthropogenic noise sources that are increasing across the landscape, like wind turbines, off-road vehicles, highways and urban development; this suggests that the impacts on greater sage-grouse observed here may be widespread. More generally, populations of many species of birds [4,70–74] and mammals [75–78] decline with proximity to noisy human activities, such as roads, urban and industrial developments. While further study is needed to determine whether chronic noise exposure contributes to the impacts of these human activities by activating the chronic stress response, this study adds to a growing body of evidence that such noise pollution is a threat to wildlife [1,2], significantly increasing our estimates of the footprint of human development beyond the boundaries of visible disturbance.

## Acknowledgments

For help and advice during the conception and execution of this project we thank Kurt Fristrup, Tom Rinkes, Sue Oberlie, Stan Harter, Tom Christiansen, Diane Blackwood and our many excellent field assistants. For statistical advice and helpful comments on the manuscript, we thank Teresa L. Iglesias, the Patricelli Lab at UC Davis and two anonymous reviewers.

## Author Contributions

Conceived and designed the experiments: JLB GLP AHK SNS. Performed the experiments: JLB AHK GLP SNS KRW JLP JCW. Analyzed the data: JLB KRW GLP AHK JLP CCT JCW. Contributed reagents/materials/analysis tools: GLP JCW. Wrote the paper: JLB KRW GLP.

## References

1. Kight CR, Swaddle JP (2011) How and why environmental noise impacts animals: an integrative, mechanistic review. Ecology Letters 14: 1052–1061.
2. Barber JR, Crooks KR, Fristrup KM (2009) The costs of chronic noise exposure for terrestrial organisms. Trends in Ecology & Evolution 25: 180–189.
3. Blickley JL, Patricelli GL (2010) Impacts of Anthropogenic Noise on Wildlife: Research Priorities for the Development of Standards and Mitigation. Journal of International Wildlife Law and Policy 13: 274–292.
4. Francis CD, Ortega CP, Cruz A (2009) Noise Pollution Changes Avian Communities and Species Interactions. Current Biology 19: 1415–1419.
5. Habib L, Bayne EM, Boutin S (2007) Chronic industrial noise affects pairing success and age structure of ovenbirds Seiurus aurocapilla. Journal of Applied Ecology 44: 176–184.
6. Bayne E, Habib L, Boutin S (2008) Impacts of Chronic Anthropogenic Noise from Energy-Sector Activity on Abundance of Songbirds in the Boreal Forest. Conservation Biology 22: 1186–1193.
7. Hu Y, Cardoso GC (2009) Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? Behavioral Ecology 20: 1268–1273.
8. Slabbekoorn H, Ripmeester EAP (2008) Birdsong and anthropogenic noise: implications and applications for conservation. Molecular Ecology 17: 72–83.
9. Warren PS, Katti M, Ermann M, Brazel A (2006) Urban bioacoustics: it's not just noise. Animal Behaviour 71: 491–502.
10. Patricelli GL, Blickley JL (2006) Overview: Avian communication in urban noise: the causes and consequences of vocal adjustment. The Auk 123: 639–649.
11. Francis CD, Kleist NJ, Ortega CP, Cruz A (2012) Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal. Proceedings of the Royal Society B: Biological Sciences.
12. Wikelski M, Cooke SJ (2006) Conservation physiology. Trends in Ecology & Evolution 21: 38–46.
13. Romero LM (2004) Physiological stress in ecology: lessons from biomedical research. Trends in Ecology & Evolution 19: 249–255.
14. Creel S, Fox JE, Hardy A, Sands J, Garrott B, et al. (2002) Snowmobile Activity and Glucocorticoid Stress Responses in Wolves and Elk. Conservation Biology 16: 809–814.
15. Wasser SK, Bevis K, King G, Hanson E (1997) Non-Invasive Physiological Measures of Disturbance in the Northern Spotted Owl. Conservation Biology 11: 1019–1022.
16. Thiel D, Jenni-Eiermann S, Palme R (2005) Measuring corticosterone metabolites in droppings of capercaillies (*Tetrao urogallus*). Bird Hormones And Bird Migrations: Analyzing Hormones In Droppings And Egg Yolks And Assessing Adaptations In Long-Distance Migration. pp. 96–108.
17. Wasser SK, Bevis K, King G, Hanson E (1997) Noninvasive Physiological Measures of Disturbance in the Northern Spotted Owl. Conservation Biology 11: 1019–1022.
18. Millspaugh JJ, Washburn BE (2004) Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation. General and Comparative Endocrinology 138: 189–199.

19. Lucas JR, Freeberg TM, Egbert J, Schwabl H (2006) Fecal corticosterone, body mass, and caching rates of Carolina chickadees (*Poecile carolinensis*) from disturbed and undisturbed sites. Hormones and Behavior 49: 634–643.
20. Wingfield JC (2005) The concept of allostasis: coping with a capricious environment. Journal of Mammalogy 86: 248–254.
21. McEwen BS, Wingfield JC (2003) The concept of allostasis in biology and biomedicine. Hormones and Behavior 43: 2–15.
22. Sapolsky RM, Romero LM, Munck AU (2000) How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory and preparative actions. Endocrine Reviews 21: 55–89.
23. Wingfield JC, Sapolsky RM (2003) Reproduction and resistance to stress: when and how. J Neuroendocrinol 15: 711–724.
24. Opplinger A, Clobert J, Lecomte J, Lorenzon P, Boudjemadi K, et al. (1998) Environmental stress increases the prevalence and intensity of blood parasite infection in the common lizard Lacerta vivipara. Ecology Letters 1: 129–138.
25. Alario P, Gamallo A, Beato MJ, Trancho G (1987) Body weight gain, food intake and adrenal development in chronic noise stressed rats. Physiology & Behavior 40: 29–32.
26. Barrett AM, Stockham MA (1963) The effect of housing conditions and simple experimental procedures upon the corticosterone level in the plasma of rats. Journal of Endocrinology 26: 97–105.
27. Davis M, Walker DL, Lee Y (1997) Amygdala and bed nucleus of the stria terminalis: differential roles in fear and anxiety measured with the acoustic startle reflex. Philosophical Transactions of the Royal Society of London, B 352: 1675–1687.
28. Atkinson H, Wood S, Kershaw Y, Bate E, Lightman S (2006) Diurnal Variation in the Responsiveness of the Hypothalamic-Pituitary-Adrenal Axis of the Male Rat to Noise Stress. Journal of neuroendocrinology 18: 526–533.
29. Thiel D, Jenni-Eiermann S, Palme R, Jenni L (2011) Winter tourism increases stress hormone levels in the Capercaillie *Tetrao urogallus*. Ibis 153: 122–133.
30. Delaney DK, Grubb TG, Beier P, Pater LL, Reiser MH (1999) Effects of helicopter noise on Mexican spotted owls. Journal of Wildlife Mangement 63: 60–76.
31. Tempel DJ, Gutiérrez RJ (2003) Fecal Corticosterone Levels in California Spotted Owls Exposed to Low-Intensity Chainsaw Sound. Wildlife Society Bulletin 31: 698–702.
32. Babisch W (2003) Stress hormones in the research on cardiovascular effects of noise. Noise Health 5: 1–11.
33. Ising H, Ising M (2002) Chronic cortisol increases in the first half of the night caused by road traffic noise. Noise Health 4: 13–21.
34. Evans GW, Lercher P, Meis M, Ising H, Kofler WW (2001) Community noise exposure and stress in children. Journal Of The Acoustical Society Of America 109: 1023–1027.
35. Evans GW, Bullinger M, Hygge S (1998) Chronic Noise Exposure and Physiological Response: A Prospective Study of Children Living under Environmental Stress. Psychological Science 9: 75–77.
36. Department of the Interior (2010) Endangered and Threatened Wildlife and Plants; 12-Month Findings for Petitions to List the Greater Sage-Grouse (*Centrocercus urophasianus*) as Threatened or Endangered. Federal Register 75: 13910–14014.
37. Connelly JW, Knick ST, Schroeder MA, Stiver SJ (2004) Conservation Assessment of Greater Sage-grouse and Sagebrush Habitats. Cheyenne, WY: West. Assn. Fish and Wildlife Agencies. 610 p.
38. Holloran MJ (2005) Greater Sage-Grouse (*Centrocercuc urophasianus*) Population Response to Natural Gas Field Development in Western Wyoming [Dissertation]. Laramie: University of Wyoming. 114 p.
39. Walker BL, Naugle DE, Doherty KE (2007) Greater Sage-Grouse Population Response to Energy Development and Habitat Loss. Journal of Wildlife Management 71: 2644–2654.
40. Holloran M, Kaiser R, Hubert W (2010) Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74: 65–72.
41. Naugle DE, Doherty KE, Walker BE, Holloran MJ, Copeland HJ (2011) Energy development and Greater Sage-Grouse. In: Knick ST, Connelly JW, editors. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Berkeley, CA.: University of California Press.
42. Blickley JL, Patricelli GL (2012) Potential acoustic masking of greater sage-grouse display components by chronic industrial noise. Ornithological Monographs 74: 23–35.
43. Blickley JL, Blackwood D, Patricelli GL (2012) Experimental Evidence for the Effects of Chronic Anthropogenic Noise on Abundance of Greater Sage-Grouse at Leks. Conservation Biology 26: 461–471.
44. Vehrencamp S, Bradbury J, Gibson R (1989) The energetic cost of display in male sage grouse. Animal Behaviour 38: 885–896.
45. Jankowski MD (2007) The influence of habitat disturbance and synergized resmethrin on avian immunocompetence: The University of Wisconsin, Madison.
46. Jankowski MD, Wittwer DJ, Heisey DM, Franson JC, Hofmeister EK (2009) The Adrenocortical Response of Greater Sage Grouse (*Centrocercus urophasianus*) to Capture, ACTH Injection, and Confinement, as Measured in Fecal Samples. Physiological and Biochemical Zoology 82: 190–201.
47. Wasser SK, Hunt KE, Brown JL, Cooper K, Crockett CM, et al. (2000) A Generalized Fecal Glucocorticoid Assay for Use in a Diverse Array of Nondomestic Mammalian and Avian Species. General and Comparative Endocrinology 120: 260–275.
48. Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach: Springer Verlag.
49. Weiss JM (1970) Somatic Effects of Predictable and Unpredictable Shock. Psychosomatic Medicine 32: 397–408.
50. Wingfield JC, Maney DL, Breuner CW, Jacobs JD, Sharon L, et al. (1998) Ecological Bases of Hormone-Behavior Interactions: The "Emergency Life History Stage". American Zoologist 38: 191–206.
51. Goymann W, Wingfield JC (2004) Allostatic load, social status and stress hormones: the costs of social status matter. Animal Behaviour 67: 591–602.
52. Angelier F, Shaffer SA, Weimerskirch H, Chastel O (2006) Effect of age, breeding experience and senescence on corticosterone and prolactin levels in a long-lived seabird: The wandering albatross. General and Comparative Endocrinology 149: 1–9.
53. Angelier F, Moe B, Weimerskirch H, Chastel O (2007) Age-specific reproductive success in a long-lived bird: do older parents resist stress better? Journal of Animal Ecology 76: 1181–1191.
54. Schwabl H (1999) Developmental Changes and Among-Sibling Variation of Corticosterone Levels in an Altricial Avian Species. General and Comparative Endocrinology 116: 403–408.
55. Wada H, Hahn TP, Breuner CW (2007) Development of stress reactivity in white-crowned sparrow nestlings: Total corticosterone response increases with age, while free corticosterone response remains low. General and Comparative Endocrinology 150: 405–413.
56. Freeman BM (1982) Stress non-responsiveness in the newly-hatched fowl. Comparative Biochemistry and Physiology Part A: Physiology 72: 251–253.
57. Dickens MJ, Romero LM (2010) Stress Responsiveness Decreases With Age in Precocial, Juvenile Chukar. The Wilson Journal of Ornithology 122: 762–766.
58. Rubenstein DR (2007) Stress hormones and sociality: integrating social and environmental stressors. Proceedings of the Royal Society B: Biological Sciences 274: 967–975.
59. Brumm H, Slabbekoorn H (2005) Acoustic Communication in Noise. Advances in the Study of Behavior 35: 151–209.
60. Mockford EJ, Marshall RC (2009) Effects of urban noise on song and response behaviour in great tits. Proceedings of the Royal Society B: Biological Sciences 276: 2979–2985.
61. Swaddle JP, Page LC (2007) High levels of environmental noise erode pair preferences in zebra finches: implications for noise pollution. Animal Behaviour 74: 363–368.
62. Rabin LA, Coss RG, Owings DH (2006) The effects of wind turbines on antipredator behavior in California ground squirrels (Spermophilus beecheyi). Biological Conservation 131: 410–420.
63. Quinn L, Whittingham J, Butler J, Cresswell W (2006) Noise, predation risk compensation and vigilance in the chaffinch Fringilla coelebs. Journal of Avian Biology 37: 601–608.
64. Dooling RJ, Popper AN (2007) The Effects of Highway Noise on Birds. Sacramento, CA: The California Department of Transportation Division of Environmental Analysis. 74 p.
65. Bonier F, Martin PR, Moore IT, Wingfield JC (2009) Do baseline glucocorticoids predict fitness? Trends in Ecology & Evolution 24: 634–642.
66. Jankowski MD, Franson JC, Möstl E, Porter WP, Hofmeister EK (2010) Testing independent and interactive effects of corticosterone and synergized resmethrin on the immune response to West Nile virus in chickens. Toxicology 269: 81–88.
67. Naugle DE, Aldridge CL, Walker BL, Cornish TE, Moynahan BJ, et al. (2004) West Nile virus: Pending crisis for Greater Sage-Grouse. Ecology Letters 7: 704–713.
68. Walker BE, Naugle DE (2011) West Nile Virus ecology in sagebrush habitat and impacts on Greater Sage-Grouse populations. In: Knick ST, Connelly JW, editors. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Berkeley, CA.: University of California Press.
69. Sheriff MJ, Wheeler H, Donker SA, Krebs CJ, Palme R, et al. (2012) Mountain-top and valley-bottom experiences: the stress axis as an integrator of environmental variability in arctic ground squirrel populations. Journal of Zoology 287: 65–75.
70. Kuitunen M, Rossi E, Stenroos A (1998) Do Highways Influence Density of Land Birds? Environmental Management 22: 297–302.
71. van der Zande AN, ter Keurs WJ, van der Weijden WJ (1980) The impact of roads on the densities of four bird species in an open field habitat–evidence of a long-distance effect. Biological Conservation 18: 299–321.
72. Rheindt FE (2003) The impact of roads on birds: Does song frequency play a role in determining susceptibility to noise pollution? J für Ornithologie 144: 295–306.
73. Ingelfinger F, Anderson S (2004) Passerine response to roads associated with natural gas extraction in a sagebrush steppe habitat. Western North American Naturalist 64: 385–395.
74. Peris SJ, Pescador M (2004) Effects of traffic noise on paserine populations in Mediterranean wooded pastures. Applied Acoustics 65: 357–366.
75. Singer FJ (1978) Behavior of Mountain Goats in Relation to US Highway 2, Glacier National Park, Montana. The Journal of Wildlife Management 42: 591–597.
76. Rost GR, Bailey JA (1979) Distribution of Mule Deer and Elk in Relation to Roads. The Journal of Wildlife Management 43: 634–641.
77. Forman RTT, Deblinger RD (2000) The Ecological Road-Effect Zone of a Massachusetts (U. S. A.) Suburban Highway. Conservation Biology 14: 36–46.
78. Sawyer H, Kauffman M, Nielson R (2009) Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73: 1052–1061.




Effects of Organophosphorus Insecticides on Sage Grouse in Southeastern Idaho
Author(s): Lawrence J. Blus, Chris S. Staley, Charles J. Henny, Grey W. Pendleton, Tim H. Craig, Erica H. Craig, Douglas K. Halford
Source: *The Journal of Wildlife Management*, Vol. 53, No. 4 (Oct., 1989), pp. 1139-1146
Published by: Allen Press
Stable URL: http://www.jstor.org/stable/3809623
Accessed: 24/02/2009 11:08

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=acg.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.




*Allen Press* is collaborating with JSTOR to digitize, preserve and extend access to *The Journal of Wildlife Management.*

http://www.jstor.org

# EFFECTS OF ORGANOPHOSPHORUS INSECTICIDES ON SAGE GROUSE IN SOUTHEASTERN IDAHO

LAWRENCE J. BLUS, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, 480 S.W. Airport Road, Corvallis, OR 97333
CHRIS S. STALEY, EG & G Idaho, Incorporated, P.O. Box 1625, Idaho Falls, ID 83415
CHARLES J. HENNY, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, 480 S.W. Airport Road, Corvallis, OR 97333
GREY W. PENDLETON, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD 20708
TIM H. CRAIG, Box 1, Lee Creek Road, Leadore, ID 83464
ERICA H. CRAIG, Box 1, Lee Creek Road, Leadore, ID 83464
DOUGLAS K. HALFORD,[1] EG & G Idaho, Incorporated, P.O. Box 1625, Idaho Falls, ID 83415

*Abstract:* Die-offs of sage grouse (*Centrocercus urophasianus*) were verified in southeastern Idaho in 1981. We captured 82 apparently healthy grouse to quantify the effects of organophosphorus insecticides (OP's) and other pesticides on sage grouse in sagebrush (*Artemisia* spp.) bordering agricultural lands in July 1985 and 1986. Grouse were fitted with radio collars and tracked through part of each summer. At least 18% of 82 radio-tagged grouse in 1985–86 subsequently occupied fields at the time they were sprayed with OP insecticides dimethoate or methamidophos. Cholinesterase (ChE) assays of brains and residue analysis of crop contents indicated that 5 and 16% of the marked sample died from OP's in 1985 and 1986, respectively. Approximately 200 sage grouse were present in a block of alfalfa sprayed with dimethoate; 63 of these were later found dead and ChE activity in 43 brains suitable for assay were depressed >50%. Maximum residues in crop contents of dead grouse were 18 μg/g methamidophos and 30 μg/g dimethoate. Intoxicated or dead grouse were observed in or near 6 fields sprayed with dimethoate or methamidophos in 1985–86. Twenty of 31 intoxicated grouse radiotagged after being found in dimethoate-sprayed (1986) alfalfa died. Our study indicates that certain pesticides have the potential for adversely affecting grouse populations.

***J. WILDL. MANAGE. 53(4):1139–1146***

Replacement of organochlorine insecticides (OC's) with shorter-lived chemicals such as organophosphorus (OP), carbamate, and other compounds alleviated many problems with persistence and bioaccumulation of lipid-soluble OC's (Blus 1982, Wiemeyer et al. 1984). Additional research revealed that serious effects, resulting from different modes of action, are also associated with use of the newer compounds, particularly from a short-term perspective where acute or subacute toxicity (Hill and Fleming 1982, Grue et al. 1983, Henny et al. 1985) and reduction in the food base are major concerns (Rands 1985, Potts 1986).

Initial evidence that OP's caused mortality of sage grouse was noted in 1981 when a die-off occurred near a potato field sprayed with methamidophos. Brain ChE activity of 5 sage grouse collected when intoxicated (sick, immobile, and showing signs of OP poisoning) and later sacrificed ranged from normal to 61% inhibition (E. F. Hill, Fish and Wildl. Serv., pers. commun.). Data collected in 1983 indicated depression of 40 to 65% in brain ChE activity of grouse collected in a potato field shortly after spraying with methamidophos. These preliminary findings and previous unverified reports of die-offs suggested a potentially serious situation and led to radio-telemetry studies in southeastern Idaho in 1985–86. The purpose of our study was to determine and quantify effects of OP's on a population of sage grouse.

We thank K. L. Stromborg, D. H. White, and B. A. Rattner for reviewing the manuscript; the many individuals assisting with field work including C. R. Breckenridge, M. C. Mondecar, and R. K. Sherwood; and J. W. Connelly, Jr. and other members of the Idaho Department of Fish and Game for ideas and assistance. This study was partially funded by the U.S. Environmental Protection Agency (Interagency Agreement DW89931370-01).

## STUDY AREA AND METHODS

The study area was located in southeastern Idaho near Mud Lake, Monteview, Hamer, and Camas in Jefferson County and Arco in Butte County (Fig. 1). This area provided summer range for sage grouse (Gates 1983, Connelly et al. 1988). Major agricultural crops included small

[1] Present address: Oak Ridge National Laboratory, P.O. Box 2567, Grand Junction, CO 81502.

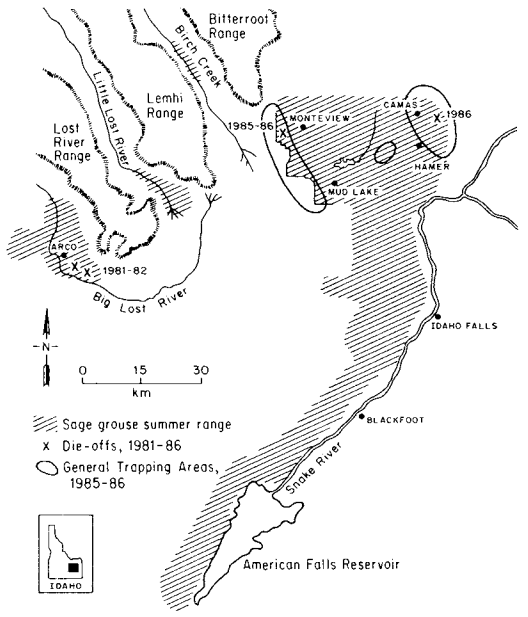



Fig. 1. Area of sage grouse study where die-offs occurred.

grains, potatoes, and alfalfa; many fields were bordered by sagebrush. Field work was conducted from April to August 1985 and from May to early September 1986. Spraying regimes employed by farmers in the study area were those normally used there.

From 9 to 26 July 1985, 39 apparently healthy sage grouse (30 juv and 9 ad F) were captured by night-lighting (Giesen et al. 1982) in sagebrush near alfalfa fields, and fitted with radio collars (Amstrup 1980, Dunn and Braun 1985). An intoxicated grouse captured in a sprayed alfalfa field was also radiotagged.

We captured apparently healthy sage grouse from 7 to 29 July 1986 by night-lighting. Radio collars were attached to 31 sage grouse taken near alfalfa fields and 12 sage grouse taken near potato fields; 31 grouse found intoxicated in sprayed fields were also radiotagged. In 1985 and 1986, individual grouse were located 2–14 times/week until the signal was permanently lost, the bird died or was collected, or the study was terminated (23 Aug 1985 and 3 Sep 1986 with a subsequent collection of 3 birds on 17 Sep 1986). Survival of radio-tagged grouse was recorded in grouse-days (i.e., 1 grouse surviving 1 day). Habitat was recorded each grouse-day that we located a bird; radio locations were verified by triangulation of several readings taken within 0.5 km of each grouse. Most radio tracking was done from trucks equipped with a null-peak system; some tracking was done on foot and from fixed-wing aircraft. Searches for radio-tagged grouse were not random; rather, we concentrated our work in areas where the grouse were last seen and expanded our search area to look for missing grouse.

Grouse found dead and those shot were placed on ice and frozen within 4 hours of collection. For analysis, grouse were thawed at room temperature and their brains were removed after medial bisection. We performed ChE assays on each half of the brain and values were averaged.

Although 2 different spectrophotometers were used, standardized methods for ChE assays (Ellman et al. 1961) with subsequent modifications (Hill and Fleming 1982) were used throughout the study. All assays were performed at 25 C and brains of apparently healthy (control) sage grouse were assayed concurrently with those of grouse exposed to OP's. Controls consisted of hunter-killed grouse and road-killed individuals picked up in non-agricultural areas. Precilip standard (Boehringer Mannheim, Indianapolis, Ind.) with an acceptable range of ChE values for freeze-dried human serum was used for quality assurance. The standard was tested $\geq 1$ time/day that grouse brains were assayed to ensure that the spectrophotometer was properly calibrated and that our procedures resulted in accurate readings. In both years, ChE assays of the standard indicated our results were in the acceptable range listed by the manufacturer.

Cholinesterase activity is expressed as micromoles of substrate (acetylthiocholine iodide) hydrolyzed/minute/g of brain tissue. Control ChE activity is expressed as the mean $\pm$ 2 standard deviations (SD). Exposure of individual grouse to an anti-ChE compound is indicated when the ChE level is $\leq$ the control $\bar{x} - 2$ SD, and anti-ChE exposure is postulated as the cause of death with inhibition $\geq 50\%$ (Ludke et al. 1975, Hill and Fleming 1982).

Crop or gizzard contents of sage grouse collected in 1985 and 1986 were homogenized, extracted, and analyzed for OP's at the Patuxent Wildlife Research Center or the Environmental Protection Agency, Corvallis Environmental Research Laboratory, with a gas chromatograph equipped with an electron capture detector (White et al. 1982; E. J. Kolbe, Fish and Wildl. Serv., pers. commun.; R. S. Bennett, Environ. Prot. Agency, pers. commun.). Approximately

Table 1. Proportion of time radio-tagged sage grouse were located in various habitats in summer range, southeastern Idaho, 1985–86.

| Yr Statistics | Grouse-days and individuals located in fields | | | | |
|---|---|---|---|---|---|
| | Alfalfa | Potatoes | Other crops | Non-cropland | Totals |
| 1985 | 119 | | 31 | 145 | 775 |
| *n* | 31 | | 11 | 35 | 39 |
| $\bar{x}$ | 3.9 | | 2.6 | 4.1 | 19.9 |
| SD | 3.9 | | 1.9 | 2.7 | 12.4 |
| Range | 1–17 | | 1–6 | 1–11 | 1–45 |
| 1986 | 342 | 96 | 44 | 390 | 1,476 |
| *n* | 27 | 9 | 7 | 41 | 43 |
| $\bar{x}$ | 13.3 | 10.7 | 3.7 | 9.5 | 34.3 |
| SD | 9.8 | 8.1 | 3.3 | 10.1 | 17.6 |
| Range | 1–34 | 1–21 | 1–10 | 1–43 | 1–57 |

10% of the residue analyses was confirmed with a mass spectrometer. Recovery of dimethoate or methamidophos from spiked samples ranged from 70 to 90%; residues were not corrected for recovery values. The lower limit of quantification ranged from 0.1 to 0.5 μg/g; residues were expressed on a wet weight basis.

Survival functions of radio-collared sage grouse were estimated with the Kaplan-Meier (product limit) non-parametric estimator (Lee 1980). Using this method we estimated the probability of grouse surviving beyond a specified time, to a specific date or number of days since marking. A staggered entry scheme was used in estimating the survival function (Pollock et al. 1989) to preserve the relationship between the survival function and the calendar date. A Chi-square test was used to compare survival of adult and juvenile grouse that were radiotagged when apparently healthy or intoxicated.

## RESULTS

### General Movements

Each of 39 healthy sage grouse radiocollared near alfalfa fields in 1985 were tracked from 1 to 45 days for 775 grouse-days (Table 1). Thirty-one grouse were observed in cropland; 19 and 15% of the grouse-days were recorded in cropland and alfalfa, respectively.

The 43 healthy sage grouse radiocollared in 1986 were divided into 2 groups: grouse captured near alfalfa ($n = 31$) or potatoes ($n = 12$). All grouse were trapped in sagebrush within 0.5 km of cropland. Each grouse trapped near alfalfa or potato fields was tracked from 1 to 57 days and 12 to 41 days, respectively (Table 1). Grouse captured near alfalfa spent 33% of the total grouse-days in cropland (31% in alfalfa), while those captured near potato fields spent 32% of the grouse-days in cropland (25% in potato fields).

During 1985 and 1986 85% of the 82 radio-tagged grouse were located ≥1 time in cropland, and the other 15% remained near cropland through much of the tracking period. Maximum distances sage grouse moved from sagebrush into cropland were 2.3 and 3.9 km in 1985 and 1986, respectively; these grouse remained in cropland for several weeks. By late August 1986, a few grouse moved back to sagebrush; some were 4 km from the nearest cropland. The daily activity pattern of about 90% of the radio-tagged sage grouse suggested feeding in cropland and roosting and loafing in nearby sagebrush. Because individuals were not located on 62 and 41% of the grouse-days in 1985 and 1986, respectively, their use of cropland and other habitats was much higher than recorded.

### Intoxication and Mortality

Six of 39 (15%) grouse radiocollared when apparently healthy in 1985 later occupied a 240-ha alfalfa field (AB alfalfa) sprayed with dimethoate on 5 August; all 6 became intoxicated and 2 birds died with 62 and 73% inhibition of brain ChE activity (Table 2). The 4 intoxicated birds could not walk or fly; they were emaciated, had diarrhea, frequently salivated, and sometimes uttered faint vocalizations. These signs are characteristic of anticholinesterase compounds such as OP's and carbamates. The biochemical lesion is phosphorylation or carbamylation of acetylcholinesterase and resultant accumulation of acetylcholine that induces problems with the nervous system (O'Brien 1960). Four intoxicat-

Table 2. Brain cholinesterase (ChE) activity of sage grouse, controls compared to birds collected or found dead in summer in or near southeastern Idaho cropland, 1985 and 1986.

| | | | | Brain ChE | | | |
|---|---|---|---|---|---|---|---|
| | | | | % change from control[a] | | % of grouse | |
| Y | *n* | OP[b] | Condition | $\bar{x}$ | Range | Exposed[c] | With ≥50% inhibition |
| 1985 | 2 | DI | Dead | −67.3 | −72.5–−62.1 | 100 | 100 |
| 1985 | 3 | — | Dead[d] | +0.6 | −9.8–13.7 | 0 | 0 |
| 1985 | 5 | DI | Shot | −34.2 | −36.8–−31.0 | 100 | 0 |
| 1985 | 11 | — | Shot | +7.1 | −61.1–37.9 | 9 | 9 |
| 1985 | 2 | DI | Sick | −66.5 | −66.8–−66.3 | 100 | 100 |
| 1986 | 43 | DI | Dead | −73.6 | −90.3–−50.6 | 100 | 100 |
| 1986 | 2 | ME | Dead | −40.8 | −42.8–−38.7 | 100 | 0 |
| 1986 | 8 | DI | Shot | −13.9 | −30.2–6.2 | 25 | 0 |
| 1986 | 1 | — | Dead[e] | | −7.8 | 0 | 0 |

[a] Results of control ChE assays ($\bar{x}$ micromoles of substrate [acetylthiocholine iodide] hydrolyzed/min/g of brain tissue ± 2 SD) were 12.54 ± 2.18 for 11 birds in 1985 and 15.30 ± 3.34 for 7 birds in 1986.
[b] Known exposure to methamidophos (ME) or dimethoate (DI) listed when known; — = no known exposure to organophosphorus insecticides (OP's).
[c] Less than control $\bar{x}$ − 2 SD.
[d] Includes roadkill, predator kill, and undetermined cause of death.
[e] Roadkill.

ed grouse recovered after approximately 1 week and left the alfalfa field; these birds appeared normal but had 31–35% inhibition of brain ChE activity when shot on 14 or 23 August (Table 2).

Three intoxicated grouse without radio collars were located in 1985 during a field search in AB alfalfa for radio-tagged grouse. Two grouse were captured and sacrificed (8–9 Aug); brain ChE activity was inhibited 66 and 67%. The third intoxicated grouse found on 9 August was fitted with a radio collar. It recovered and seemed healthy when shot on 23 August; however, its brain ChE was still inhibited 37% (Table 2). On 6 August, 2 grouse without radio collars were shot on the ground in sagebrush near AB alfalfa. The brain ChE activity of 1 grouse was normal but the other showed 61% inhibition (Table 2).

In 1985, residue analysis of the gizzard contents of 3 grouse adversely affected by dimethoate sprayed on AB alfalfa (2 found dead and 1 sacrificed 3–4 days post-spray) revealed that only 1 grouse had residues of dimethoate (0.2 μg/g); crops of all 3 were empty. Seven grouse that were shot, including 5 that had recovered from OP intoxication in AB alfalfa and were collected 9 or 18 days post-spray, contained no residues of dimethoate in crop or gizzard contents.

Nine of 43 (21%) grouse radiocollared when healthy in 1986 later occupied fields sprayed with OP's. Eight of the 9 became intoxicated and 7 died from OP's. Five juveniles died after being sprayed with dimethoate in AB alfalfa at 0600 on 1 August; an adult female in the same field left shortly after spraying and showed no signs of intoxication. On 5 August, 2 partially eaten juvenile grouse were found buried in or near a potato field that was sprayed with methamidophos the previous day; these birds were probably eaten by a coyote (*Canis latrans*). A radio-tagged adult male that occupied a small alfalfa field sprayed with dimethoate on 6 August was intoxicated for several days; this was the only sick grouse found in the field adjacent to AB alfalfa.

We observed 100 sick or dead grouse around 3 alfalfa and 2 potato fields that were sprayed with OP's in 1986; the major die-off occurred in the AB alfalfa fields where we noted dead grouse in 1985. A flock of about 200 sage grouse occupied the AB alfalfa sprayed on 1 August; about 30 intoxicated and dead grouse were observed on 2 August with the last verified OP mortality occurring there on 12 August. We found 63 dead sage grouse in the AB alfalfa; these included 5 grouse radiotagged when healthy, 20 radiocollared when intoxicated, and 38 birds without radios (Table 3). In the large block of AB alfalfa sprayed with dimethoate on 1 August, we radiotagged 29 sage grouse found intoxicated; 20 of these apparently died from dimethoate and 10 deaths were verified by brain ChE assays.

Intoxicated sage grouse in the AB fields exhibited the same signs noted in 1985. Most of the sick grouse attempted to move into sagebrush. At least 2 grouse fell to the ground from

Table 3. Incidence of organophosphorus-related mortality of sage grouse by age and sex, southeastern Idaho, 1986.

| Marking Physical condition | No. grouse | | | | | |
|---|---|---|---|---|---|---|
| | F | | M | | Unknown sex | Unknown sex and age |
| | Ad | Juv | Ad | Juv | Juv | |
| Radiotagged | | | | | | |
| Healthy | 11 (0)[a] | 9 (3) | 4 (0) | 9 (4) | 10 (0) | |
| Intoxicated | 4 (4) | 11 (5) | 1 (1) | 14 (9) | | 1 (1) |
| Unmarked | (1) | (7) | (1) | (13) | (3) | (13) |

[a] Grouse radiotagged with organophosphorus insecticide-induced mortalities in parentheses.

flight. Most grouse died in or at the edge of the AB alfalfa, but 2 grouse radiotagged when intoxicated died in sagebrush 0.8 and 1 km from the field border. Avian and mammalian predators were attracted to the dead and dying grouse. We found 17 depredated carcasses in or near the AB fields ≤2 weeks after spray.

Assays of brains of 43 sage grouse found dead in AB alfalfa in 1986 revealed 51–90% inhibition of ChE activity (Table 2). Brains of 9 depredated grouse were suitable for ChE assay; activity was depressed from 51 to 86%. Of the 9 grouse that were radiocollared in AB alfalfa when intoxicated and subsequently recovered, 5 shot on 3 September had brain ChE activity inhibited from 9 to 30%; 3 other grouse shot on 17 September had brain ChE activity that ranged from −13 to 6% of control values. Unlike the 2 grouse that died from OP's in 1985, some of the birds in 1986 died soon after spraying; crops of 16 of 18 grouse found on 2 August contained alfalfa. Dimethoate residues in crop contents of 12 grouse found dead the day after spray ranged from 3 to 30 μg/g.

Two depredated radio-collared grouse that were found buried in or near a potato field the day after it was sprayed with methamidophos had brain ChE activity depressed 39 and 43% and crop contents of 1 grouse contained 18 μg/g methamidophos; these were the only 2 suspected OP mortalities during this study that had <50% inhibition of ChE activity.

## Survival Analysis

Survival analysis of the 39 sage grouse radiotagged when apparently healthy in 1985 indicated that the probability of these grouse dying during the 45-day tracking period was 0.25 (mortality = 1 − survival); however, only 2 (juv) of 9 documented deaths (1 ad F and 8 juv) were related to OP intoxication (probability of dying from OP's = 0.10). Four radio-tagged grouse were killed by predators, 2 by farm machinery, and 1 died from an unknown cause; ChE activity in brains of 2 of these grouse was similar to control values. Two young killed by farm machinery died the day after they were trapped and were not included in the mortality estimates. Of the 7 deaths unrelated to OP poisoning, 5 occurred from 10 to 27 July and 2 occurred in early August. As a result of the short range of the transmitters (<1.3 km) and related problems, signals from 17 grouse were lost before the study ended; thus, the mortality values are minimal estimates with low precision.

Of the 43 sage grouse radiocollared when healthy in 1986, 10 died (7 from OP's) before the end of the study with an overall mortality rate of 0.32. The probability of a grouse dying during the 72-day study from OP poisoning was 0.25. Aside from the 7 juvenile grouse that died from OP's, 3 additional radio-tagged grouse (2 juv and 1 ad F) were depredated on 15 and 20 August and 17 September. Although these 3 grouse were located in cropland from 3 to 20 days, there is no evidence of their exposure to OP sprays and their brains were not available for ChE assays. Radio collars were removed from apparently healthy grouse on 1 August (1 grouse) and 2 August (4 grouse); these units were then placed on intoxicated grouse.

The probability of mortality for 31 grouse, radiotagged when intoxicated in alfalfa from 25 July to 7 August 1986, was 0.76 to 12 August when the die-off from dimethoate in AB alfalfa apparently ended and 0.78 to 3 September when several of these grouse were collected. Dimethoate apparently accounted for deaths of 20 of these grouse; ChE activity was inhibited >50% in brains of 10 birds. Mortality of grouse instrumented when intoxicated was highest in 8 marked in AB alfalfa on 2 August (1 day post-spray) and all died by 5 August; 12 of 21 grouse radiocollared when intoxicated on 3–7 August

died from 4 to 12 August and 1 was depredated on 1 September. The grouse that died on 12 August was depredated; however, its brain ChE activity was inhibited 55.3%. The longer range (2.0–2.5 km) of the transmitters used in 1986 resulted in more efficient tracking compared to 1985; nevertheless, signals of 5 grouse were lost before the end of the study.

*Age Effects.*—Concerning sage grouse radiotagged when healthy in 1986, juveniles were more likely to die from OP poisoning than adults (Table 3); 7 of 28 juveniles died compared with zero of 15 adults ($P < 0.05$). There was no significant difference ($P > 0.05$) in survival of adults and juveniles radiocollared when intoxicated; however, all 5 adults died compared with 14 of 25 juveniles. Two adults were among 38 nonradioed birds that probably died from dimethoate in the AB alfalfa fields; however, sex and age of 13 birds were unknown. Considering the 6 grouse radiotagged when healthy and subsequently sprayed in AB alfalfa, an adult female showed no ill effects but all 5 juveniles died. The first 2 grouse radiocollared when sick were found in several cm of water in an alfalfa field on 25 July; the field was sprayed with dimethoate 2 days previously and was subsequently flood irrigated. One grouse flew from the field the same day it was radiotagged and the other left the field the next day.

## DISCUSSION

Generally, sage grouse in southeastern Idaho are migratory (Dalke et al. 1963, Connelly and Ball 1983); movements to summer range, including cropland, begin in June. Maximum movement of adult sage grouse from winter range to summer range was 82 km (Connelly and Markham 1983, Connelly et al. 1988). Distances moved from nests to summer range by 6 females with broods ranged from 3 to 21 km (Gates 1983). Gates (1983) also noted that 82% of 22 sage grouse trapped and marked on leks subsequently moved to irrigated cropland. Based on this study and previous work by Gates (1983), most of the Idaho population uses cropland for summer range; such use increases sharply during extended periods of extremely hot and dry weather (J. W. Connelly, Id. Dep. Fish and Game, pers. commun.). In our study area, spraying crops with pesticides is initiated in late spring, but most applications occur in July and August at the height of cropland use by sage grouse.

The die-offs during our study were apparently the first verified records for wildlife losses that resulted from dimethoate application. There are no toxicity data relating to sage grouse tolerance to OP insecticides. Factors that increased risk of OP's to sage grouse were their use of alfalfa fields for feeding, roosting, and loafing, and their extensive feeding on alfalfa foliage after spraying.

The conditions associated with methamidophos application to potatoes that result in risk to sage grouse were similar to those associated with dimethoate applications to alfalfa. Some sage grouse used potato fields extensively during this study. The crops of grouse shot or found dead in potato fields contained foliage of weeds and small amounts of insect material; sage grouse may occasionally eat potato leaves (J. W. Connelly, Id. Dep. Fish and Game, pers. commun.). We are uncertain whether repellency of dietary methamidophos to experimental birds (Stromborg 1986) is an important factor mediating toxicity to wild sage grouse, especially in view of the 18 μg/g methamidophos detected in crop contents of a sage grouse. Although the acute toxicity of methamidophos is higher than for dimethoate (Hudson et al. 1984), we located only 1 record of a die-off of wild birds (house sparrow [*Passer domesticus*] and killdeer [*Charadrius vociferus*]) from this compound (Smith 1987). On the basis of survival of about 35% of the sage grouse found intoxicated, some of the sick birds may have survived effects of OP's had they not been depredated. In any case, OP exposure was considered the primary cause of death when ChE assay results and residues were available for verification. Although the 2 depredated sage grouse found in or near the potato field sprayed with methamidophos had brain ChE activity depressed <50%, recent experimental evidence supports the probability that their deaths resulted from the spraying. Japanese quail (*Coturnix japonica*) were critically intoxicated when euthanized 1 hour after receiving an oral dose of the OP dicrotophos; however, brain ChE activity was inhibited about 40% (Hill 1989).

In other studies, half-time of dimethoate and methamidophos on plants was <4 days; however, low residues of these systemic insecticides may persist for several weeks (Szeto et al. 1984, Westcott et al. 1987). Thus, intoxicated sage grouse in cropland may be exposed to additional residues of OP's when ChE reversal is initiated and the grouse resume feeding on contaminated foliage. Sublethal depression of ChE activity in

the brain did not have lasting physiological effects in experimental birds in earlier studies (Metz 1958, Glow and Rose 1966, Banks and Russell 1967), but more recent studies present evidence that OP's similar to dimethoate and methamidophos are capable of inducing long-term effects (Farage-Elawar and Francis 1987, 1988). There are few data for free-ranging birds (Hill and Fleming 1982). European starling (*Sturnus vulgaris*) nestlings exhibited 19% mortality within 48 hours of receiving a dose of the OP dicrotophos compared with no mortality among controls; thereafter, survival of dosed and control young was similar for 1 month (Stromborg et al. 1988). We found no short-term effects after recovery of locomotive abilities by grouse, but the sample size was small and mortality was the only factor considered. The approximate time for renewal of ChE activity in intoxicated sage grouse in this study was similar to the 26-day recovery period (from 55 to 64% inhibition to within 2 SD of the control $\bar{x}$) measured for 5 avian species given diets containing dicrotophos (Fleming and Grue 1981).

Our findings suggest that OP's may adversely affect sage grouse populations, but this study only involved that segment of the population whose summer range included cropland. The mortality rate and sublethal intoxication of our marked population, induced by OP's and possibly other pesticides used in the area, was probably underestimated because sage grouse were radiotracked only during part of the season when OP's and other pesticides were applied, signals were lost from a number of grouse before the study terminated each year, radio collars were removed from 5 healthy birds in 1986 for use on intoxicated grouse, and some unrecorded exposure of marked grouse may have occurred between radio locations because the birds were not tracked continuously.

## MANAGEMENT IMPLICATIONS

In all fields where grouse were affected, the spray pilot reported the maximum allowable rates of dimethoate (0.56 kg active ingredient [ai]/ha) and methamidophos (1.13 kg ai/ha) were applied. Use of the minimal recommended application rates of 0.37 kg ai/ha for dimethoate and 0.85 kg ai/ha for methamidophos may reduce the hazard to grouse. General wildlife repellents are being tested by ≥1 chemical company for use with pesticides; successful short-lived repellents may deter sage grouse from ingesting contaminated foliage and may force them to leave sprayed fields. Die-offs of sage grouse and other species of birds including ring-necked pheasants (*Phasianus colchicus*) and gray partridge (*Perdix perdix*) are possible throughout much of their range in Idaho and in other states where cropland is available. The situation may worsen if intensive spraying of OP's on small grains is expanded in efforts to control the newly invading Russian wheat aphid (*Diuraphis noxia*). Our study provides evidence for claims that pesticides are at least partially responsible for declining populations of upland game birds in the United States and Europe; however, additional data are needed for verification.

## LITERATURE CITED

AMSTRUP, S. C. 1980. A radio-collar for game birds. J. Wildl. Manage. 44:214–217.

BANKS, A., AND R. W. RUSSELL. 1967. Effects of chronic reductions in acetylcholinesterase activity on serial problem-solving behavior. J. Comp. Physiol. Psychol. 64:262–267.

BLUS, L. J. 1982. Further interpretation of the relation of organochlorine residues in brown pelican eggs to reproductive success. Environ. Pollut. 28:15–33.

CONNELLY, J. W., JR., AND I. J. BALL. 1983. Sage grouse census methods and populations in southeastern Idaho. Pages 325–337 *in* O. D. Markham, ed. Idaho National Engineering Laboratory Radioecology and Ecology Programs 1983. Prog. Rep. NTIS, Springfield, Va.

———, H. W. BROWERS, AND R. J. GATES. 1988. Seasonal movements of sage grouse in southeastern Idaho. J. Wildl. Manage. 52:116–122.

———, AND O. D. MARKHAM. 1983. Movements and radionuclide concentrations of sage grouse in southeastern Idaho. J. Wildl. Manage. 47:169–177.

DALKE, P. D., D. B. PYRAH, D. C. STANTON, J. E. CRAWFORD, AND E. F. SCHLATTERER. 1963. Ecology, productivity, and management of sage grouse in Idaho. J. Wildl. Manage. 27:811–841.

DUNN, P. O., AND C. E. BRAUN. 1985. Natal dispersal and lek fidelity of sage grouse. Auk 102: 621–627.

ELLMAN, G. L., K. D. COURTNEY, V. ANDRES, JR., AND R. M. FEATHERSTONE. 1961. A new and rapid colorimetric determination of acetylcholinesterase activity. Biochem. Pharmacol. 7:88–95.

FARAGE-ELAWAR, M., AND R. M. FRANCIS. 1987. Acute and delayed effects of fenthion in young chicks. J. Toxicol. Environ. Health 21:455–469.

———, AND ———. 1988. Effects of multiple dosing of fenthion, fenitrothion, and desbromoleptophos in young chicks. J. Toxicol. Environ. Health 23:217–228.

FLEMING, W. J., AND C. E. GRUE. 1981. Recovery of cholinesterase activity in five avian species

exposed to dicrotophos, an organophosphorous pesticide. Pestic. Biochem. Physiol. 16:129–135.

GATES, R. J. 1983. Sage grouse, lagomorph, and pronghorn use of a sagebrush grassland site on the Idaho National Engineering Laboratory. M.S. Thesis, Montana State Univ., Bozeman. 135pp.

GIESEN, K. M., T. J. SCHOENBERG, AND C. E. BRAUN. 1982. Methods for trapping sage grouse in Colorado. Wildl. Soc. Bull. 10:224–231.

GLOW, P. H., AND S. ROSE. 1966. Cholinesterase levels and operant extinction. J. Comp. Physiol. Psychol. 61:165–172.

GRUE, C. E., W. J. FLEMING, D. G. BUSBY, AND E. F. HILL. 1983. Assessing hazards of organophosphate pesticides to wildlife. Trans. North Am. Wildl. Nat. Resour. Conf. 48:200–220.

HENNY, C. J., L. J. BLUS, E. J. KOLBE, AND R. E. FITZNER. 1985. Organophosphate insecticide (famphur) topically applied to cattle kills magpies and hawks. J. Wildl. Manage. 49:648–658.

HILL, E. F. 1989. Divergent effects of postmortem ambient temperature on organophosphorus—and carbamate—inhibited brain cholinesterase activity in birds. Pesticide Biochem. Physiol. 33:In Press.

———, AND W. J. FLEMING. 1982. Anticholinesterase poisoning in birds: field monitoring and diagnosis of acute poisoning. Environ. Toxicol. Chem. 1:27–38.

HUDSON, R. H., R. K. TUCKER, AND M. A. HAEGELE. 1984. Handbook of toxicity of pesticides to wildlife. Second ed. U.S. Fish Wildl. Serv. Resour. Publ. 153. Washington, D.C. 90pp.

LEE, E. T. 1980. Statistical methods for survival data analysis. Lifetime Learning Publ., Belmont, Calif. 557pp.

LUDKE, J. L., E. F. HILL, AND M. P. DIETER. 1975. Cholinesterase (ChE) responses and related mortality among birds fed ChE inhibitors. Arch. Environ. Contam. Toxicol. 3:1–21.

METZ, B. 1958. Brain acetylcholinesterase and a respiratory reflex. Am. J. Physiol. 192:101–105.

O'BRIEN, R. D. 1960. Toxic phosphorus esters. Academic Press, New York, N.Y. 434pp.

POLLOCK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, AND P. D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. J. Wildl. Manage. 53:7–15.

POTTS, G. R. 1986. The partridge. Collins, London, U.K. 274pp.

RANDS, M. R. W. 1985. Pesticide use on cereals and the survival of grey partridge chicks: a field experiment. J. Appl. Ecol. 22:49–54.

SMITH, G. J. 1987. Pesticides used and toxicology in relation to wildlife: organophosphorus and carbamate compounds. U.S. Fish and Wildl. Serv. Resour. Publ. 170. 171pp.

STROMBORG, K. L. 1986. Reproduction of bobwhites fed different dietary concentrations of an organophosphate insecticide, methamidophos. Arch. Environ. Contam. Toxicol. 15:143–147.

———, C. E. GRUE, J. D. NICHOLS, G. R. HEPP, J. E. HINES, AND H. C. BOURNE. 1988. Postfledging survival of European starlings exposed as nestlings to an organophosphorus insecticide. Ecology 69:590–601.

SZETO, S. Y., J. R. MACKENZIE, AND M. J. BROWN. 1984. Disappearance of dimethoate, methamidophos and pirimicarb in lettuce. J. Environ. Sci. Health B19:225–235.

WESTCOTT, N. D., Y. W. LEE, AND K. S. MCKINLAY. 1987. Persistence of dimethoate on wheat herbage and sweetclover herbage. J. Environ. Sci. Health 22B:379–390.

WHITE, D. H., C. A. MITCHELL, L. D. WYNN, E. L. FLICKINGER, AND E. J. KOLBE. 1982. Organophosphate insecticide poisoning of Canada geese in the Texas Panhandle. J. Field Ornithol. 53: 22–27.

WIEMEYER, S. N., T. G. LAMONT, C. M. BUNCK, C. R. SINDELAR, F. J. GRAMLICH, J. D. FRASER, AND M. A. BYRD. 1984. Organochlorine pesticide, polychlorobiphenyl, and mercury residues in bald eagle eggs—1969–1979—and their relationship to shell thinning and reproduction. Arch. Environ. Contam. Toxicol. 13:529–549.

*Received 9 September 1988.*
*Accepted 5 April 1989.*

# CHANGES IN SAGE GROUSE LEK COUNTS WITH ADVENT OF SURFACE COAL MINING

CLAIT E. BRAUN, Colorado Division of Wildlife, Research Center, 317 W. Prospect Road, Fort Collins, Colorado 80526.

*Abstract*: Intensive investigations of sage grouse (*Centrocerus urophasianus*) in North Park, Jackson County, Colorado were initiated in 1973. Three surface coal mines became active for varying periods in northeastern North Park during 1973–83. Numbers of known active sage grouse leks in North Park increased from 1973 through 1979, decreased in 1980, and were stable through 1983. Average number of males counted per lek in North Park was stable from 1973 through 1977, increased in 1978, and remained stable through 1983. Between 1974 and 1983, 9 leks were located in the mining area of which 7 (77.8%) were active in 1983. During this same interval in areas not impacted by mining, 18 new leks were located of which 13 (72.2%) were active in 1983. Average number of males counted per lek within 2 km of mining activity was low from 1974 to 1976 (9–14/lek), variable from 1977 to 1981 (46–60/lek), and decreased in 1982 and 1983 (47–25/lek). Outside the mining area, average numbers of males counted per lek were stable from 1973 to 1977 (29–33/lek), increased in 1978, and remained at the higher level through 1983 (39–44/lek). Number of males counted on leks closest to the 3 active surface coal mines decreased markedly (average = 60/lek in 1981; 25 in 1983) with increased mine preparation and mining activity.

Responses of sage grouse to mining disturbances are poorly understood even though sage grouse occur near or on many coal mines (53% of 51 mines surveyed) in western North America (Scott and Zimmerman 1984). The scientific literature concerning the impacts of surface coal mining on sage grouse is sparse with 2 of the 3 published papers relating to relocating display areas (leks) (Eng et al. 1979, Tate et al. 1979). The other paper develops criteria for reclamation of sage grouse habitats on areas altered by surface coal mining (Colenso et al. 1980). Considerable effort has been expended by energy companies in gathering baseline data on sage grouse on areas to be mined. These data are not available in the published literature and are generally available only from the mining companies that did the original work (Overthrust Industrial Assoc. 1984). Reasons for the lack of understanding of mining impacts on sage grouse relate to the short term approach of most studies, a lack of understanding of what to measure, failure of sage grouse populations to immediately and dramatically respond to small scale habitat alterations, and inadequate resources directed to the question. This paper describes the changes in a subpopulation of sage grouse and possible explanations of the changes in an area where surface coal mining was planned and implemented.

## STUDY AREA AND METHODS

Counts of male sage grouse on leks were conducted from 1973 through 1983 in North Park, Jackson County, Colorado. North Park is a large basin at an elevation of about 2,500 m with surrounding mountains to 3,800 m. Topography is irregular with drainage to the north through a series of small streams that flow into the North Platte River. Sagebrush, primarily *Artemisia tridentata wyomingensis* and *A. t. vaseyana*, is the dominant shrub and occurs with native bunchgrasses and forbs. Many stream bottoms have been developed for raising hay; livestock grazing is the dominant land use (Beck 1975).

Coal mining presently occurs east of Walden in northeastern North Park, south of Jackson County Road 10, east of Colorado 125, and north of Colorado 14. That portion of North Park east of Colorado 125, south and west of the Canadian River, and north of Colorado 14 is termed the mining area and encompasses the 3 surface coal mines that were active sometime in the 1973–83 interval (Figure 1).

Counts of males present on all known sage grouse leks throughout North Park were made in April–May each year following procedures described by Braun and Beck (1976). Three to 4 counts of all birds present on each lek were scheduled at 7–10 day intervals from early April through mid-May. The desired schedule of counts was not uniformly attained because of poor access, predator or other disturbance, and inclement weather. Searches for new leks were made every year using ground vehicles and at 2–3 year intervals using fixed-wing aircraft or helicopters.

Sage grouse throughout North Park were located with spotlights where they roosted on leks or along trails and were captured with long-handled nets (Giesen et al. 1982). Captured birds were classified to age and sex (Beck et al. 1975) and marked with individually numbered aluminum leg bands and colored plastic bandettes coded to either area or year of banding. Locations of recaptured or recovered (dead) birds were recorded.

## RESULTS

Numbers of known active leks throughout North Park increased from 1973 to 1979 (17 to 35), decreased between 1979 (35) and 1980 (30), and stabilized from 1981 through 1983 (31). No leks were found in northeastern North



1986 Proc. Issues and Technology in the Management of Impacted Western Wildlife 2:227-231.

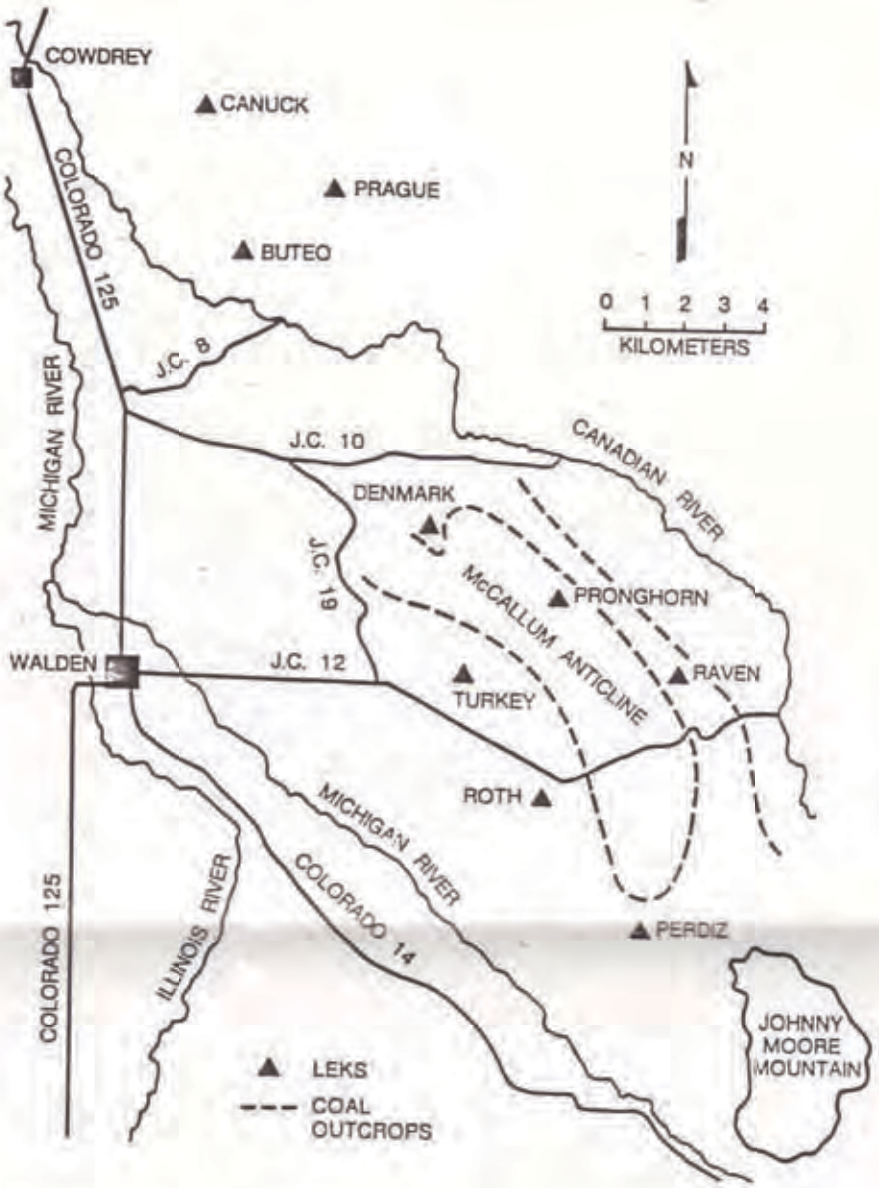



Figure 1. Sage grouse leks and coal outcrops in northeastern North Park, Jackson County, Colorado. Adapted from Schoenberg 1982.

Park in 1973, but 2 were found in 1974. Known numbers of active leks in this area increased from 2 to 7 between 1974 and 1979 and remained stable at 6–7 leks from 1978 through 1983. Male sage grouse were observed displaying at 4 other locations in northeastern North Park in 1981–83. These sites were not included because they were active only sporadically or not at all in 1 or 2 of the years. Numbers of active leks within 2 km of mines that were being developed or were in operation increased from 1 in 1974–76 to 3–4 in 1977–83 (Table 1).

Average numbers of males counted on leks throughout North Park fluctuated little between 1973 and 1977 (28–33), increased in 1978, and stabilized at the higher level through 1983. Numbers of males on leks within the northeastern portion of North Park fluctuated more widely (1977–80) and declined in 1982–83 (Table 1). The same pattern occurred on the 3–4 leks closest to mining activities although the decline in 1983 was far more marked (47 to 25) than elsewhere in North Park.

One small (8–14 males) lek (Roth) became inactive within 3 years of upgrading the haul road to the Wyoming Fuels Mine. This road passed within 50 m of the display site. With opening of the Walden Coal Company Mine in late 1980 and development of a modern haul road, numbers of males on Denmark Lek (0.5 km west of the mine site)

Table 1. Trends in numbers of active leks and average number of males per lek, North Park, Colorado, 1973–83.

| | North Park | | Outside of mining area | | Mining area | | Leks ± 2 km of mining activity | |
|---|---|---|---|---|---|---|---|---|
| Year | N leks | N males/lek | N leks | N males/lek | N leks | N males/lek | N leks | N males/lek |
| 1973 | 17 | 33 | 17 | 33 | 0 | 0 | 0 | 0 |
| 1974 | 19 | 28 | 17 | 29 | 2 | 19 | 1 | 10 |
| 1975 | 19 | 31 | 17 | 32 | 2 | 18 | 1 | 14 |
| 1976 | 21 | 32 | 19 | 33 | 2 | 19 | 1 | 9 |
| 1977 | 26 | 31 | 21 | 30 | 5 | 36 | 3 | 46 |
| 1978 | 34 | 39 | 28 | 39 | 6 | 60 | 3 | 58 |
| 1979 | 35 | 43 | 28 | 44 | 7 | 42 | 4 | 54 |
| 1980 | 30 | 40 | 24 | 40 | 6 | 83 | 4 | 49 |
| 1981 | 31 | 41 | 25 | 41 | 6 | 82 | 3 | 60 |
| 1982 | 31 | 41 | 24 | 44 | 7 | 64 | 3 | 47 |
| 1983 | 31 | 39 | 24 | 43 | 7 | 56 | 3 | 25 |

decreased 24% in the first year and 83% by the third spring. Numbers of males on 2 other leks (Perdiz, Raven) closest to coal mining activity also decreased (8 and 69%) as the mines were prepared for expansion (Table 2).

## DISCUSSION

Numbers of sage grouse in North Park as measured by numbers of active leks and average numbers of males present per lek increased from 1973 to 1983. This increase occurred throughout the area and was pronounced within the area where coal mines were developed in the late 1970s and early 1980s. Reasons for the increase are not clearly known, but are probably related to improvement in habitat conditions following cessation of large-scale sagebrush manipulation projects that occurred throughout North Park in the late 1960's (Braun and Beck 1976).

Coal mining has occurred sporadically near Coalmont and northeast of Walden for many years (Beekly 1915). Expansion of coal mining activities in northeastern North Park in the late 1970s and early 1980s occurred at the same time that the sage grouse population was expanding. However, as haul roads were improved (3 mines), site preparation increased (2 mines), and one mine became fully operational (Walden Coal Company Mine) numbers of sage grouse counted on leks closest to the mining activity began to decrease and one lek became inactive. The declines at 2 leks were precipitous (69% in 5 years, 83% in 3 years). Both of these leks are expected to be inactive by 1986.

Why have numbers of males decreased on the leks closest to mine development? Why did one lek become inactive with prospects for two more leks to become inactive in the near future? Numbers of sage grouse present on leks in spring are largely controlled by recruitment of yearlings. The average annual mortality rate of adult male sage grouse approximates 50% (C. E. Braun, unpubl. data). Thus, to maintain stability, numbers of yearlings recruited must equal the number of adults that died. If no yearlings are recruited, the number of males present on leks will decrease 50% each year. Trapping data for the two leks (Denmark, Raven) experiencing the largest declines indicated that no yearling males were recruited to one (Denmark) in 1982 and 1983 and the other (Raven) in 1983. Failure to recruit yearlings was also the problem at the lek (Roth) that became inactive as the last 1–2 birds present at this lek had been banded prior to full development of the adjacent haul road.

Why do yearling males fail to recruit to a lek? Failure to recruit may be related to dispersal, poor nesting success of hens, and/or decreased survival of young. It may also be related to acoustical or physical factors that deter yearling males from becoming established. It is well documented that adult males tend to return to the same lek year after year once they become established (Braun and Beck 1976; C. E. Braun, unpubl. data). If young are produced and survive to

Table 2. Numbers of male sage grouse per lek on leks ≤ 2 km of surface coal mining activity, North Park, Colorado, 1974–83.

| Year | Lek | | | | |
|---|---|---|---|---|---|
| | Denmark | Perdiz | Raven | Roth | Average |
| 1974 | | | | 10 | 10 |
| 1975 | | | | 14 | 14 |
| 1976 | | | | 9 | 9 |
| 1977 | 58 | | 73 | 8 | 46 |
| 1978 | 80 | | 94 | 1 | 58 |
| 1979 | 136 | 16 | 63 | 2 | 54 |
| 1980 | 144 | 8 | 43 | 1 | 49 |
| 1981 | 109 | 23 | 49 | 0 | 60 |
| 1982 | 71 | 27 | 44 | 0 | 47 |
| 1983 | 24 | 21 | 29 | 0 | 25 |

recruit to established leks, but fail to do so, they should either establish new leks or recruit to other, more favorable established leks. One new lek (Turkey) has become established 4 km south of the lek (Denmark) experiencing the greatest decline. Since establishment, this new lek has increased from 22 to 59 males. This is less than the number of males "lost" from the declining lek. Numbers of males on other leks in northeastern North Park have not increased. Thus, the evidence suggests that the overall sage grouse population in the area impacted by mining has decreased without a concomitant increase elsewhere in North Park. This decrease is attributed to decreased recruitment of yearling males.

Analysis of banding, recapture, and recovery data indicate that few sage grouse (only 4 recoveries from 4,491 bandings) migrate from North Park. Recaptures of adult males during the display period further than 5 km from where captured previously on leks have not occurred. Also, no movements of banded males from leks with decreasing number of males to other leks within the area have been documented. Thus, declines in numbers of males on leks over a several year period cannot be attributed to emigration. The declines documented fit the hypothesis that adult males return to leks where they are established until they die and that no or few yearlings are recruited to replace those adults dying. Thus, a lek can go to extinction in 4–6 years. Research should now focus on the factors that make established leks unattractive to yearling males in areas affected by mining disturbance.

## ACKNOWLEDGMENTS

Counts of male sage grouse on leks were made by personnel of the Colorado Division of Wildlife; I especially thank J. L. Wagner and S. H. Porter. T. E. Remington and T. J. Schoenberg of the Department of Fishery and Wildlife Biology, Colorado State University, who were intimately involved with and made valuable contributions to all phases of the sage grouse investigations in North Park. I thank K. M. Giesen and R. W. Hoffman for review of a draft of the manuscript, and N. W. McEwen and J. E. Black for typing assistance. This study was supported in part by the Bureau of Land Management, Colorado State and Kremmling Area offices, and throughout by the Colorado Division of Wildlife through Federal Aid in Wildlife Restoration Project W-37-R.

## LITERATURE CITED

Beekly, A.L. 1915. Geology and coal resources of North Park, Colorado. U.S. Geol. Surv. Bull. 596. 121 pp.

Beck, T.D.I. 1975. Attributes of a wintering population of sage grouse, North Park, Colorado. M.S. Thesis, Colorado State Univ., Fort Collins. 49 pp.

____, R.B. Gill, and C.E. Braun. 1975. Sex and age determination of sage grouse from wing characteristics. Colorado Div. Wildl., Game. Inf. Leafl. 49(Rev.). 4 pp.

Braun, C.E. and T.D.I. Beck. 1976. Effects of sagebrush control on distribution and abundance of sage grouse. Final Rep., Colorado Div. Wildl. Fed. Aid Wildl. Rest. Proj. W-37-R-29. Pp. 21–84.

Colenso, B.E., M.S. Boyce, and J.T. Tate. 1980. Developing criteria for reclamation of sage grouse habitat on a surface coal mine in northeastern Wyoming. Pp. 27–31 *In*: Proc., symposium: surface mining hydrology, sedimentology, and reclamation. Univ. Kentucky, Lexington.

Eng, R.L., E.J. Pitcher, S.J. Scott, and R.J. Green. 1979. Minimizing the effect of surface coal mining on a sage grouse population by a directed shift of breeding activities. Pp. 464–468 *In*: G.A. Swanson, (Tech. Coord.). The mitigation symposium: a national workshop on mitigating losses of fish and wildlife habitats. U.S. Dept. Agric., For. Serv. Gen. Tech. Rep. RM–65.

Giesen, K.M., T.J. Schoenberg, and C.E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildl. Soc. Bull. 10:224–231.

Overthrust Industrial Association. 1984. Cooperative wildlife program. Phase I. Literature search and review project report. Overthrust Industrial Assoc., Denver, Colo. (Not consecutively paginated).

Schoenberg, T.J. 1982. Sage grouse movements and habitat selection in North Park, Colorado. M.S. Thesis, Colorado State Univ., Fort Collins. 86 pp.

Scott, M.D., and G.M. Zimmerman. 1984. Wildlife management at surface coal mines in the Northwest. Wildl. Soc. Bull. 12:364–370.

Tate, J., Jr., M.S. Boyce, and T.R. Smith. 1979. Response of sage grouse to artificially created display ground. Pp. 459–463 *In*: G.A. Swanson, (Tech. Coord.). The mitigation symposium: a national workshop on mitigating losses of fish and wildlife habitats. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. RM-65.

# Fall Population Structure of Sage-grouse in Colorado and Oregon

Wildlife Technical Report 005 - 2015




OREGON DEPARTMENT OF FISH AND WILDLIFE
In cooperation with Grouse Inc., Colorado Parks and Wildlife, and Washington Department of Fish and Wildlife



Frontispiece: George Keister (left) of ODFW and Dr. Clait Braun of Grouse Inc. examine a greater sage-grouse wing.

# Fall Population Structure of Sage-grouse in Colorado and Oregon

**CLAIT E. BRAUN,**[1] *Grouse Inc., 5572 North Ventana Vista Road, Tucson, AZ 85750, USA*
**DAVID A. BUDEAU,** *Oregon Department of Fish and Wildlife, 4034 Fairview Industrial Drive SE, Salem, OR 97302, USA*
**MICHAEL A. SCHROEDER,** *Washington Department of Fish and Wildlife, P.O. Box 1077, Bridgeport, WA 98813, USA*

**ABSTRACT** We studied the population structure of sage-grouse (*Centrocercus* spp.) based on collection and analysis of 67,679 wings from hunter-harvested birds in 10 areas in Colorado and 12 areas in Oregon during 1973–1998 and 1993–2013, respectively. The harvest age structure for greater sage-grouse (*C. urophasianus*) varied from 42 to 63% juveniles in Colorado and 27 to 58% in Oregon. Approximately 59% of the Gunnison sage-grouse (*C. minimus*) harvest was juvenile. The overall adult male:female sex ratio was 28:72 for greater sage-grouse in Colorado, 41:59 (this includes an unknown proportion of yearlings) for greater sage-grouse in Oregon, and 34:66 for Gunnison sage-grouse in Colorado. Proportions of females increased in all fall populations from juvenile to yearling to adult age classes. Estimated breeding success was similar for greater sage-grouse in Colorado (47%) and Oregon (49%), but Gunnison sage-grouse appeared to have higher (60%) breeding success. The average number of juveniles in the harvest per breeding-age female varied from 1.2 to 2.4. There was high annual variation within and among areas. Composite estimated annual survival varied from 46 to 48% for adult males and 56 to 59% for adult females.

**KEY WORDS** age and sex composition, *Centrocercus minimus, C. urophasianus*, chicks per hen, Colorado, harvest, nest success, Oregon, sage-grouse, survival, turnover
[1]*E-mail: sgwtp66@gmail.com*

Sage-grouse (*Centrocercus* spp.) are charismatic large grouse of the sagebrush (*Artemisia* spp.) steppe in western North America (Schroeder et al. 1999). They historically occurred in at least 16 states and 3 provinces of Canada. Greater sage-grouse (*C. urophasianus*) are currently considered an endangered species in Canada but are hunted in 8 states (as of 2014). The distribution of sage-grouse has markedly declined from their apparent historical distribution (Schroeder et al. 2004) as have apparent numbers (Braun 1998). The reasons for the declines are related to degradation, loss, and fragmentation of sagebrush-dominated habitats (Braun 1987, Connelly and Braun 1997, Braun 1998). This has led to concern about their status and both species have been repeatedly petitioned for listing under the Endangered Species Act (Knick and Connelly 2011). The U.S. Fish and Wildlife Service has filed a ruling to list Gunnison sage-grouse (*C. minimus*) as threatened (USDI 2014) and the greater sage-grouse is presently listed as warranted but precluded because of higher priorities (USDI 2010).

Data on the structure of sage-grouse populations are not readily available as individuals may occur seasonally in widely-spaced sex-specific flocks in winter (Beck 1977) and also in summer and fall. All individuals cannot be counted, even on leks where males congregate in spring, because all locations of active leks are not known, not all males attend leks, and hen presence on leks is not simultaneous (Beck and Braun 1980). Our objectives were to (1) describe

the fall structure of sage-grouse populations, and (2) test hypotheses that the fall structure of sage-grouse populations does not differ among populations of greater sage-grouse within a State, between states, and between greater and Gunnison sage-grouse. This analysis is based on examination and classification of the age and sex of over 67,000 individual sage-grouse harvested in Colorado and Oregon over the periods, 1973–1998, and 1993–2013, respectively. These data have not been examined or published across the range of sage-grouse and are important in understanding the population dynamics of both species. Some harvest data are present in unpublished reports of State wildlife agencies.

## METHODS

We collected sage-grouse wings from hunters in Colorado at check stations on highways and roads leading from hunting areas as well as from voluntary wing collection stations placed along access roads (Hoffman and Braun 1975). A wing was clipped from each sage-grouse examined at check stations, the gonads were checked (primarily juveniles) when possible to ascertain sex, and the wings were labeled, and stored cold or frozen until analysis. Hunters in Oregon were requested to return one wing of each sage-grouse harvested in mail-in envelopes that were sent to, or dropped off at a central location for frozen storage.

Wings were thawed prior to analysis and were grouped into young of the year (juveniles), yearlings (young from the previous year), and adults following standardized procedures (Beck et al. 1975, Braun and Schroeder 2015). Sex of juveniles was ascertained based on measurements of primaries (from birds for which gonads were examined at check stations) and appearance of primaries, secondaries, wing coverts, and tertial feathers as described by Braun and Schroeder (2015). The adult category included some yearlings that had progressed enough in the molt, that characteristic yearling feathers (Braun and Schroeder 2015) were no longer present. Breeding success was estimated based on old (prior year) primaries retained at time of harvest. The primary molt of successful hens starts later than for hens losing their clutch during egg laying and or incubation based on recapture data in Colorado (Braun 1984). Annual turnover was estimated based on either the proportion of yearlings (Colorado) or juveniles (Oregon) compared to the proportion of adults (including yearlings) of each sex in the fall harvest. This assumes a population is stable. A population can be stable, increasing, or decreasing and the proportion of yearlings and or juveniles is a measure of overwinter survival (yearlings) or first summer survival to September (juveniles). We present raw data and averages by specific harvest area (Colorado) and by Management Unit (Oregon).

## STUDY AREAS

### Colorado

Sage-grouse were historically widely distributed in Colorado (Rogers 1964, Schroeder et al. 2004). Their distribution in the state has been greatly reduced (Braun 1995, Schroeder et al. 2004) (Fig. 1). Small Game Management Units historically followed the distribution of sage-grouse in Colorado and were first numbered in 1968, which continued through 1973; they were renumbered continuing through 1986. Numbering of all Big and Small Game Management units in Colorado was standardized in 1987. The distribution of sage-grouse in Colorado is within range-wide sage-grouse management zones II and VII (Stiver et al. 2006). Colorado shares sage-grouse populations with Utah and Wyoming. Sage-grouse in Colorado occur in three Environmental Protection Agency Level III ecoregions: Colorado Plateau, Southern Rockies, and

Wyoming Basin.

*North Park* - This area is within Jackson County and includes portions of Game Management Units 6, 7, 16, 17, 161, and 171. This area was formerly Small Game Management Unit 4 (1968–1973) and 12 (1974–1986). The area used by greater sage-grouse in North Park is at elevations of 2315–2745 m within a broad basin with numerous streams flowing to the north. Wet meadows and seasonally irrigated hay meadows are abundant. The area is rolling with numerous low and several higher ridges. There are no agricultural crops other than native hay as the growing season is short. Timing of sage-grouse breeding activities can be delayed in some years following severe winters.

*Middle Park* - This area includes portions of Game Management Units 18, 27, 28, 37, 171, and 181 in Grand and Summit counties. This area was formerly Small Game Unit 11 (1968–1973) and 28 (1974–1986). Middle Park is an open basin at ~2100–2300 m surrounded mostly by higher mountains. It has numerous streams flowing from the south and north, and then west. There is no agriculture other than native hay, and wet meadows are common. The length of the growing season is similar to that in North Park and greater sage-grouse breeding seasons can be late depending upon winter severity.

*Eagle* - This area includes portions of Game Management Units 25, 35, and 36 in Eagle (north of the Eagle River) and extreme northeastern Garfield counties. This area was formerly part of Small Game Management Units 9 and 10 (1968–1973) and Small Game Management Unit 54 (1974–1986). The Eagle area ranges from mid elevation (< 2000 m) sagebrush meadows to areas sloping sharply to the Eagle and Colorado rivers. Greater sage-grouse use the available sagebrush areas that are disjunct within a larger mosaic of pinyon-juniper (*Pinus-Juniperus*) shrubs and trees. Agriculture is limited to small hay meadows. Overall, the area is narrow, linear, and highly dissected by non-sagebrush habitat.

*Yampa* - This area includes parts of Game Management Units 15, 26, 131, and 231 in southern Routt County. This area was formerly Small Game Management Units 9 and 10 (1968–1973) and parts of Units 26 and 54 (1974–1986). The Yampa area supports greater sage-grouse from mid elevation (~ 2000 m) rolling sagebrush hills to irrigated hay meadows. Overall, the area is dissected by non-sagebrush habitat and hay meadows with more open areas near Yampa.

*Piceance Basin* - This area is primarily in Rio Blanco County and northern Garfield County in Game Management Unit 22 (1974 to present). It was formerly Small Game Management Unit 8 (1968–1973). This area is highly dissected by drainages and narrow ridges at elevations ranging from 1830 to 2285 m. Wider stream bottoms have been developed for hay production including some non-native species (primarily alfalfa). The population of greater sage-grouse is disjunct and occurs primarily along ridgetops dominated by sagebrush. The growing season is longer and warmer than in higher elevation areas, but little of the area is suitable for agriculture. Development for the extraction of oil, gas, and soda is common throughout the area.

*Blue Mountain* - This area includes part of Game Management Unit 10 (1987 to present) in far western Moffat County east of the Utah State Line and north of U.S. Highway 40 and west

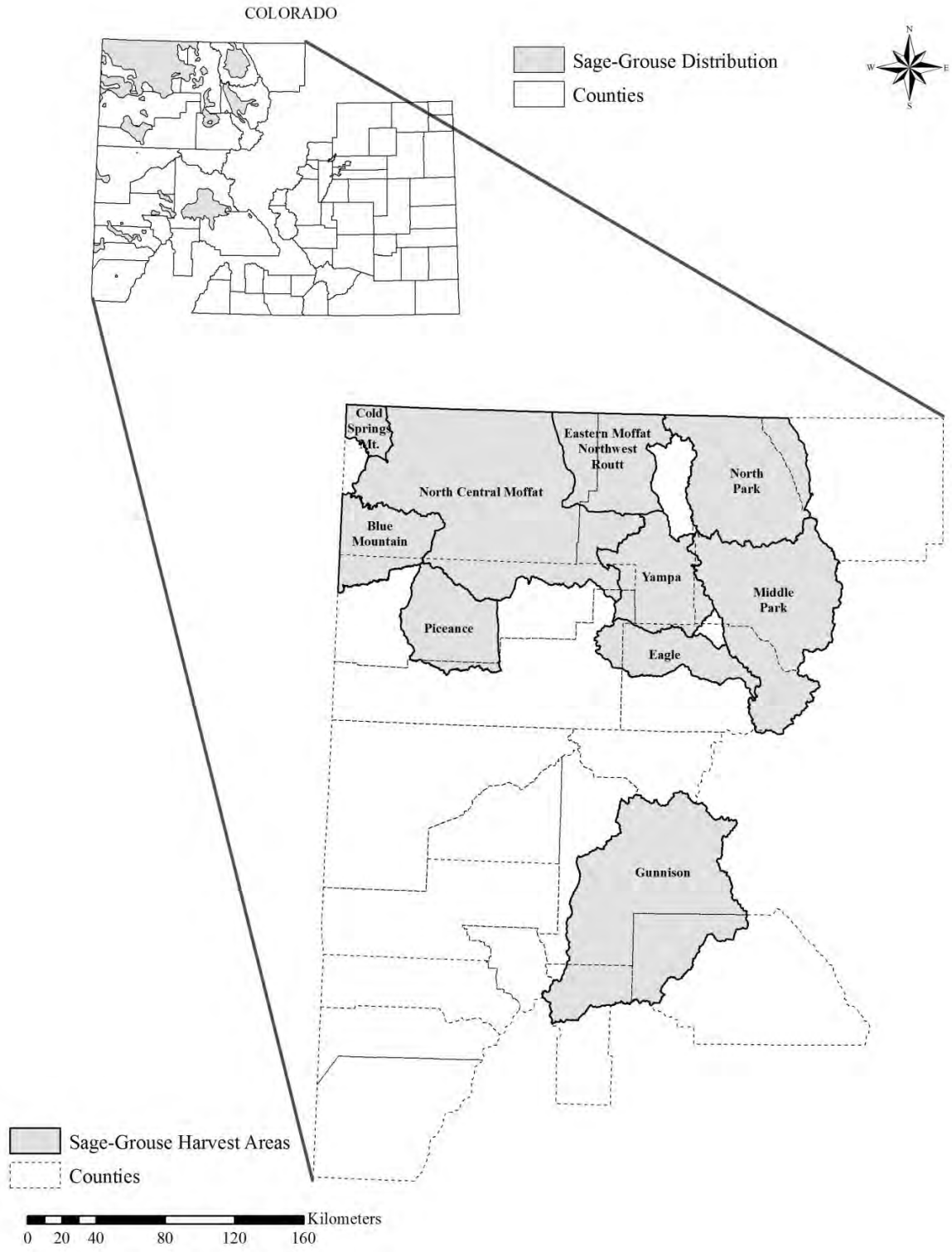



**Figure 1.** Sage-grouse harvest areas, county boundaries, and current distribution of sage-grouse in Colorado.

of Moffat County Road 16 north to the Yampa River. This was formerly part of Small Game Management Unit 7 (1968–1973) and parts of Units 18 and 20 (1974–1986). Blue Mountain is a higher elevation (~ 2785 m) area with rolling topography and intermittent springs and wet meadows. Greater sage-grouse breeding activity is later than in low elevations to the east and south.

*Cold Springs Mountain* - This area is in Game Management Unit 201 (1987 to present). It was formerly in Small Game Management Unit 18 (1974–1986) and in Unit 7 from 1968 to 1973. It is in the northwest corner of Moffat County bordered by Utah on the west, Wyoming on the north, Moffat County Road 10 on the east, and Colorado Highway 318 on the south. Cold Springs Mountain is a higher elevation (up to 2785 m) area with rolling topography and an abundance of intermittent springs and wet meadows. Greater sage-grouse breeding activity is later than in low elevations to the east and south. There is no agriculture including production of hay, except on one ranch, in the Unit.

*Eastern Moffat County and Northwestern Routt County* - This area includes Game Management Units 4, 5, 214, and 441 (1987 to present) and formerly Small Game Management Unit 5 (1968–1973) and Unit 14 (1974–1986) and is primarily east of Colorado Highway 13, north of U.S. Highway 40, and east and northeast of Craig. The topography of this area varies from rolling wheat fields at an elevation slightly over 1525 m along the west side near Craig to elevations of about 2875 m south of the Little Snake River which flows to the west and the Elkhead River that flows south to the Yampa River. Higher precipitation occurs to the northeast. Greater sage-grouse breeding is later at the higher elevations. Most suitable areas at low elevations have been developed for hay or wheat production, particularly along the Little Snake River. Overall, agricultural development is minimal.

*Northcentral Moffat County* - This large area includes Game Management Units 2, 3, 11, 12, 13, 211, and 301 and is west, northwest, southwest, and southeast of Craig. It formerly included all or parts of Small Game Management Units 6, 7, 8, 9, and 10 (1968–1973) and 16, 18, 20, and 26 (1974–1986). The Northcentral Moffat County area is diverse with extensive areas of small grain production as well as coal mining and oil and gas development. Most of the area supporting greater sage-grouse is at an elevation of 1525 to 1830 m and has a longer growing season. The remaining sagebrush habitats are highly fragmented and used by domestic livestock including both sheep and cattle. Hay production occurs along the Yampa River and other streams.

*Gunnison Basin* - This was the area supporting most Gunnison sage-grouse. It lies primarily in Gunnison and Saguache counties and marginally south into Hinsdale County west of the Continental Divide within Game Management Units 54, 55, 66, 67, and 551.This area was formerly Small Game Management Unit 20 (1968–1973) and then 66 (1974–1986). The Gunnison area is a large open basin dissected by streams that flow from the north, south, and east to form the west-flowing Gunnison River. The topography is irregular and slopes uphill to the north, east, and south. It lies at an elevation ranging from 2315 to 2745 m with cold winters and a short growing season. Agriculture, other than production of mostly native hay, is not common.

**Oregon**

Hunting of greater sage-grouse in Oregon is permitted in 12 of 21 state-defined wildlife management units in which sage-grouse are known to occur (Fig. 2). Habitat within each of the units is highly variable ranging from high elevation conifer forests to low elevation arid landscapes dominated by Wyoming big sagebrush (*A. tridentata wyomingensis*). The distribution of sage-grouse in Oregon is within range-wide sage-grouse management zones IV and V (Stiver et al. 2006). Oregon shares sage-grouse populations with California, Idaho, and Nevada. Sage-grouse in Oregon occur in the following four Environmental Protection Agency Level III ecoregions: Blue Mountains, Snake River Plain, Central Basin and Range, and Eastern Cascade Slopes and Foothills. Cattle ranching is the primary agricultural activity in all of the hunted management units.

*Sumpter (Management Unit 51*) - The Sumpter Wildlife Management Unit (51) occurs mostly within Baker and a small part of northern Malheur counties. The western portion is forested and within the Wallowa-Whitman National Forest of the Blue Mountains of Oregon. Much of this unit is drained by the Burnt River, a tributary of the Snake River. Most of the sage-grouse habitat is below 1000 m in elevation. Most (55%) of the land is in private ownership.

*Lookout Mountain (Management Unit 64*) - The Lookout Mountain Wildlife Management Unit (64) occurs entirely within Baker County. It is bordered on east by the Snake River and on the west by Interstate 84. Most of the unit is low to mid elevation sagebrush habitat with the highest point being Lookout Mountain at 3,048 m. Ranching was the primary agricultural activity, but hay production in lower elevation areas is also significant. This unit contains the smallest portion of public land (38%) of any Oregon unit open to sage-grouse hunting.

*Beulah (Management Unit 65*) - Most of the Beulah Wildlife Management Unit (65) is in the north part of Malheur County, but also includes the extreme northeast part of Harney, southwest extreme of Baker, and eastern part of Grant counties. The Baker and Grant county portions are primarily conifer forests and non-habitat for sage-grouse. This is a large unit with the Snake River forming the eastern border and the Malheur River forming the southern border. The eastern portion is characterized by higher human density and intensive row crop agriculture, but the principal agricultural activity throughout the unit is cattle ranching. The unit contains large contiguous expanses of sagebrush-steppe bisected by riparian areas and associated meadows which are often used for hay production. Most of the sage-grouse habitat is below 1000 m in elevation, but some buttes approach 2000 m. The Beulah unit consists of 57% public lands.

*Malheur River (Management Unit 66*) - The Malheur River Wildlife Management Unit (66) includes most of northeast Harney County, but also portions of Grant and Malheur counties. The Grant County portion is primarily conifer forest in the Malheur National Forest with little habitat for sage-grouse. The Malheur River, a tributary of the Snake River, drains most of the unit. The western portion includes the Malheur Basin with large portions dedicated to pivot irrigation and hay production. In modern history, western juniper (*Juniperus occidentalis*) has expanded into much of the large contiguous expanses of sagebrush-steppe, particularly at higher elevations. The unit is about 69% public lands.




**Figure 2.** Sage-grouse management units, county boundaries, and current distribution of greater sage-grouse in Oregon.

*Owyhee (Management Unit 67*) - The Owyhee Wildlife Management Unit (67) is entirely within Malheur County. The Owyhee River, a tributary of the Snake River, bisects the unit from south to north and Idaho forms the eastern border. Historically, this unit contained large expanses of sagebrush-steppe, but large areas were converted to crested wheatgrass (*Agropyron cristatum*) seedings in the 1960s as part of Bureau of Land Management's Vale Project. Sagebrush-steppe has also been lost from frequent lightning-caused wildfires. The relatively low elevation of this unit makes it highly vulnerable to invasive annual grasses. Juniper and conifers only exist on some of the highest points such as Mahogany Mountain (~1988 m). The BLM is the principal land manager with 82% of the area in the public domain.

*Whitehorse (Management Unit 68*) - The Whitehorse Wildlife Management Unit (68) encompasses the extreme southeast portion of Oregon and includes southern Malheur and southeast Harney counties. This is a large diverse unit and the Owyhee River and associated tributaries drain the northeast portion. The Trout Creek Mountains in the southwest part of the unit are generally below 2000 m and consist of large expanses of low (*A. arbuscula*) and mountain big (*A. t. vaseyana*) sagebrush with stands of aspen (*Populus tremuloides*). The Trout Creek Mountains have consistently had some of the highest densities of sage-grouse in Oregon. The north part of the unit experiences frequent lightning-caused wildfires, but the entire unit is susceptible. Fires of unprecedented scale in modern history impacted approximately 323,760 ha of this unit in 2012, including the Trout Creek Mountains. The unit is largely under the management of the BLM as 90% is public lands.

*Steens Mountain (Management Unit 69*) - The Steens Mountain Wildlife Management Unit (69) is in Harney County. The north part of the unit includes low elevations dominated by wet meadows and marsh and includes Malheur National Wildlife Refuge (NWR). The southern part of the unit is dominated by Steens Mountain. Steens Mountain is approximately 80 km in length and is a large fault-block mountain. The east side of the mountain drops precipitously by more than a 1000 m, but gradually slopes to the west. The western slopes are bisected by several large glacially-formed valleys. Encroachment by western juniper is an issue at lower elevations, but at higher elevations the juniper transitions to stands of aspen interspersed with meadows and mountain big sagebrush. Areas of low sage dominate some of the higher elevations or ridges with shallow soils. About 64% of the unit is in public ownership.

*Beatys Butte (Management Unit 70*) - The Beatys Butte Wildlife Management Unit (70) is in the southwest portion of Harney and southeast portion of Lake counties. Most of Hart Mountain National Antelope Refuge (NAR) occupies the northwest part of the unit. This area contains large contiguous expanses of low and big sagebrush with large areas of gentle topography. The western portion of the unit includes the Warner Wetlands and has some areas of western juniper encroachment. The Pueblo Mountains (~2659 m) are on the eastern border, while Hart Mountain (2347 m) is to the northwest and Beatys Butte (~2400 m) is near the middle of the unit. The Beatys Butte unit is 82% public lands.

*Juniper (Management Unit 71*) - The Juniper Wildlife Management Unit (71) lies mostly within Harney County but includes a portion of eastern Lake County. The southwest portion of the unit includes the Warner Basin and a portion of Hart Mountain NAR while the northeast part of the unit contains Harney Lake on Malheur NWR. Large contiguous expanses of intact

sagebrush-steppe with numerous playas dominate this arid unit. Lightning-caused wildfires are periodic and sometimes exceed 40,470 ha. There is little cultivated agriculture with most of the land use influenced by cattle ranching. The Juniper Unit is 89% public lands.

*Silvies (Management Unit 72*) - The Silvies Wildlife Management Unit (72) is primarily in Harney County but also includes portions of Lake, Deschutes, Crook, and Grant counties. Much of the unit is conifer forest in the Ochoco National Forest. The south and west portions are sagebrush-dominated landscapes, but western juniper distribution has expanded rapidly in this region. Cultivated agriculture occupies a small part of the unit. About 67% of the unit is in public ownership.

*Wagontire (Management Unit 73*) - The Wagontire Wildlife Management Unit (73) is primarily in Lake County but also includes portions of Harney and eastern Deschutes counties. This arid unit is dominated by large expanses of lower elevation Wyoming big sagebrush with numerous playas and two large closed basins (Summer Lake and Abert) in the south. Post-settlement encroachment of western juniper is compromising sage-grouse habitat quality in the western and northern areas of this unit. Cultivated agriculture is limited to a few irrigated pivots used for hay production. The unit is 85% public lands with the BLM being the principal land management agency.

*Warner (Management Unit 74*) - The Warner Wildlife Management Unit (74) is entirely within Lake County and is comparatively small. The western portion is bordered by U.S. Highway 395 at the base of Abert Rim and the Warner Mountains to the south. The Warner Mountains are dominated by conifer forest and are part of the Fremont National Forest. The western portion is higher in elevation (1800–2500 m) and receives more precipitation than the eastern area of the unit. The higher elevations with numerous wet meadows are attractive summer and late brood-rearing habitat. Western juniper encroachment is a serious threat to the sagebrush-steppe habitat and thousands of hectares of juniper have been cut in this unit in recent years. The unit is 70% public lands with the U.S. Forest Service and BLM the largest land managers.

## HUNTING SEASON REGULATIONS

In general, the length of sage-grouse hunting seasons in Colorado was progressively lengthened from 3 days in 1974 to 16–34 days in the 1983–1994 period, depending upon the area (Table 1). Between 1994 and 1998 the seasons were generally reduced to 7–16 days in most areas, and in some cases closed (Eagle, Yampa, Piceance Basin, and Eastern Moffat and Northwestern Routt management units). Daily bag and possession limits were much more consistent throughout 1974–1998, varying from a bag limit of 1 to 3 and a possession limit of 2 to 9 (Table 2). The largest bag and possession limits (3 and 9 respectively) were in place in 1992–1994.

The sage-grouse season length in Oregon varied from 2 (1993–1994), to 5 (1995–2004), and to 9 days (2005–2013). The daily bag and season limits were 2 and 2, respectively. Permits specific to a particular Management Unit were required in all years and allocated based on the estimated fall population for each unit. Hunting was closed or permit numbers were reduced in several Management Units in some years because of West Nile virus or large wildfires.

## RESULTS

Sex and age were ascertained for 48,599 greater sage-grouse and 7,547 Gunnison sage-grouse wings in Colorado and 11,533 greater sage-grouse wings in Oregon. Sex and age ratios in the harvest were calculated for each year and area for greater sage-grouse in Colorado (Appendix A1–A9), for greater sage-grouse in all Colorado hunting areas combined (Table 3), for Gunnison sage-grouse in Colorado (Table 4), for greater sage-grouse for each year and management area in Oregon (Appendix A10–A21), and for greater sage-grouse in management areas in Oregon combined (Table 5). The male:female sex ratio among juveniles varied from 41:59 to 52:48 for the 22 areas examined (Table 6). The harvest age structure for greater sage-grouse varied by year from 42 to 63% juveniles (Table 3) in Colorado (mean = 53.9%) and 27 to 58% (Table 5) in Oregon (mean = 48.0%); the Gunnison sage-grouse harvest that was juvenile ranged from 43 to 69% (Table 4) (mean = 59.5%).

The sex ratio changed with age as the male:female sex ratio for adult greater sage-grouse varied from 22:78 in Colorado to 41:59 (including an unknown proportion of yearlings) in Oregon (not counting the 2 areas with sample sizes < 100, Table 6), and 34:66 for Gunnison sage-grouse in Colorado (Table 6). The annual proportion of juveniles in the harvest for greater sage-grouse in Colorado (1974–1998) and Oregon (1993-2013) appeared to decline less than the proportion of juvenile Gunnison sage-grouse in Colorado (1977–1998) (Fig. 3).

Productivity was estimated for each year and area for greater sage-grouse in Colorado (Appendix B1–B9), for greater sage-grouse in all Colorado areas combined (Table 7), for Gunnison sage-grouse in Colorado (Table 8), for greater sage-grouse in Oregon (Appendix B10–B21), and for greater sage-grouse in all Oregon areas combined (Table 9). Estimated breeding success was similar for greater sage-grouse in Colorado (46.9%) and Oregon (48.8%), but was higher (60.0%) for Gunnison sage-grouse (Table 6). There was variability, 35.9–63.2%, in rates of breeding success among units (Table 6, not counting the 2 samples < 100). The average number of juveniles in the harvest per breeding-age female varied from 1.2 to 2.4 and the average number of juveniles per successful female varied from 2.2 to 4.8 (Table 6, excluding the samples <100). Generally, percent breeding success tracked the percent juveniles in the harvest (Table 6). Also notable was that breeding success of yearling females of both species in Colorado (Tables 8 and 9) was lower than for adult females. This comparison had no validity in Oregon (Table 9) as most unsuccessful females (both age classes) had completed replacement of primary flight feathers because of earlier timing of breeding.

Annual turnover of the sage-grouse populations in Colorado was based on the percent of yearlings in the fall harvest. This assumes the population was stable over time. Thus, the proportion of yearlings in the harvest should equal the proportion of adults that died. The survival estimate for greater sage-grouse in Colorado was 48.1% for males and 59.0% for females (Table 6). The survival estimate for Gunnison sage-grouse was 46.3% for males and 56.1% for females. A similar procedure was used for greater sage-grouse in Oregon, except that percent of juveniles was used because it was assumed many yearlings had completed their wing molt by time of harvest. The survival estimate in Oregon was 46.7% for males and 55.8% for females (Table 6). Gunnison sage-grouse generally were more productive (higher percent of juveniles in the harvest, higher estimated breeding success, more juveniles per hen) but had lower survival than greater sage-grouse.

**Table 1.** Sage-grouse hunting season length by year and area in Colorado, 1974–1998. Only years for which harvest data are available are shown.

| Year | North Park | Middle Park | Eagle | Yampa | Piceance Basin | Blue Mountain | Cold Spring Mountain | E Moffat and NW Routt | N-central Moffat | Gunnison Basin |
|---|---|---|---|---|---|---|---|---|---|---|
| 1974 | 3 | | | | | | | | | |
| 1975 | 9 | 3 | | | | | | | | |
| 1976 | 9 | 3 | | | | 3 | 3 | 3 | 3 | |
| 1977 | 16 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 3 |
| 1978 | 16 | 9 | 9 | 9[a] | 9 | 9 | 9 | 9[a] | 9 | 7 |
| 1979 | 16 | 9 | 9 | 9 | 9 | 16 | 16 | 9 | 16 | 9 |
| 1980 | 16 | 16 | 16 | 9 | 16 | 25 | 25 | 25 | 25 | 16 |
| 1981 | 23 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 |
| 1982 | 30 | 16 | 16 | 16 | 16 | 16 | 7 | 16 | 16 | 16 |
| 1983 | 30 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 |
| 1984 | 30 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 |
| 1985 | 23 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 |
| 1986 | 23 | 23 | 23 | 23 | 23 | 23 | 23 | 23 | 23 | 16 |
| 1987 | 23 | 23 | 23 | 23 | 23 | 23 | 23 | 23 | 23 | 16 |
| 1988 | 23 | 23 | 23 | 23 | 23 | 23 | 23 | 23 | 23 | 16 |
| 1989 | 30 | 30 | 30 | 30 | 30 | 30 | 30 | 30 | 30 | 30 |
| 1990 | 30 | 30 | 30 | 30 | 30 | 30 | 30 | 30 | 30 | 30 |
| 1991 | 30 | 30 | 30 | 30 | 30 | 30 | 30 | 30 | 30 | 30 |
| 1992 | 34 | 34 | 34 | 34 | 34 | 34 | 34 | 34 | 34 | 34 |
| 1993 | 33 | 33 | 33 | 33 | 33 | 33 | 33 | 33 | 33 | 33 |
| 1994 | 32 | 32 | 32 | 32 | 32 | 32 | 32 | 32 | 32 | 16 |
| 1995 | 17 | 17 | Closed | 17[b] | Closed | 17 | 17 | 17 | 17 | 17 |
| 1996 | 22 | 22 | Closed | 22 | Closed | 22 | 22 | 22 | 22 | 16 |
| 1997 | 16 | 16 | Closed | 16 | Closed | 16 | 16 | 16 | 16 | 16 |
| 1998 | 16 | 16 | Closed | Closed | Closed | 7 | 7 | Closed | 7 | 16 |

[a] Season was only 7 days in Yampa area east of Colorado Highway 131 and in the Elk River drainage, and east of Colorado Highway 131 in the Eastern Moffat and Northwestern Routt area.
[b] Unit 26 was closed in the Yampa area in 1995.

**Table 2.** Sage-grouse hunting season bag and possession limits (in parentheses) by year and area in Colorado, 1974–1998. Only years for which harvest data are available are shown.

| Year | North Park | Middle Park | Eagle | Yampa | Piceance Basin | Blue Mountain | Cold Spring Mountain | E Moffat and NW Routt | N-central Moffat | Gunnison Basin |
|---|---|---|---|---|---|---|---|---|---|---|
| 1974 | 2 (4) | | | | | | | | | |
| 1975 | 2 (4) | 2 (2) | | | | | | | | |
| 1976 | 3 (6) | 2 (4) | | | | 2 (4) | 2 (4) | 2 (4) | 2 (4) | |
| 1977 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 2 (2) |
| 1978 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) |
| 1979 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) |
| 1980 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) |
| 1981 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) |
| 1982 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) |
| 1983 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) |
| 1984 | 3 (6) | 2 (4) | 2 (4) | 2 (4) | 2 (4) | 2 (4) | 1 (2) | 2 (4) | 2 (4) | 2 (4) |
| 1985 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) |
| 1986 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 1 (2) | 3 (6) | 3 (6) | 3 (6) |
| 1987 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 1 (2) | 3 (6) | 3 (6) | 3 (6) |
| 1988 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 1 (2) | 3 (6) | 3 (6) | 3 (6) |
| 1989 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) |
| 1990 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) |
| 1991 | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) | 3 (6) |
| 1992 | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) |
| 1993 | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) |
| 1994 | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 3 (9) | 1 (2) |
| 1995 | 2 (4) | 1 (2) | Closed | 1 (2) | Closed | 2 (4) | 1 (2) | 1 (2) | 1 (2) | 2 (4) |
| 1996 | 2 (4) | 1 (2) | Closed | 1 (2) | Closed | 2 (4) | 1 (2) | 1 (2) | 1 (2) | 2 (4) |
| 1997 | 2 (4) | 1 (2) | Closed | 1 (2) | Closed | 2 (4) | 1 (2) | 1 (2) | 1 (2) | 2 (4) |
| 1998 | 2 (4) | 2 (4) | Closed | Closed | Closed | 2 (4) | 2 (4) | Closed | 2 (4) | 2 (4) |

**Table 3.** Age and gender composition of the greater sage-grouse harvest in Colorado, 1974–1998.

| Year | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1974 | 171 | 179 | 350 | 48.9:51.1 | 50.1 | 49 | 89 | 138 | 35.5:64.5 | 19.8 | 45 | 165 | 210 | 21.4:78.6 | 30.1 |
| 1975 | 124 | 142 | 266 | 46.6:53.4 | 45.4 | 56 | 67 | 123 | 45.5:54.5 | 21.0 | 56 | 141 | 197 | 28.4:71.6 | 33.6 |
| 1976 | 341 | 415 | 756 | 45.1:54.9 | 55.9 | 96 | 159 | 255 | 37.6:62.4 | 18.8 | 76 | 266 | 342 | 22.2:77.8 | 25.3 |
| 1977 | 343 | 431 | 774 | 44.3:55.7 | 46.9 | 144 | 216 | 360 | 40.0:60.0 | 21.8 | 148 | 367 | 515 | 28.7:71.3 | 31.2 |
| 1978 | 1008 | 1060 | 2068 | 48.7:51.3 | 63.5 | 154 | 265 | 419 | 36.8:63.2 | 12.9 | 224 | 546 | 770 | 29.1:70.9 | 23.6 |
| 1979 | 1113 | 1247 | 2360 | 47.2:52.8 | 54.9 | 523 | 662 | 1185 | 44.1:55.9 | 27.6 | 242 | 511 | 753 | 32.1:67.9 | 17.5 |
| 1980 | 871 | 1070 | 1941 | 44.9:55.1 | 53.6 | 265 | 444 | 709 | 37.4:62.6 | 19.6 | 351 | 618 | 969 | 36.2:63.8 | 26.8 |
| 1981 | 709 | 883 | 1592 | 44.5:55.5 | 50.3 | 222 | 441 | 663 | 33.5:66.5 | 20.9 | 248 | 664 | 912 | 27.2:72.8 | 28.8 |
| 1982 | 569 | 647 | 1216 | 46.8:53.2 | 58.0 | 128 | 222 | 350 | 36.6:63.4 | 16.7 | 140 | 391 | 531 | 26.4:73.6 | 25.3 |
| 1983 | 874 | 983 | 1857 | 47.1:52.9 | 57.6 | 254 | 399 | 653 | 38.9:61.1 | 20.2 | 168 | 547 | 715 | 23.5:76.5 | 22.2 |
| 1984 | 542 | 608 | 1150 | 47.1:52.9 | 56.9 | 155 | 280 | 435 | 35.6:64.4 | 21.5 | 106 | 331 | 437 | 24.3:75.7 | 21.6 |
| 1985 | 633 | 737 | 1370 | 46.2:53.8 | 60.0 | 146 | 293 | 439 | 33.3:66.7 | 19.2 | 123 | 353 | 476 | 25.8:74.2 | 20.8 |
| 1986 | 720 | 828 | 1548 | 46.5:53.5 | 60.0 | 185 | 352 | 537 | 34.5:65.5 | 20.8 | 132 | 362 | 494 | 26.7:73.3 | 19.2 |
| 1987 | 793 | 929 | 1722 | 46.1:53.9 | 57.8 | 222 | 414 | 636 | 34.9:65.1 | 21.4 | 158 | 461 | 619 | 25.5:74.5 | 20.8 |
| 1988 | 510 | 628 | 1138 | 44.8:55.2 | 49.4 | 220 | 346 | 566 | 38.9:61.1 | 24.6 | 182 | 417 | 599 | 30.4:69.6 | 26.0 |
| 1989 | 678 | 801 | 1479 | 45.8:54.2 | 50.8 | 265 | 342 | 607 | 43.7:56.3 | 20.9 | 293 | 531 | 824 | 35.6:64.4 | 28.3 |
| 1990 | 588 | 711 | 1299 | 45.3:54.7 | 46.0 | 224 | 416 | 640 | 35.0:65.0 | 22.7 | 270 | 614 | 884 | 30.5:69.5 | 31.3 |
| 1991 | 365 | 505 | 870 | 42.0:58.0 | 46.3 | 124 | 227 | 351 | 35.3:64.7 | 18.7 | 174 | 484 | 658 | 26.4:73.6 | 35.0 |
| 1992 | 236 | 331 | 567 | 41.6:58.4 | 42.3 | 130 | 176 | 306 | 42.5:57.5 | 22.8 | 101 | 368 | 469 | 21.5:78.5 | 34.9 |
| 1993 | 273 | 308 | 581 | 47.0:53.0 | 53.1 | 43 | 99 | 142 | 30.3:69.7 | 13.0 | 87 | 285 | 372 | 23.4:76.6 | 34.0 |
| 1994 | 207 | 267 | 474 | 43.7:56.3 | 53.0 | 63 | 95 | 158 | 39.9:60.1 | 17.7 | 52 | 210 | 262 | 19.8:80.2 | 29.3 |
| 1995 | 90 | 89 | 179 | 50.3:49.7 | 59.7 | 12 | 40 | 52 | 23.1:76.9 | 17.3 | 18 | 51 | 69 | 26.1:73.9 | 23.0 |
| 1996 | 127 | 166 | 293 | 43.3:56.7 | 56.8 | 29 | 60 | 89 | 32.6:67.4 | 17.2 | 34 | 100 | 134 | 25.4:74.6 | 26.0 |
| 1997 | 99 | 90 | 189 | 52.4:47.6 | 52.6 | 29 | 46 | 75 | 38.7:61.3 | 20.9 | 28 | 67 | 95 | 29.5:70.5 | 26.5 |
| 1998 | 77 | 90 | 167 | 46.1:53.9 | 45.6 | 24 | 64 | 88 | 27.3:72.7 | 24.0 | 27 | 84 | 111 | 24.3:75.7 | 30.3 |
| Average | 482 | 566 | 1048 | 46.0:54.0 | 53.9 | 150 | 249 | 399 | 37.6:62.4 | 20.5 | 139 | 357 | 497 | 28.0:72.0 | 25.6 |

**Table 4.** Age and gender composition of the Gunnison sage-grouse harvest, Gunnison Basin, Colorado, 1977–1998.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1977 | 67 | 75 | 142 | 47.2:52.8 | 60.4 | 18 | 35 | 53 | 34.0:66.0 | 22.6 | 15 | 25 | 40 | 37.5:62.5 | 17.0 |
| 1978 | 151 | 168 | 319 | 47.3:52.7 | 61.7 | 16 | 38 | 54 | 29.6:70.4 | 10.4 | 56 | 88 | 144 | 38.9:61.1 | 27.9 |
| 1979 | 216 | 219 | 435 | 49.7:50.3 | 62.9 | 63 | 66 | 129 | 48.8:51.2 | 18.6 | 41 | 87 | 128 | 32.0:68.0 | 18.5 |
| 1980 | 127 | 144 | 271 | 46.9:53.1 | 64.5 | 41 | 43 | 84 | 48.8:51.2 | 20.0 | 25 | 40 | 65 | 38.5:61.5 | 15.5 |
| 1981 | 56 | 33 | 89 | 62.9:37.1 | 42.6 | 43 | 34 | 77 | 55.8:44.2 | 36.8 | 19 | 24 | 43 | 44.2:55.8 | 20.6 |
| 1982 | 94 | 79 | 173 | 54.3:45.7 | 64.6 | 14 | 13 | 27 | 51.9:48.1 | 10.1 | 22 | 46 | 68 | 32.4:67.6 | 25.4 |
| 1983 | 205 | 231 | 436 | 47.0:53.0 | 64.5 | 55 | 81 | 136 | 40.4:59.6 | 20.1 | 33 | 71 | 104 | 31.7:68.3 | 15.4 |
| 1984 | 130 | 197 | 327 | 39.8:60.2 | 66.3 | 32 | 46 | 78 | 41.0:59.0 | 15.8 | 32 | 56 | 88 | 36.4:63.6 | 17.8 |
| 1985 | 137 | 107 | 244 | 56.1:43.9 | 62.9 | 24 | 45 | 69 | 34.8:65.2 | 17.8 | 38 | 37 | 75 | 50.7:49.3 | 19.3 |
| 1986 | 165 | 139 | 304 | 54.3:45.7 | 54.8 | 74 | 60 | 134 | 55.2:44.8 | 24.1 | 33 | 84 | 117 | 28.2:71.8 | 21.1 |
| 1987 | 159 | 184 | 343 | 46.4:53.6 | 69.0 | 28 | 47 | 75 | 37.3:62.7 | 15.1 | 33 | 46 | 79 | 41.8:58.2 | 15.9 |
| 1988 | 99 | 119 | 218 | 45.4:54.6 | 60.1 | 36 | 35 | 71 | 50.7:49.3 | 19.6 | 25 | 49 | 74 | 33.8:66.2 | 20.4 |
| 1989 | 126 | 133 | 259 | 48.6:51.4 | 50.0 | 57 | 70 | 127 | 44.9:55.1 | 24.5 | 37 | 95 | 132 | 28.0:72.0 | 25.5 |
| 1990 | 69 | 98 | 167 | 41.3:58.7 | 45.6 | 41 | 65 | 106 | 38.7:61.3 | 29.0 | 21 | 72 | 93 | 22.6:77.4 | 25.4 |
| 1991 | 75 | 107 | 182 | 41.2:58.8 | 58.9 | 14 | 25 | 39 | 35.9:64.1 | 12.6 | 29 | 59 | 88 | 33.0:67.0 | 28.5 |
| 1992 | 68 | 67 | 135 | 50.4:49.6 | 50.6 | 29 | 31 | 60 | 48.3:51.7 | 22.5 | 27 | 45 | 72 | 37.5:62.5 | 27.0 |
| 1993 | 63 | 80 | 143 | 44.1:55.9 | 69.4 | 8 | 15 | 23 | 34.8:65.2 | 11.2 | 13 | 27 | 40 | 32.5:67.5 | 19.4 |
| 1994 | 12 | 13 | 25 | 48.0:52.0 | 65.8 | 5 | 2 | 7 | 71.4:28.6 | 18.4 | 3 | 3 | 6 | 50.0:50.0 | 15.8 |
| 1995 | 40 | 40 | 80 | 50.0:50.0 | 54.4 | 16 | 16 | 32 | 50.0:50.0 | 21.8 | 9 | 26 | 35 | 25.7:74.3 | 23.8 |
| 1996 | 32 | 42 | 74 | 43.2:56.8 | 51.0 | 11 | 24 | 35 | 31.4:68.6 | 24.1 | 15 | 21 | 36 | 41.7:58.3 | 24.8 |
| 1997 | 33 | 38 | 71 | 46.5:53.5 | 53.8 | 9 | 17 | 26 | 34.6:65.4 | 19.7 | 12 | 23 | 35 | 34.3:65.7 | 26.5 |
| 1998 | 24 | 26 | 50 | 48.0:52.0 | 47.2 | 2 | 16 | 18 | 11.1:88.9 | 17.0 | 11 | 27 | 38 | 28.9:71.1 | 35.8 |
| Average | 98 | 106 | 204 | 48.0:52.0 | 59.5 | 29 | 37 | 66 | 43.9:56.1 | 19.2 | 25 | 48 | 73 | 34.2:65.8 | 21.3 |

**Table 5.** Age and gender composition of the greater sage-grouse harvest in Oregon, 1993–2013.

| Year | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1993 | 103 | 99 | 202 | 51.0:49.0 | 47.4 | 5 | 14 | 19 | 26.3:73.7 | 4.5 | 80 | 125 | 205 | 39.0:61.0 | 48.1 |
| 1994 | 145 | 168 | 313 | 46.3:53.7 | 42.7 | 6 | 45 | 51 | 11.8:88.2 | 7.0 | 116 | 253 | 369 | 31.4:68.6 | 50.3 |
| 1995 | 68 | 93 | 161 | 42.2:57.8 | 35.5 | 1 | 20 | 21 | 4.8:95.2 | 4.6 | 86 | 185 | 271 | 31.7:68.3 | 59.8 |
| 1996 | 105 | 148 | 253 | 41.5:58.5 | 51.3 | 1 | 23 | 24 | 4.2:95.8 | 4.9 | 68 | 148 | 216 | 31.5:68.5 | 43.8 |
| 1997 | 147 | 169 | 316 | 46.5:53.5 | 53.9 | 7 | 37 | 44 | 15.9:84.1 | 7.5 | 88 | 138 | 226 | 38.9:61.1 | 38.6 |
| 1998 | 110 | 119 | 229 | 48.0:52.0 | 49.1 | 1 | 17 | 18 | 5.6:94.4 | 3.9 | 86 | 133 | 219 | 39.3:60.7 | 47.0 |
| 1999 | 173 | 201 | 374 | 46.3:53.7 | 55.7 | 5 | 31 | 36 | 13.9:86.1 | 5.4 | 108 | 153 | 261 | 41.4:58.6 | 38.9 |
| 2000 | 120 | 139 | 259 | 46.3:53.7 | 44.3 | 11 | 38 | 49 | 22.4:77.6 | 8.4 | 131 | 145 | 276 | 47.5:52.5 | 47.3 |
| 2001 | 181 | 179 | 360 | 50.3:49.7 | 54.0 | 5 | 45 | 50 | 10.0:90.0 | 7.5 | 113 | 144 | 257 | 44.0:56.0 | 38.5 |
| 2002 | 192 | 181 | 373 | 51.5:48.5 | 57.6 | 4 | 39 | 43 | 9.3:90.7 | 6.6 | 106 | 126 | 232 | 45.7:54.3 | 35.8 |
| 2003 | 145 | 171 | 316 | 45.9:54.1 | 48.3 | 4 | 30 | 34 | 11.8:88.2 | 5.2 | 142 | 162 | 304 | 46.7:53.3 | 46.5 |
| 2004 | 178 | 222 | 400 | 44.5:55.5 | 51.5 | 4 | 43 | 47 | 8.5:91.5 | 6.1 | 130 | 199 | 329 | 39.5:60.5 | 42.4 |
| 2005 | 171 | 201 | 372 | 46.0:54.0 | 44.9 | 2 | 38 | 40 | 5.0:95.0 | 4.8 | 189 | 227 | 416 | 45.4:54.6 | 50.2 |
| 2006 | 147 | 169 | 316 | 46.5:53.5 | 47.4 | 9 | 20 | 29 | 31.0:69.0 | 4.3 | 157 | 165 | 322 | 48.8:51.2 | 48.3 |
| 2007 | 58 | 74 | 132 | 43.9:56.1 | 27.4 | 3 | 28 | 31 | 9.7:90.3 | 6.4 | 121 | 198 | 319 | 37.9:62.1 | 66.2 |
| 2008 | 117 | 124 | 241 | 48.5:51.5 | 54.4 | 0 | 17 | 17 | 0.0:100.0 | 3.8 | 56 | 129 | 185 | 30.3:69.7 | 41.8 |
| 2009 | 131 | 148 | 279 | 47.0:53.0 | 56.7 | 0 | 24 | 24 | 0.0:100.0 | 4.9 | 92 | 97 | 189 | 48.7:51.3 | 38.4 |
| 2010 | 96 | 125 | 221 | 43.4:56.6 | 47.7 | 1 | 22 | 23 | 4.3:95.7 | 5.0 | 79 | 140 | 219 | 36.1:63.9 | 47.3 |
| 2011 | 78 | 102 | 180 | 43.3:56.7 | 42.7 | 2 | 20 | 22 | 9.1:90.9 | 5.2 | 105 | 115 | 220 | 47.7:52.3 | 52.1 |
| 2012 | 39 | 56 | 95 | 41.1:58.9 | 29.2 | 14 | 33 | 47 | 29.8:70.2 | 14.5 | 89 | 94 | 183 | 48.6:51.4 | 56.3 |
| 2013 | 74 | 73 | 147 | 50.3:49.7 | 57.9 | 2 | 16 | 18 | 11.1:88.9 | 7.1 | 32 | 57 | 89 | 36.0:64.0 | 35.0 |
| Average | 123 | 141 | 264 | 46.5:53.5 | 48.0 | 4 | 29 | 33 | 12.7:87.3 | 6.0 | 104 | 149 | 253 | 41.0:59.0 | 46.0 |

**Table 6.** Summary of sample size, sex ratio, breeding success, and survival for greater and Gunnison sage-grouse in Colorado and Oregon.

| Species and area | Wings (*n*) | Male:female sex ratio | | | Survival (%)[a] | | Female success (%) | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Juveniles | Yearlings | Adults | Male | Female | | In harvest (%) | Per female | Per successful female |
| Greater sage-grouse in Colorado | 48599 | 46:54 | 38:62 | 28:72 | 48.1 | 59.0 | 46.9 | 53.9 | 1.7 | 3.7 |
| North Park | 13424 | 47:53 | 35:65 | 25:75 | 46.9 | 58.4 | 49.1 | 50.7 | 1.5 | 3.0 |
| Middle Park | 1903 | 50:50 | 39:61 | 26:74 | 41.4 | 57.7 | 55.9 | 52.6 | 1.6 | 2.9 |
| Eagle | 694 | 50:50 | 40:60 | 33:67 | 46.5 | 58.2 | 63.2 | 59.3 | 2.3 | 3.6 |
| Yampa | 920 | 50:50 | 46:54 | 36:64 | 42.1 | 54.4 | 47.9 | 43.2 | 1.2 | 2.6 |
| Piceance Basin | 817 | 47:53 | 43:57 | 30:70 | 41.3 | 54.8 | 57.1 | 57.6 | 2.1 | 3.7 |
| Blue Mountain | 5408 | 47:53 | 41:59 | 29:71 | 40.4 | 53.2 | 45.0 | 58.3 | 2.2 | 4.8 |
| Cold Spring Mountain | 2520 | 45:55 | 35:65 | 21:79 | 47.1 | 63.0 | 53.9 | 59.4 | 1.8 | 3.4 |
| E Moffat and NW Routt counties | 3539 | 48:52 | 33:67 | 25:75 | 42.6 | 53.5 | 39.6 | 53.5 | 1.6 | 4.1 |
| Northcentral Moffat County | 19374 | 44:56 | 39:61 | 31:69 | 53.3 | 62.1 | 44.2 | 54.6 | 1.8 | 4.1 |
| Gunnison sage-grouse in Colorado | 7547 | 48:52 | 44:56 | 34:66 | 46.3 | 56.1 | 60.0 | 59.5 | 2.4 | 4.0 |
| Greater sage-grouse in Oregon | 11533 | 47:53 | 12:88 | 41:59 | 46.7 | 55.8 | 48.8 | 48.0 | 1.5 | 3.0 |
| Sumpter, Hunt Unit 51 | 47 | 41:59 | 0:100 | 43:57 | 63.2 | 64.3 | 33.3 | 36.2 | 0.9 | 2.8 |
| Lookout Mountain, Hunt Unit 64 | 92 | 51:49 | 0:100 | 60:40 | 64.0 | 59.5 | 20.0 | 38.0 | 1.4 | 7.0 |
| Beulah, Hunt Unit 65 | 990 | 52:48 | 4:96 | 36:64 | 40.0 | 58.4 | 39.6 | 49.4 | 1.5 | 3.7 |
| Malheur River, Hunt Unit 66 | 780 | 45:55 | 16:84 | 41:59 | 45.8 | 53.8 | 43.1 | 49.5 | 1.6 | 3.6 |
| Owyhee, Hunt Unit 67 | 693 | 51:49 | 7:93 | 40:60 | 50.7 | 63.1 | 35.9 | 42.3 | 1.2 | 3.3 |
| Whitehorse, Hunt Unit 68 | 2721 | 47:53 | 7:93 | 41:59 | 43.3 | 53.2 | 48.5 | 51.0 | 1.7 | 3.4 |
| Steens Mountain, Hunt Unit 69 | 1193 | 47:53 | 17:83 | 52:48 | 61.4 | 59.4 | 50.5 | 39.6 | 1.3 | 2.5 |
| Beatys Butte, Hunt Unit 70 | 1999 | 46:54 | 19:81 | 43:57 | 48.5 | 54.7 | 54.8 | 48.0 | 1.5 | 2.8 |
| Juniper, Hunt Unit 71 | 868 | 44:56 | 9:91 | 36:64 | 49.7 | 59.7 | 54.2 | 44.1 | 1.2 | 2.2 |
| Silvies, Hunt Unit 72 | 202 | 43:57 | 10:90 | 26:74 | 35.3 | 56.0 | 49.3 | 51.0 | 1.4 | 2.8 |
| Wagontire, Hunt Unit 73 | 546 | 46:54 | 19:81 | 31:69 | 40.8 | 58.2 | 53.0 | 48.4 | 1.3 | 2.5 |
| Warner, Hunt Unit 74 | 1402 | 44:56 | 6:94 | 37:63 | 38.9 | 51.3 | 53.3 | 53.5 | 1.7 | 3.2 |

[a] Survival for greater sage-grouse in Oregon was estimated using annual turnover of juveniles and survival for sage-grouse in Colorado was estimated using annual turnover of yearlings.

**Table 7.** Greater sage-grouse productivity data, Colorado, 1974–1998.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1974 | 64.8 | 165 | 46.1 | 89 | 58.3 | 254 | 50.1 | 1.4 | 2.4 |
| 1975 | 56.0 | 141 | 38.8 | 67 | 50.5 | 208 | 45.4 | 1.3 | 2.5 |
| 1976 | 54.9 | 266 | 34.0 | 159 | 47.1 | 425 | 55.9 | 1.8 | 3.8 |
| 1977 | 51.5 | 367 | 25.9 | 216 | 42.0 | 583 | 46.9 | 1.3 | 3.2 |
| 1978 | 65.2 | 546 | 46.4 | 265 | 59.1 | 811 | 63.5 | 2.5 | 4.3 |
| 1979 | 62.6 | 511 | 47.7 | 662 | 54.2 | 1173 | 54.9 | 2.0 | 3.7 |
| 1980 | 50.3 | 618 | 34.0 | 444 | 43.5 | 1062 | 53.6 | 1.8 | 4.2 |
| 1981 | 41.4 | 665 | 28.2 | 440 | 36.1 | 1105 | 50.3 | 1.4 | 4.0 |
| 1982 | 53.5 | 391 | 31.5 | 222 | 45.5 | 613 | 58.0 | 2.0 | 4.4 |
| 1983 | 62.7 | 547 | 45.3 | 408 | 55.3 | 955 | 57.6 | 2.0 | 3.5 |
| 1984 | 67.2 | 326 | 50.5 | 285 | 59.4 | 611 | 56.9 | 1.9 | 3.2 |
| 1985 | 62.0 | 353 | 41.3 | 293 | 52.6 | 646 | 60.0 | 2.1 | 4.0 |
| 1986 | 57.5 | 362 | 40.9 | 352 | 49.3 | 714 | 60.0 | 2.2 | 4.4 |
| 1987 | 50.9 | 462 | 36.1 | 413 | 43.9 | 875 | 57.8 | 2.0 | 4.5 |
| 1988 | 50.2 | 416 | 30.3 | 347 | 41.2 | 763 | 49.4 | 1.5 | 3.6 |
| 1989 | 48.0 | 531 | 29.2 | 342 | 40.7 | 873 | 50.8 | 1.7 | 4.2 |
| 1990 | 44.8 | 614 | 19.2 | 416 | 34.5 | 1030 | 46.0 | 1.3 | 3.7 |
| 1991 | 49.8 | 484 | 32.2 | 227 | 44.2 | 711 | 46.3 | 1.2 | 2.8 |
| 1992 | 40.5 | 368 | 23.3 | 176 | 34.9 | 544 | 42.3 | 1.0 | 3.0 |
| 1993 | 66.7 | 285 | 43.4 | 99 | 60.7 | 384 | 53.1 | 1.5 | 2.5 |
| 1994 | 61.0 | 210 | 38.9 | 95 | 54.1 | 305 | 53.0 | 1.6 | 2.9 |
| 1995 | 66.7 | 51 | 57.5 | 40 | 62.6 | 91 | 59.7 | 2.0 | 3.1 |
| 1996 | 64.0 | 100 | 36.7 | 60 | 53.8 | 160 | 56.8 | 1.8 | 3.4 |
| 1997 | 56.7 | 67 | 48.9 | 47 | 53.5 | 114 | 52.6 | 1.7 | 3.1 |
| 1998 | 50.6 | 85 | 23.4 | 64 | 38.9 | 149 | 45.6 | 1.1 | 2.9 |
| Totals | 54.2 | 8931 | 36.4 | 6228 | 46.9 | 15159 | 53.9 | 1.7 | 3.7 |

**Table 8.** Gunnison sage-grouse productivity data, Gunnison Basin, Colorado, 1977–1998.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1977 | 92.0 | 25 | 68.6 | 35 | 78.3 | 60 | 60.4 | 2.4 | 3.0 |
| 1978 | 76.1 | 88 | 60.5 | 38 | 71.4 | 126 | 61.7 | 2.5 | 3.5 |
| 1979 | 67.8 | 87 | 72.7 | 66 | 69.9 | 153 | 62.9 | 2.8 | 4.1 |
| 1980 | 67.5 | 40 | 69.8 | 43 | 68.7 | 83 | 64.5 | 3.3 | 4.8 |
| 1981 | 50.0 | 24 | 29.4 | 34 | 37.9 | 58 | 42.6 | 1.5 | 4.0 |
| 1982 | 65.2 | 46 | 46.2 | 13 | 61.0 | 59 | 64.6 | 2.9 | 4.8 |
| 1983 | 74.6 | 71 | 49.4 | 81 | 61.2 | 152 | 64.5 | 2.9 | 4.7 |
| 1984 | 69.6 | 56 | 69.6 | 46 | 69.6 | 102 | 66.3 | 3.2 | 4.6 |
| 1985 | 62.2 | 37 | 73.3 | 45 | 68.3 | 82 | 62.9 | 3.0 | 4.4 |
| 1986 | 66.7 | 84 | 51.7 | 60 | 60.4 | 144 | 54.8 | 2.1 | 3.5 |
| 1987 | 71.7 | 46 | 40.4 | 47 | 55.9 | 93 | 69.0 | 3.7 | 6.6 |
| 1988 | 77.6 | 49 | 62.9 | 35 | 71.4 | 84 | 60.1 | 2.6 | 3.6 |
| 1989 | 58.9 | 95 | 38.6 | 70 | 50.3 | 165 | 50.0 | 1.6 | 3.1 |
| 1990 | 48.6 | 72 | 15.4 | 65 | 32.8 | 137 | 45.6 | 1.2 | 3.7 |
| 1991 | 66.1 | 59 | 36.0 | 25 | 57.1 | 84 | 58.9 | 2.2 | 3.8 |
| 1992 | 55.6 | 45 | 25.8 | 31 | 43.4 | 76 | 50.6 | 1.8 | 4.1 |
| 1993 | 81.5 | 27 | 66.7 | 15 | 76.2 | 42 | 69.4 | 3.4 | 4.5 |
| 1994 | 100.0 | 3 | 0.0 | 2 | 60.0 | 5 | 65.8 | 5.0 | 8.3 |
| 1995 | 65.4 | 26 | 87.5 | 16 | 73.8 | 42 | 54.4 | 1.9 | 2.6 |
| 1996 | 61.9 | 21 | 45.8 | 24 | 53.3 | 45 | 51.0 | 1.6 | 3.1 |
| 1997 | 65.2 | 23 | 58.8 | 17 | 62.5 | 40 | 53.8 | 1.8 | 2.8 |
| 1998 | 66.7 | 27 | 31.3 | 16 | 53.5 | 43 | 47.2 | 1.2 | 2.2 |
| Totals | 66.9 | 1051 | 51.2 | 824 | 60.0 | 1875 | 59.5 | 2.4 | 4.0 |

**Table 9.** Greater sage-grouse productivity data, Oregon, 1993–2013. Successful yearling females were more likely to be detected because those that were unsuccessful had likely completed replacement of all primaries from the previous year.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1993 | 55.2 | 125 | 100.0 | 14 | 59.7 | 139 | 47.4 | 1.5 | 2.4 |
| 1994 | 40.3 | 253 | 37.8 | 45 | 39.9 | 298 | 42.7 | 1.1 | 2.6 |
| 1995 | 35.7 | 185 | 30.0 | 20 | 35.1 | 205 | 35.5 | 0.8 | 2.2 |
| 1996 | 51.4 | 148 | 47.8 | 23 | 50.9 | 171 | 51.3 | 1.5 | 2.9 |
| 1997 | 54.3 | 138 | 81.1 | 37 | 60.0 | 175 | 53.9 | 1.8 | 3.0 |
| 1998 | 45.1 | 133 | 100.0 | 17 | 51.3 | 150 | 49.1 | 1.5 | 3.0 |
| 1999 | 66.0 | 153 | 100.0 | 31 | 71.7 | 184 | 55.7 | 2.0 | 2.8 |
| 2000 | 42.1 | 145 | 55.3 | 38 | 44.8 | 183 | 44.3 | 1.4 | 3.2 |
| 2001 | 42.0 | 144 | 64.4 | 45 | 47.3 | 189 | 54.0 | 1.9 | 4.0 |
| 2002 | 57.1 | 126 | 100.0 | 39 | 67.3 | 165 | 57.6 | 2.3 | 3.4 |
| 2003 | 52.5 | 162 | 63.3 | 30 | 54.2 | 192 | 48.3 | 1.6 | 3.0 |
| 2004 | 42.7 | 199 | 100.0 | 43 | 52.9 | 242 | 51.5 | 1.7 | 3.1 |
| 2005 | 45.4 | 227 | 100.0 | 38 | 53.2 | 265 | 44.9 | 1.4 | 2.6 |
| 2006 | 49.1 | 165 | 55.0 | 20 | 49.7 | 185 | 47.4 | 1.7 | 3.4 |
| 2007 | 32.3 | 198 | 53.6 | 28 | 35.0 | 226 | 27.4 | 0.6 | 1.7 |
| 2008 | 47.3 | 129 | 76.5 | 17 | 50.7 | 146 | 54.4 | 1.7 | 3.3 |
| 2009 | 44.3 | 97 | 66.7 | 24 | 48.8 | 121 | 56.7 | 2.3 | 4.7 |
| 2010 | 35.0 | 140 | 50.0 | 22 | 37.0 | 162 | 47.7 | 1.4 | 3.7 |
| 2011 | 40.0 | 115 | 60.0 | 20 | 43.0 | 135 | 42.7 | 1.3 | 3.1 |
| 2012 | 31.9 | 94 | 15.2 | 33 | 27.6 | 127 | 29.2 | 0.7 | 2.7 |
| 2013 | 45.6 | 57 | 56.3 | 16 | 47.9 | 73 | 57.9 | 2.0 | 4.2 |
| Totals | 45.2 | 3133 | 67.8 | 600 | 48.8 | 3733 | 47.6 | 1.5 | 3.0 |

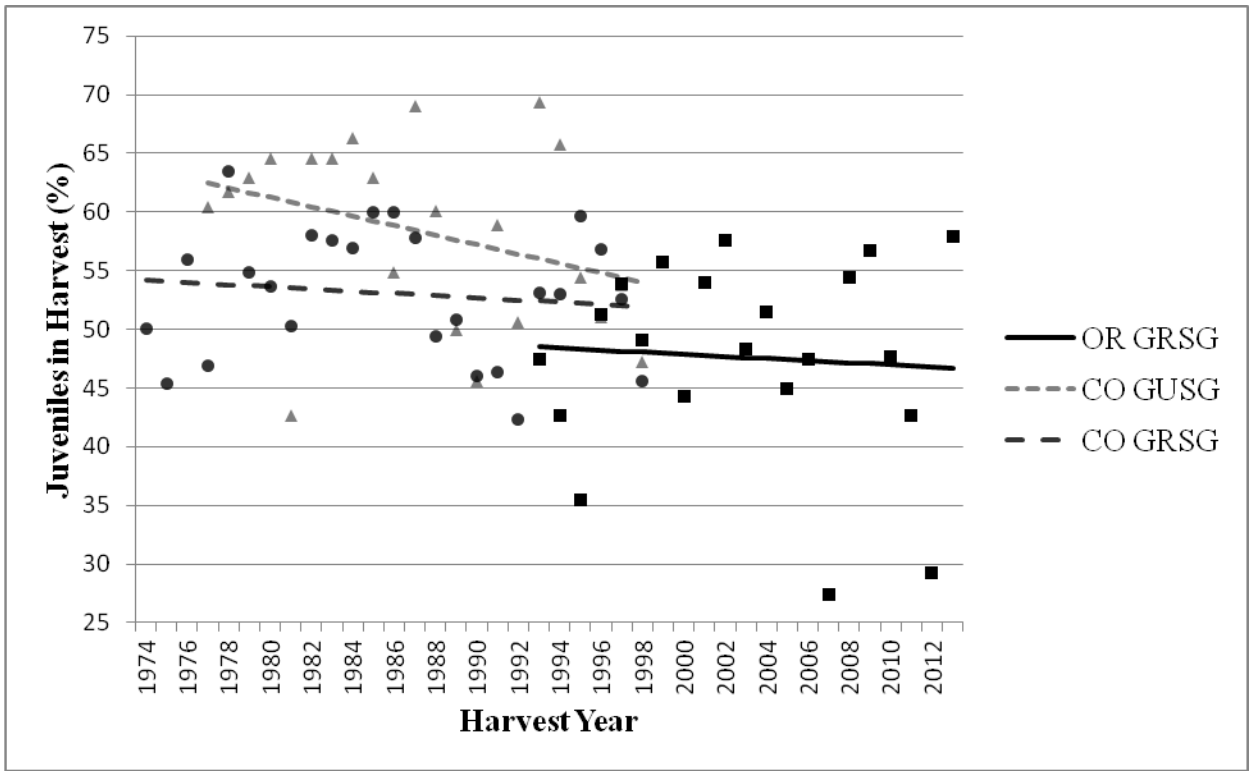



**Figure 3.** Trends (%) in juvenile sage-grouse as a proportion of harvest for Colorado (1974–1998) and Oregon (1993–2013) (OR GRSG = Oregon greater sage-grouse [squares], CO GUSG = Colorado Gunnison sage-grouse [triangles], CO GRSG = Colorado greater sage-grouse [circles]).

## DISCUSSION

The structure of sage-grouse populations has been of interest for many years starting with the work of Patterson (1952). Wings from hunter-harvested sage-grouse were collected in Montana (Eng 1955) and Colorado starting in the 1950s (Rogers 1964) and later in other states (even though understanding the usefulness of wing analysis was rudimentary) (Dalke et al. 1963). Collection and classification of wings (Beck et al. 1975) were not standardized until the early 1970s in Colorado (Braun 1984) when sage-grouse wing collection was instituted in all areas open to sage-grouse hunting. This effort led other states (such as Idaho [Autenrieth 1981]) to follow standard procedures promoted by the Western States Sage Grouse Committee (Autenrieth et al. 1982; reviewed by Connelly and Schroeder 2007). This led to the first compilations of sage-grouse harvest data based on large samples (e.g., Braun 1984).

Several concerns arose from these data sets (Braun 1984) including the high percentage of females in the adult and yearling segments of the harvested sample and the apparent increase in females in the harvest from the juvenile (young of the year = 52%), to yearling (64%), to adult (72%) segments of the fall population. Sex ratios of juveniles in the harvest were approximately 1:1 (10-year average from 1974 to 1983 = 48:52, $n$ = 4060 juveniles). This led Braun (1984:153) to indicate that survival favored females in all age classes. He also used progression of the molt

of primary flight feathers to estimate nest success of adult and yearling females (page 154) and reported a difference between yearlings (10-year average = 51%) and adults (10-year average = 68%). Braun's (1984) assumption of even sex ratios at hatch is consistent with the findings of Atamian and Sedinger (2010) and Guttery et al. (2013). Recent research indicates differences in juvenile to adult ratios and juveniles per hen may be related to moisture as Blomberg et al. (2014a) documented that clutch size was larger in years with more moisture (generally at higher elevations). These authors suggest that resource availability affects clutch size. A companion paper (Blomberg et al. 2014b) found that postfledging survival of juveniles was higher during cooler and wetter growing seasons compared to hot and dry growing seasons. Thus, those sites in Colorado with adequate sample sizes such as in the higher elevation areas of the Gunnison Basin (59%), Blue Mountain (58%), and Cold Spring Mountain (60%) would be expected to have higher proportions of juveniles in the harvest than in the lower elevation area of northcentral Moffat County (55%). This did not hold for the high elevation area of North Park (51% juveniles in the harvest).

Knowledge of the structure of sage-grouse populations is thus important for understanding the dynamics of changes over time. Most previous projections dating to Patterson's (1952) work have focused on male attendance at leks (Emmons and Braun 1984), even though the proportion of males in the population that attend leks is poorly understood. Females congregate in sex-specific flocks in winter and Beck's (1977) work in North Park, Colorado indicated there were 2 hens per male in winter flocks. Our work has supported that finding using harvest data. All populations studied had about 62–70% adult and yearling females in the adult and yearling segment of the fall harvest. These findings are not surprising as the mating system of sage-grouse is one where a few males do most of the breeding (Wiley 1973, 1978). Thus, even sex ratios are neither necessary nor desirable. The shift from an expected sex ratio of 50:50 at hatch to a ratio favoring females starts at a young age, probably because of the need for large amounts of high protein foods to meet the growth demands of the larger juvenile males (Swenson 1986). This shift continues as adult males especially have low annual survival (37% vs. adult females = 59%) (Zablan et al. 2003), possibly because of higher rates of predation during the breeding season (Connelly et al. 2000, Hagen 2011). Thus, based on the above discussion of the data, we were unable to detect differences using the available techniques to indicate that the fall structure of sage-grouse populations based on harvest differed among populations of greater sage-grouse within a State, between states, and between greater and Gunnison sage-grouse.

Estimates of breeding success of sage-grouse have primarily been based on studies of radio-marked hens (Schroeder 1997, Hagen et al. 2007). Ours is the first to derive breeding success (which includes nesting effort, nesting success, and chick survival to the hunting season) estimates from examination of hunter-harvested sage-grouse. This provides a less expensive way to estimate this important parameter even if it is not precise. More recently, Hagen and Loughin (2008) devised a method to estimate variance in sample sizes needed to provide estimates of productivity based on sage-grouse wing collections from hunters.

Estimated annual turnover (mortality) based on examination of wings varied slightly among areas (and years depending upon sample sizes) and was lower than rates for adult males

(63%), but similar for adult females (41%) published for banded and recovered sage-grouse in North Park, Colorado based on 6,000+ bandings over the period 1973–1990 and recovered in 1973–1993 (Zablan et al. 2003). These data suggest that estimating annual turnover of adult males and females from hunter-harvested sage-grouse has merit in both Colorado and Oregon.

Differential vulnerability to hunting is unknown for sage-grouse but juveniles may be more vulnerable than older age classes (Caudill et al. 2014). Anecdotal comments from hunters suggest there is selection for smaller birds (females and young). However, this is not supported by return of bands from marked sage-grouse of all age classes in Moffat County (unpubl. data) or of birds banded in spring as yearlings and adults in North Park. The data from North Park (Zablan et al. 2003) indicate that adult males had the highest harvest rates. This can be understood as males are larger (Beck and Braun 1978) and appear to flush later than females or juveniles.

## MANAGEMENT IMPLICATIONS

The data on population composition of sage-grouse provided in this report span a 40-year period from small to large populations in a variety of habitats from high mountain valleys, which have substantial wet meadows, to low elevations that approach semi-deserts, all within a matrix of live sagebrush and mostly native herbaceous plants. Thus, data can be compared for the 1973–1998 period with that from 1993–2013. Of importance is the overlap from 1993 through 1998 between Colorado and Oregon. Data from small populations (Eagle = 695 wings [1977–1998], Piceance = 817 wings [1977–1994], and Yampa = 920 wings [1977–1998]) in Colorado have value as none of these populations is now hunted and none is likely to be hunted again. The same is true for some Harvest Management Units in Oregon. Even in situations where harvest is continuing, the long-term trend is declining samples of hunter-harvested wings. Consequently, it is unlikely that this quantity of data will ever be replicated.

These small populations have characteristics similar to the larger populations, but with larger variances in parameter estimates. Both species of sage-grouse are candidates for threatened or endangered listing and it is certain that at least one species will be subject to development of a recovery plan in the near future. Thus, it is important to know the characteristics of the populations prior to cessation of hunting and possible ESA listing.

The Gunnison sage-grouse population studied had the highest proportion of young in the fall harvest, the highest young per hen ratio, and was among those with the highest estimated breeding success. Despite these attributes, it still had estimated annual turnover that was quite similar (but somewhat higher) to other populations (Oregon; and especially North Park, Colorado which has similar habitat associations) that had adequate samples of wing receipts. Of interest is the similarity of most parameters measured including age and sex ratios with females comprising larger segments of fall populations in all older age classes. Clearly, the data indicate the mating system of sage-grouse which focuses on large, showy males and nondescript females is negative for male survival. It is also clear that all populations studied did not differ over time periods or geographical regions in their core attributes.

The data represented long periods from two states and indicates the need for population

monitoring over time as recommended by Nichols and Williams (2006). Unfortunately, the opportunity to collect large samples may not exist but we show that even small samples collected over time can provide reasonable estimates of the structure of the fall population of sage-grouse.

**ACKNOWLEDGMENTS**

We thank hunters in Colorado and Oregon for graciously allowing us to examine the sage-grouse they harvested and or for providing wings for analysis. T. D. I. Beck was helpful in the early years of the effort in Colorado as was R. W. Hoffman in operating check stations and wing collection barrels. Numerous graduate students, technicians, and personnel of the Colorado Division of Wildlife worked with us at check stations and in recording data. Personnel of the Oregon Department of Fish and Wildlife (ODFW) processed wings under our supervision at annual wing bees. Ken Durbin of ODFW invited CEB to be involved starting in 1993 as did John Crawford of Oregon State University. Mitch Willis and George Keister of ODFW were also helpful in the early years. Personnel of other agencies and students at several universities helped in Oregon. We especially thank C. A. Hagen and R. W. Hoffman for review of the data sets. Comments received from J. H. Gammonley were also helpful. We thank all of those who helped over the 40-year period of data collection. D. Joanne Saher prepared the distribution figure for Colorado while Kelly M. Walton prepared the distribution figure for Oregon. We thank them for their help with this project. This is a joint contribution of the Colorado Division of Parks and Wildlife, Oregon Department of Fish and Wildlife, and Grouse Inc.

**LITERATURE CITED**

Atamian, M. T., and J. S. Sedinger. 2010. Balanced sex ratio at hatch in a greater sage-grouse (*Centrocercus urophasianus*) population. Auk 127:16–22.

Autenrieth, R. E. 1981. Sage grouse management in Idaho. Wildlife Bulletin 9. Idaho Department of Fish and Game, Boise, USA.

Autenrieth, R., W. Molini, and C. Braun. 1982. Sage grouse management practices. Technical Bulletin 1. Western States Sage Grouse Committee, Twin Falls, Idaho, USA.

Beck, T. D. I. 1977. Sage grouse flock characteristics and habitat selection in winter. Journal of Wildlife Management 41:18–26.

Beck, T. D. I., and C. E. Braun. 1978. Weights of Colorado sage grouse. Condor 80:241–243.

Beck, T. D. I., and C. E. Braun. 1980. The strutting ground count: variation, traditionalism, management needs. Proceedings of the Western Association of Fish and Wildlife Agencies 60:558–566.

Beck, T. D. I., R. B. Gill, and C. E. Braun. 1975. Sex and age determination of sage grouse from wing characteristics. Outdoor Facts, Game Information Leaflet 49. Colorado Division of Game, Fish and Parks, Fort Collins, USA.

Blomberg, E. J., D. Gibson, M. T. Atamian, and J. S. Sedinger. 2014a. Individual and

environmental effects on egg allocations of female greater sage-grouse. Auk 131:507–523.

Blomberg, E. J., J. S. Sedinger, D. Gibson, P. S. Coates, and M. L. Casazza. 2014b. Carryover effects and climatic conditions influence the postfledging survival of greater sage-grouse. Ecology and Evolution 4: doi:10.1002/ece3.1139.

Braun, C. E. 1984. Attributes of a hunted sage grouse population in Colorado, U.S.A. Pages 148–162 *in* P. J. Hudson and T. W. I. Lovel, Editors. Third International Grouse Symposium, York University, York, United Kingdom.

Braun, C. E. 1987. Current issues in sage grouse management. Proceedings of the Western Association of Fish and Wildlife Agencies 67:134–144.

Braun, C. E. 1995. Distribution and status of sage grouse in Colorado. Prairie Naturalist 27:1–9.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of Fish and Wildlife Agencies 78:139–156.

Braun, C. E., and M. A. Schroeder. 2015. Age and sex identification from wings of sage-grouse. Wildlife Society Bulletin 39: In Press.

Caudill, D., T. A. Messmer, B. Bibles, and M. R. Guttery. 2014. Greater sage-grouse juvenile survival in Utah. Journal of Wildlife Management 78:808–817.

Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. Wildlife Biology 3:229–234.

Connelly, J. W., and M. A. Schroeder. 2007. Historical and current approaches to monitoring greater sage-grouse. Pages 3–9 in Monitoring populations of sage-grouse (K. P. Reese and R. T. Bowyer, Editors). Experiment Station Bulletin 88. College of Natural Resources, University of Idaho, Moscow, USA.

Connelly, J. W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. Wildlife Biology 6:227–232.

Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. Journal of Wildlife Management 27:811–841.

Emmons, S. R., and C. E. Braun. 1984. Lek attendance of male sage grouse. Journal of Wildlife Management 48:1023–1028.

Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal of Wildlife Management 19:267–272.

Guttery, M. R., T. A. Messmer, E. T. Thacker, N. Gruber, and C. M. Culumber. 2013. Greater sage-grouse sex ratios in Utah: implications for reporting population trends. Journal of Wildlife Management 77:1593–1597.

Hagen, C. A. 2011. Predation of greater sage-grouse: facts, process, and effects. Pages 95–100 *in* S. T. Knick and J. W. Connelly, Editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Number 38. University of California Press, Berkeley, USA.

Hagen, C. A., and T. M. Loughin. 2008. Productivity estimates from upland bird harvests: estimating variance and necessary sample sizes. Journal of Wildlife Management 72:1369–1375.

Hagen, C. A., J. W. Connelly, and M. A. Schroeder. 2007. A meta analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. Wildlife Biology 13:42–50.

Hoffman, R. W., and C. E. Braun. 1975. A volunteer wing collection station. Outdoors Facts, Game Information Leaflet 101. Colorado Division of Wildlife, Fort Collins, USA.

Knick, S. T., and J. W. Connelly, Editors. 2011. Greater sage-grouse: ecology and conservation of a landscape species. Studies in Avian Biology Number 38. University of California Press, Berkeley, USA.

Nichols, J. D., and B. K. Williams. 2006. Monitoring for conservation. Trends in Ecology and Evolution 21:668–673.

Patterson, R. L. 1952. The sage grouse in Wyoming. Sage Books Inc., Denver, Colorado, USA.

Rogers, G. E. 1964. Sage grouse investigations in Colorado. Colorado Game, Fish and Parks Department Technical Publication Number 16.

Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99:933–941.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse. Number 425 in A. Poole and F. Gill, Editors. The birds of North America. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

Stiver, S. J., A. D. Apa, J. Bohne, S. D. Bunnell, P. Deibert, S. Gardner, M. Hilliard, C. McCarthy, and M. A. Schroeder. 2006. Greater sage-grouse comprehensive conservation

strategy. Unpublished Report. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Swenson, J. E. 1986. Differential survival by sex in juvenile sage grouse and gray partridge. Ornis Scandinavica 17:14–17.

U. S. Department of the Interior (USDI). 2010. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Federal Register 75:13910-13958.

U. S. Department of the Interior (USDI). 2014. Endangered and threatened wildlife and plants; Threatened status for Gunnison sage-grouse. Federal Register 79:69191–69310.

Wiley Jr., R. H. 1973. Territoriality and nonrandom mating in sage-grouse, *Centrocercus urophasianus*. Animal Behavior Monographs 6:85–169.

Wiley Jr., R. H. 1978. The lek mating system of the sage grouse Scientific American 238:114–125.

Zablan, M. A., C. E. Braun, and G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal of Wildlife Management 67:144–154.

**Appendix A1.** Age and gender composition of the greater sage-grouse harvest, North Park, Colorado, 1974–1998.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1974 | 171 | 179 | 350 | 48.9:51.1 | 50.1 | 49 | 89 | 138 | 35.5:64.5 | 19.8 | 45 | 165 | 210 | 21.4:78.6 | 30.1 |
| 1975 | 101 | 111 | 212 | 47.6:52.4 | 42.0 | 52 | 59 | 111 | 46.8:53.2 | 22.0 | 55 | 127 | 182 | 30.2:69.8 | 36.0 |
| 1976 | 104 | 106 | 210 | 49.5:50.5 | 42.3 | 46 | 71 | 117 | 39.3:60.7 | 23.5 | 49 | 121 | 170 | 28.8:71.2 | 34.2 |
| 1977 | 136 | 154 | 290 | 46.9:53.1 | 45.9 | 47 | 76 | 123 | 38.2:61.8 | 19.5 | 48 | 171 | 219 | 21.9:78.1 | 34.7 |
| 1978 | 184 | 201 | 385 | 47.8:52.2 | 53.2 | 62 | 81 | 143 | 43.4:56.6 | 19.8 | 67 | 129 | 196 | 34.2:65.8 | 27.1 |
| 1979 | 306 | 318 | 624 | 49.0:51.0 | 57.7 | 102 | 154 | 256 | 39.8:60.2 | 23.7 | 72 | 129 | 201 | 35.8:64.2 | 18.6 |
| 1980 | 207 | 254 | 461 | 44.9:55.1 | 49.1 | 80 | 170 | 250 | 32.0:68.0 | 26.6 | 70 | 158 | 228 | 30.7:69.3 | 24.3 |
| 1981 | 234 | 255 | 489 | 47.9:52.1 | 47.4 | 78 | 151 | 229 | 34.1:65.9 | 22.2 | 87 | 227 | 314 | 27.7:72.3 | 30.4 |
| 1982 | 197 | 196 | 393 | 50.1:49.9 | 50.6 | 53 | 80 | 133 | 39.8:60.2 | 17.1 | 81 | 170 | 251 | 32.3:67.7 | 32.3 |
| 1983 | 295 | 352 | 647 | 45.6:54.4 | 57.4 | 90 | 155 | 245 | 36.7:63.3 | 21.7 | 53 | 183 | 236 | 22.5:77.5 | 20.9 |
| 1984 | 236 | 251 | 487 | 48.5:51.5 | 57.0 | 68 | 132 | 200 | 34.0:66.0 | 23.4 | 37 | 131 | 168 | 22.0:78.0 | 19.6 |
| 1985 | 163 | 190 | 353 | 46.2:53.8 | 53.6 | 47 | 112 | 159 | 29.6:70.4 | 24.2 | 33 | 113 | 146 | 22.6:77.4 | 22.2 |
| 1986 | 168 | 236 | 404 | 41.6:58.4 | 61.8 | 27 | 93 | 120 | 22.5:77.5 | 18.3 | 25 | 105 | 130 | 19.2:80.8 | 19.9 |
| 1987 | 153 | 216 | 369 | 41.5:58.5 | 54.2 | 54 | 114 | 168 | 32.1:67.9 | 24.7 | 29 | 115 | 144 | 20.1:79.9 | 21.1 |
| 1988 | 80 | 101 | 181 | 44.2:55.8 | 42.9 | 52 | 81 | 133 | 39.1:60.9 | 31.5 | 18 | 90 | 108 | 16.7:83.3 | 25.6 |
| 1989 | 89 | 98 | 187 | 47.6:52.4 | 46.1 | 25 | 92 | 117 | 21.4:78.6 | 28.8 | 17 | 85 | 102 | 16.7:83.3 | 25.1 |
| 1990 | 69 | 66 | 135 | 51.1:48.9 | 38.7 | 21 | 59 | 80 | 26.3:73.8 | 22.9 | 25 | 109 | 134 | 18.7:81.3 | 38.4 |
| 1991 | 47 | 64 | 111 | 42.3:57.7 | 43.0 | 18 | 28 | 46 | 39.1:60.9 | 17.8 | 18 | 83 | 101 | 17.8:82.2 | 39.1 |
| 1992 | 37 | 35 | 72 | 51.4:48.6 | 36.7 | 26 | 20 | 46 | 56.5:43.5 | 23.5 | 15 | 63 | 78 | 19.2:80.8 | 39.8 |
| 1993 | 53 | 53 | 106 | 50.0:50.0 | 45.1 | 6 | 20 | 26 | 23.1:76.9 | 11.1 | 25 | 78 | 103 | 24.3:75.7 | 43.8 |
| 1994 | 65 | 68 | 133 | 48.9:51.1 | 56.1 | 15 | 16 | 31 | 48.4:51.6 | 13.1 | 15 | 58 | 73 | 20.5:79.5 | 30.8 |
| 1995 | 10 | 13 | 23 | 43.5:56.5 | 36.5 | 4 | 15 | 19 | 21.1:78.9 | 30.2 | 10 | 11 | 21 | 47.6:52.4 | 33.3 |
| 1996 | 38 | 32 | 70 | 54.3:45.7 | 54.7 | 5 | 15 | 20 | 25.0:75.0 | 15.6 | 7 | 31 | 38 | 18.4:81.6 | 29.7 |
| 1997 | 31 | 41 | 72 | 43.1:56.9 | 51.4 | 12 | 18 | 30 | 40.0:60.0 | 21.4 | 10 | 28 | 38 | 26.3:73.7 | 27.1 |
| 1998 | 22 | 26 | 48 | 45.8:54.2 | 37.2 | 4 | 34 | 38 | 10.5:89.5 | 29.5 | 9 | 34 | 43 | 20.9:79.1 | 33.3 |
| Average | 128 | 145 | 272 | 46.9:53.1 | 50.7 | 42 | 77 | 119 | 35.3:64.7 | 22.2 | 37 | 109 | 145 | 25.3:74.7 | 27.0 |

**Appendix A2.** Age and gender composition of the greater sage-grouse harvest, Middle Park, Colorado, 1975–1998.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1975 | 23 | 31 | 54 | 42.6:57.4 | 66.7 | 4 | 8 | 12 | 33.3:66.7 | 14.8 | 1 | 14 | 15 | 6.7:93.3 | 18.5 |
| 1976 | 34 | 35 | 69 | 49.3:50.7 | 63.9 | 9 | 14 | 23 | 39.1:60.9 | 21.3 | 2 | 14 | 16 | 12.5:87.5 | 14.8 |
| 1977 | 49 | 40 | 89 | 55.1:44.9 | 57.1 | 11 | 20 | 31 | 35.5:64.5 | 19.9 | 9 | 27 | 36 | 25.0:75.0 | 23.1 |
| 1978 | 52 | 37 | 89 | 58.4:41.6 | 45.9 | 24 | 27 | 51 | 47.1:52.9 | 26.3 | 16 | 38 | 54 | 29.6:70.4 | 27.8 |
| 1979 | 41 | 43 | 84 | 48.8:51.2 | 50.0 | 20 | 21 | 41 | 48.8:51.2 | 24.4 | 13 | 30 | 43 | 30.2:69.8 | 25.6 |
| 1980 | 22 | 27 | 49 | 44.9:55.1 | 51.6 | 7 | 17 | 24 | 29.2:70.8 | 25.3 | 7 | 15 | 22 | 31.8:68.2 | 23.2 |
| 1981 | 5 | 4 | 9 | 55.6:44.4 | 22.0 | 11 | 9 | 20 | 55.0:45.0 | 48.8 | 3 | 9 | 12 | 25.0:75.0 | 29.3 |
| 1982 | 23 | 24 | 47 | 48.9:51.1 | 75.8 | 1 | 4 | 5 | 20.0:80.0 | 8.1 | 1 | 9 | 10 | 10.0:90.0 | 16.1 |
| 1983 | 28 | 37 | 65 | 43.1:56.9 | 51.6 | 10 | 18 | 28 | 35.7:64.3 | 22.2 | 12 | 21 | 33 | 36.4:63.6 | 26.2 |
| 1984 | 31 | 30 | 61 | 50.8:49.2 | 56.0 | 10 | 15 | 25 | 40.0:60.0 | 22.9 | 10 | 13 | 23 | 43.5:56.5 | 21.1 |
| 1985 | 13 | 11 | 24 | 54.2:45.8 | 38.7 | 6 | 14 | 20 | 30.0:70.0 | 32.3 | 4 | 14 | 18 | 22.2:77.8 | 29.0 |
| 1986 | 29 | 36 | 65 | 44.6:55.4 | 58.6 | 4 | 16 | 20 | 20.0:80.0 | 18.0 | 3 | 23 | 26 | 11.5:88.5 | 23.4 |
| 1987 | 26 | 49 | 75 | 34.7:65.3 | 66.4 | 6 | 10 | 16 | 37.5:62.5 | 14.2 | 4 | 18 | 22 | 18.2:81.8 | 19.5 |
| 1988 | 29 | 21 | 50 | 58.0:42.0 | 54.3 | 11 | 10 | 21 | 52.4:47.6 | 22.8 | 5 | 16 | 21 | 23.8:76.2 | 22.8 |
| 1989 | 14 | 12 | 26 | 53.8:46.2 | 38.2 | 10 | 7 | 17 | 58.8:41.2 | 25.0 | 10 | 15 | 25 | 40.0:60.0 | 36.8 |
| 1990 | 14 | 13 | 27 | 51.9:48.1 | 38.6 | 14 | 9 | 23 | 60.9:39.1 | 32.9 | 10 | 10 | 20 | 50.0:50.0 | 28.6 |
| 1991 | 19 | 16 | 35 | 54.3:45.7 | 47.9 | 9 | 7 | 16 | 56.3:43.8 | 21.9 | 4 | 18 | 22 | 18.2:81.8 | 30.1 |
| 1992 | 16 | 18 | 34 | 47.1:52.9 | 45.3 | 7 | 7 | 14 | 50.0:50.0 | 18.7 | 6 | 21 | 27 | 22.2:77.8 | 36.0 |
| 1993 | 12 | 17 | 29 | 41.4:58.6 | 54.7 | 1 | 12 | 13 | 7.7:92.3 | 24.5 | 1 | 10 | 11 | 9.1:90.9 | 20.8 |
| 1994 | 1 | 1 | 2 | 50.0:50.0 | 100.0 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 |
| 1995 | 2 | 2 | 4 | 50.0:50.0 | 30.8 | 2 | 1 | 3 | 66.7:33.3 | 23.1 | 2 | 4 | 6 | 33.3:66.7 | 46.2 |
| 1996 | 7 | 6 | 13 | 53.8:46.2 | 68.4 | 0 | 3 | 3 | 0.0:100.0 | 15.8 | 1 | 2 | 3 | 33.3:66.7 | 15.8 |
| 1997 | 2 | 1 | 3 | 66.7:33.3 | 30.0 | 0 | 3 | 3 | 0.0:100.0 | 30.0 | 1 | 3 | 4 | 25.0:75.0 | 40.0 |
| 1998 | 0 | 0 | 0 | | 0.0 | 0 | 1 | 1 | 0.0:100.0 | 50.0 | 0 | 1 | 1 | 0.0:100.0 | 50.0 |
| Average | 21 | 21 | 42 | 50.0:50.0 | 52.5 | 7 | 11 | 18 | 38.9:61.1 | 22.5 | 5 | 14 | 20 | 26.3:73.7 | 25.0 |

**Appendix A3.** Age and gender composition of the greater sage-grouse harvest, Eagle, Colorado, 1977–1998.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1977 | 7 | 16 | 23 | 30.4:69.6 | 65.7 | 0 | 8 | 8 | 0.0:100.0 | 22.9 | 0 | 4 | 4 | 0.0:100.0 | 11.4 |
| 1978 | 27 | 20 | 47 | 57.4:42.6 | 59.5 | 5 | 3 | 8 | 62.5:37.5 | 10.1 | 5 | 19 | 24 | 20.8:79.2 | 30.4 |
| 1979 | 19 | 17 | 36 | 52.8:47.2 | 48.6 | 15 | 6 | 21 | 71.4:28.6 | 28.4 | 9 | 8 | 17 | 52.9:47.1 | 23.0 |
| 1980 | 22 | 25 | 47 | 46.8:53.2 | 69.1 | 0 | 7 | 7 | 0.0:100.0 | 10.3 | 4 | 10 | 14 | 28.6:71.4 | 20.6 |
| 1981 | 5 | 5 | 10 | 50.0:50.0 | 76.9 | 1 | 1 | 2 | 50.0:50.0 | 15.4 | 0 | 1 | 1 | 0.0:100.0 | 7.7 |
| 1982 | 8 | 6 | 14 | 57.1:42.9 | 100.0 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 |
| 1983 | 26 | 25 | 51 | 51.0:49.0 | 56.7 | 8 | 16 | 24 | 33.3:66.7 | 26.7 | 3 | 12 | 15 | 20.0:80.0 | 16.7 |
| 1984 | 8 | 3 | 11 | 72.7:27.3 | 42.3 | 4 | 6 | 10 | 40.0:60.0 | 38.5 | 2 | 3 | 5 | 40.0:60.0 | 19.2 |
| 1985 | 13 | 7 | 20 | 65.0:35.0 | 58.8 | 0 | 2 | 2 | 0.0:100.0 | 5.9 | 5 | 7 | 12 | 41.7:58.3 | 35.3 |
| 1986 | 11 | 16 | 27 | 40.7:59.3 | 69.2 | 0 | 4 | 4 | 0.0:100.0 | 10.3 | 0 | 8 | 8 | 0.0:100.0 | 20.5 |
| 1987 | 18 | 17 | 35 | 51.4:48.6 | 55.6 | 6 | 10 | 16 | 37.5:62.5 | 25.4 | 4 | 8 | 12 | 33.3:66.7 | 19.0 |
| 1988 | 8 | 12 | 20 | 40.0:60.0 | 54.1 | 1 | 5 | 6 | 16.7:83.3 | 16.2 | 4 | 7 | 11 | 36.4:63.6 | 29.7 |
| 1989 | 4 | 2 | 6 | 66.7:33.3 | 75.0 | 0 | 1 | 1 | 0.0:100.0 | 12.5 | 0 | 1 | 1 | 0.0:100.0 | 12.5 |
| 1990 | 9 | 7 | 16 | 56.3:43.8 | 61.5 | 1 | 0 | 1 | 100.0:0.0 | 3.8 | 1 | 8 | 9 | 11.1:88.9 | 34.6 |
| 1991 | 11 | 17 | 28 | 39.3:60.7 | 63.6 | 7 | 5 | 12 | 58.3:41.7 | 27.3 | 2 | 2 | 4 | 50.0:50.0 | 9.1 |
| 1992 | 3 | 7 | 10 | 30.0:70.0 | 45.5 | 5 | 1 | 6 | 83.3:16.7 | 27.3 | 3 | 3 | 6 | 50.0:50.0 | 27.3 |
| 1993 | 0 | 1 | 1 | 0.0:100.0 | 25.0 | 0 | 0 | 0 | | 0.0 | 1 | 2 | 3 | 33.3:66.7 | 75.0 |
| 1994 | 3 | 1 | 4 | 75.0:25.0 | 36.4 | 1 | 0 | 1 | 100.0:0.0 | 9.1 | 4 | 2 | 6 | 66.7:33.3 | 54.5 |
| 1995 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 1996 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 1997 | 0 | 1 | 1 | 0.0:100.0 | 50.0 | 0 | 1 | 1 | 0.0:100.0 | 50.0 | 0 | 0 | 0 | | 0.0 |
| 1998 | 2 | 2 | 4 | 50.0:50.0 | 80.0 | 0 | 0 | 0 | | 0.0 | 0 | 1 | 1 | 0.0:100.0 | 20.0 |
| Average | 9 | 9 | 19 | 50.0:50.0 | 59.4 | 2 | 3 | 6 | 40.0:60.0 | 18.8 | 2 | 5 | 7 | 33.3:66.7 | 21.9 |

**Appendix A4.** Age and gender composition of the greater sage-grouse harvest, Yampa, Colorado, 1977–1998.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1977 | 30 | 28 | 58 | 51.7:48.3 | 58.6 | 9 | 16 | 25 | 36.0:64.0 | 25.3 | 5 | 11 | 16 | 31.3:68.8 | 16.2 |
| 1978 | 28 | 28 | 56 | 50.0:50.0 | 45.5 | 5 | 14 | 19 | 26.3:73.7 | 15.4 | 16 | 32 | 48 | 33.3:66.7 | 39.0 |
| 1979 | 20 | 31 | 51 | 39.2:60.8 | 37.0 | 23 | 28 | 51 | 45.1:54.9 | 37.0 | 17 | 19 | 36 | 47.2:52.8 | 26.1 |
| 1980 | 31 | 30 | 61 | 50.8:49.2 | 42.4 | 21 | 19 | 40 | 52.5:47.5 | 27.8 | 16 | 27 | 43 | 37.2:62.8 | 29.9 |
| 1981 | 7 | 10 | 17 | 41.2:58.8 | 21.3 | 17 | 26 | 43 | 39.5:60.5 | 53.8 | 3 | 17 | 20 | 15.0:85.0 | 25.0 |
| 1982 | 8 | 11 | 19 | 42.1:57.9 | 57.6 | 5 | 4 | 9 | 55.6:44.4 | 27.3 | 0 | 5 | 5 | 0.0:100.0 | 15.2 |
| 1983 | 16 | 8 | 24 | 66.7:33.3 | 57.1 | 4 | 7 | 11 | 36.4:63.6 | 26.2 | 1 | 6 | 7 | 14.3:85.7 | 16.7 |
| 1984 | 7 | 7 | 14 | 50.0:50.0 | 51.9 | 5 | 3 | 8 | 62.5:37.5 | 29.6 | 2 | 3 | 5 | 40.0:60.0 | 18.5 |
| 1985 | 2 | 6 | 8 | 25.0:75.0 | 34.8 | 2 | 3 | 5 | 40.0:60.0 | 21.7 | 3 | 7 | 10 | 30.0:70.0 | 43.5 |
| 1986 | 4 | 3 | 7 | 57.1:42.9 | 63.6 | 0 | 2 | 2 | 0.0:100.0 | 18.2 | 0 | 2 | 2 | 0.0:100.0 | 18.2 |
| 1987 | 3 | 1 | 4 | 75.0:25.0 | 33.3 | 2 | 4 | 6 | 33.3:66.7 | 50.0 | 0 | 2 | 2 | 0.0:100.0 | 16.7 |
| 1988 | 3 | 2 | 5 | 60.0:40.0 | 16.7 | 11 | 2 | 13 | 84.6:15.4 | 43.3 | 8 | 4 | 12 | 66.7:33.3 | 40.0 |
| 1989 | 7 | 9 | 16 | 43.8:56.3 | 43.2 | 10 | 3 | 13 | 76.9:23.1 | 35.1 | 6 | 2 | 8 | 75.0:25.0 | 21.6 |
| 1990 | 2 | 6 | 8 | 25.0:75.0 | 47.1 | 1 | 2 | 3 | 33.3:66.7 | 17.6 | 2 | 4 | 6 | 33.3:66.7 | 35.3 |
| 1991 | 7 | 6 | 13 | 53.8:46.2 | 48.1 | 1 | 5 | 6 | 16.7:83.3 | 22.2 | 3 | 5 | 8 | 37.5:62.5 | 29.6 |
| 1992 | 1 | 2 | 3 | 33.3:66.7 | 25.0 | 5 | 0 | 5 | 100.0:0.0 | 41.7 | 1 | 3 | 4 | 25.0:75.0 | 33.3 |
| 1993 | 12 | 11 | 23 | 52.2:47.8 | 54.8 | 0 | 2 | 2 | 0.0:100.0 | 4.8 | 3 | 14 | 17 | 17.6:82.4 | 40.5 |
| 1994 | 1 | 1 | 2 | 50.0:50.0 | 18.2 | 3 | 1 | 4 | 75.0:25.0 | 36.4 | 4 | 1 | 5 | 80.0:20.0 | 45.5 |
| 1995 | 1 | 3 | 4 | 25.0:75.0 | 50.0 | 0 | 0 | 0 | | 0.0 | 0 | 4 | 4 | 0.0:100.0 | 50.0 |
| 1996 | 1 | 1 | 2 | 50.0:50.0 | 100.0 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 |
| 1997 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 1998 | 2 | 0 | 2 | 100.0:0.0 | 100.0 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 |
| Average | 9 | 9 | 18 | 50.0:50.0 | 42.9 | 6 | 6 | 12 | 45.5:54.5 | 28.6 | 4 | 8 | 12 | 36.4:63.6 | 28.6 |

**Appendix A5.** Age and gender composition of the greater sage-grouse harvest, Piceance Basin, Colorado, 1977–1994.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1977 | 13 | 19 | 32 | 40.6:59.4 | 49.2 | 6 | 9 | 15 | 40.0:60.0 | 23.1 | 3 | 15 | 18 | 16.7:83.3 | 27.7 |
| 1978 | 33 | 42 | 75 | 44.0:56.0 | 65.8 | 4 | 12 | 16 | 25.0:75.0 | 14.0 | 6 | 17 | 23 | 26.1:73.9 | 20.2 |
| 1979 | 23 | 16 | 39 | 59.0:41.0 | 54.9 | 10 | 4 | 14 | 71.4:28.6 | 19.7 | 8 | 10 | 18 | 44.4:55.6 | 25.4 |
| 1980 | 22 | 31 | 53 | 41.5:58.5 | 67.9 | 8 | 6 | 14 | 57.1:42.9 | 17.9 | 5 | 6 | 11 | 45.5:54.5 | 14.1 |
| 1981 | 9 | 11 | 20 | 45.0:55.0 | 83.3 | 1 | 1 | 2 | 50.0:50.0 | 8.3 | 0 | 2 | 2 | 0.0:100.0 | 8.3 |
| 1982 | 24 | 17 | 41 | 58.5:41.5 | 69.5 | 2 | 6 | 8 | 25.0:75.0 | 13.6 | 1 | 9 | 10 | 10.0:90.0 | 16.9 |
| 1983 | 17 | 15 | 32 | 53.1:46.9 | 62.7 | 5 | 9 | 14 | 35.7:64.3 | 27.5 | 1 | 4 | 5 | 20.0:80.0 | 9.8 |
| 1984 | 15 | 11 | 26 | 57.7:42.3 | 61.9 | 1 | 5 | 6 | 16.7:83.3 | 14.3 | 3 | 7 | 10 | 30.0:70.0 | 23.8 |
| 1985 | 12 | 13 | 25 | 48.0:52.0 | 69.4 | 2 | 2 | 4 | 50.0:50.0 | 11.1 | 1 | 6 | 7 | 14.3:85.7 | 19.4 |
| 1986 | 9 | 16 | 25 | 36.0:64.0 | 37.9 | 10 | 12 | 22 | 45.5:54.5 | 33.3 | 8 | 11 | 19 | 42.1:57.9 | 28.8 |
| 1987 | 17 | 17 | 34 | 50.0:50.0 | 63.0 | 3 | 10 | 13 | 23.1:76.9 | 24.1 | 3 | 4 | 7 | 42.9:57.1 | 13.0 |
| 1988 | 8 | 7 | 15 | 53.3:46.7 | 55.6 | 2 | 5 | 7 | 28.6:71.4 | 25.9 | 0 | 5 | 5 | 0.0:100.0 | 18.5 |
| 1989 | 7 | 11 | 18 | 38.9:61.1 | 36.7 | 12 | 8 | 20 | 60.0:40.0 | 40.8 | 6 | 5 | 11 | 54.5:45.5 | 22.4 |
| 1990 | 5 | 4 | 9 | 55.6:44.4 | 37.5 | 4 | 2 | 6 | 66.7:33.3 | 25.0 | 6 | 3 | 9 | 66.7:33.3 | 37.5 |
| 1991 | 0 | 1 | 1 | 0.0:100.0 | 14.3 | 1 | 1 | 2 | 50.0:50.0 | 28.6 | 1 | 3 | 4 | 25.0:75.0 | 57.1 |
| 1992 | 3 | 6 | 9 | 33.3:66.7 | 47.4 | 1 | 5 | 6 | 16.7:83.3 | 31.6 | 0 | 4 | 4 | 0.0:100.0 | 21.1 |
| 1993 | 6 | 2 | 8 | 75.0:25.0 | 57.1 | 1 | 1 | 2 | 50.0:50.0 | 14.3 | 0 | 4 | 4 | 0.0:100.0 | 28.6 |
| 1994 | 9 | 3 | 12 | 75.0:25.0 | 70.6 | 1 | 0 | 1 | 100.0:0.0 | 5.9 | 0 | 4 | 4 | 0.0:100.0 | 23.5 |
| Average | 13 | 13 | 26 | 47.4:52.6 | 56.5 | 4 | 5 | 10 | 42.9:57.1 | 21.7 | 3 | 7 | 10 | 30.0:70.0 | 21.7 |

**Appendix A6.** Age and gender composition of the greater sage-grouse harvest, Blue Mountain, Colorado, 1976–1998.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1976 | 32 | 37 | 69 | 46.4:53.6 | 61.6 | 7 | 10 | 17 | 41.2:58.8 | 15.2 | 4 | 22 | 26 | 15.4:84.6 | 23.2 |
| 1977 | 26 | 38 | 64 | 40.6:59.4 | 60.4 | 10 | 7 | 17 | 58.8:41.2 | 16.0 | 11 | 14 | 25 | 44.0:56.0 | 23.6 |
| 1978 | 166 | 164 | 330 | 50.3:49.7 | 62.1 | 28 | 68 | 96 | 29.2:70.8 | 18.1 | 31 | 74 | 105 | 29.5:70.5 | 19.8 |
| 1979 | 97 | 107 | 204 | 47.5:52.5 | 45.0 | 76 | 74 | 150 | 50.7:49.3 | 33.1 | 29 | 70 | 99 | 29.3:70.7 | 21.9 |
| 1980 | 102 | 136 | 238 | 42.9:57.1 | 68.8 | 11 | 31 | 42 | 26.2:73.8 | 12.1 | 13 | 53 | 66 | 19.7:80.3 | 19.1 |
| 1981 | 27 | 40 | 67 | 40.3:59.7 | 54.9 | 13 | 19 | 32 | 40.6:59.4 | 26.2 | 11 | 12 | 23 | 47.8:52.2 | 18.9 |
| 1982 | 58 | 100 | 158 | 36.7:63.3 | 70.5 | 23 | 21 | 44 | 52.3:47.7 | 19.6 | 4 | 18 | 22 | 18.2:81.8 | 9.8 |
| 1983 | 41 | 50 | 91 | 45.1:54.9 | 63.2 | 6 | 17 | 23 | 26.1:73.9 | 16.0 | 4 | 26 | 30 | 13.3:86.7 | 20.8 |
| 1984 | 78 | 81 | 159 | 49.1:50.9 | 63.1 | 28 | 28 | 56 | 50.0:50.0 | 22.2 | 9 | 28 | 37 | 24.3:75.7 | 14.7 |
| 1985 | 125 | 98 | 223 | 56.1:43.9 | 67.4 | 25 | 36 | 61 | 41.0:59.0 | 18.4 | 18 | 29 | 47 | 38.3:61.7 | 14.2 |
| 1986 | 116 | 115 | 231 | 50.2:49.8 | 59.5 | 41 | 50 | 91 | 45.1:54.9 | 23.5 | 17 | 49 | 66 | 25.8:74.2 | 17.0 |
| 1987 | 150 | 151 | 301 | 49.8:50.2 | 66.3 | 35 | 41 | 76 | 46.1:53.9 | 16.7 | 21 | 56 | 77 | 27.3:72.7 | 17.0 |
| 1988 | 69 | 79 | 148 | 46.6:53.4 | 50.0 | 32 | 48 | 80 | 40.0:60.0 | 27.0 | 32 | 36 | 68 | 47.1:52.9 | 23.0 |
| 1989 | 74 | 75 | 149 | 49.7:50.3 | 41.3 | 51 | 58 | 109 | 46.8:53.2 | 30.2 | 42 | 61 | 103 | 40.8:59.2 | 28.5 |
| 1990 | 70 | 89 | 159 | 44.0:56.0 | 55.4 | 27 | 38 | 65 | 41.5:58.5 | 22.6 | 10 | 53 | 63 | 15.9:84.1 | 22.0 |
| 1991 | 40 | 81 | 121 | 33.1:66.9 | 54.0 | 15 | 35 | 50 | 30.0:70.0 | 22.3 | 15 | 38 | 53 | 28.3:71.7 | 23.7 |
| 1992 | 32 | 41 | 73 | 43.8:56.2 | 45.9 | 16 | 23 | 39 | 41.0:59.0 | 24.5 | 14 | 33 | 47 | 29.8:70.2 | 29.6 |
| 1993 | 43 | 60 | 103 | 41.7:58.3 | 65.2 | 3 | 11 | 14 | 21.4:78.6 | 8.9 | 8 | 33 | 41 | 19.5:80.5 | 25.9 |
| 1994 | 17 | 38 | 55 | 30.9:69.1 | 48.7 | 11 | 22 | 33 | 33.3:66.7 | 29.2 | 7 | 18 | 25 | 28.0:72.0 | 22.1 |
| 1995 | 41 | 29 | 70 | 58.6:41.4 | 74.5 | 1 | 13 | 14 | 7.1:92.9 | 14.9 | 1 | 9 | 10 | 10.0:90.0 | 10.6 |
| 1996 | 39 | 43 | 82 | 47.6:52.4 | 56.6 | 11 | 16 | 27 | 40.7:59.3 | 18.6 | 10 | 26 | 36 | 27.8:72.2 | 24.8 |
| 1997 | 20 | 14 | 34 | 58.8:41.2 | 50.0 | 9 | 9 | 18 | 50.0:50.0 | 26.5 | 8 | 8 | 16 | 50.0:50.0 | 23.5 |
| 1998 | 10 | 10 | 20 | 50.0:50.0 | 50.0 | 1 | 6 | 7 | 14.3:85.7 | 17.5 | 6 | 7 | 13 | 46.2:53.8 | 32.5 |
| Average | 64 | 73 | 137 | 46.7:53.3 | 58.3 | 21 | 30 | 50 | 41.2:58.8 | 21.3 | 14 | 34 | 48 | 29.2:70.8 | 20.4 |

**Appendix A7.** Age and gender composition of the greater sage-grouse harvest, Cold Spring Mountain, Colorado, 1976–1998. Wings were not identifiable to specific hunting area in 1978 and 1979.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n* ) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1976 | 18 | 20 | 38 | 47.4:52.6 | 73.1 | 2 | 2 | 4 | 50.0:50.0 | 7.7 | 0 | 10 | 10 | 0.0:100.0 | 19.2 |
| 1977 | 18 | 43 | 61 | 29.5:70.5 | 59.8 | 6 | 12 | 18 | 33.3:66.7 | 17.6 | 3 | 20 | 23 | 13.0:87.0 | 22.5 |
| 1978 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 1979 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 1980 | 25 | 22 | 47 | 53.2:46.8 | 60.3 | 2 | 4 | 6 | 33.3:66.7 | 7.7 | 4 | 21 | 25 | 16.0:84.0 | 32.1 |
| 1981 | 75 | 81 | 156 | 48.1:51.9 | 61.7 | 8 | 28 | 36 | 22.2:77.8 | 14.2 | 19 | 42 | 61 | 31.1:68.9 | 24.1 |
| 1982 | 25 | 26 | 51 | 49.0:51.0 | 64.6 | 5 | 8 | 13 | 38.5:61.5 | 16.5 | 2 | 13 | 15 | 13.3:86.7 | 19.0 |
| 1983 | 97 | 79 | 176 | 55.1:44.9 | 68.0 | 15 | 24 | 39 | 38.5:61.5 | 15.1 | 3 | 41 | 44 | 6.8:93.2 | 17.0 |
| 1984 | 4 | 14 | 18 | 22.2:77.8 | 39.1 | 3 | 8 | 11 | 27.3:72.7 | 23.9 | 4 | 13 | 17 | 23.5:76.5 | 37.0 |
| 1985 | 50 | 73 | 123 | 40.7:59.3 | 62.1 | 12 | 22 | 34 | 35.3:64.7 | 17.2 | 3 | 38 | 41 | 7.3:92.7 | 20.7 |
| 1986 | 39 | 31 | 70 | 55.7:44.3 | 61.4 | 8 | 12 | 20 | 40.0:60.0 | 17.5 | 2 | 22 | 24 | 8.3:91.7 | 21.1 |
| 1987 | 15 | 20 | 35 | 42.9:57.1 | 49.3 | 9 | 12 | 21 | 42.9:57.1 | 29.6 | 4 | 11 | 15 | 26.7:73.3 | 21.1 |
| 1988 | 23 | 23 | 46 | 50.0:50.0 | 54.1 | 6 | 13 | 19 | 31.6:68.4 | 22.4 | 6 | 14 | 20 | 30.0:70.0 | 23.5 |
| 1989 | 46 | 52 | 98 | 46.9:53.1 | 51.3 | 12 | 24 | 36 | 33.3:66.7 | 18.8 | 24 | 33 | 57 | 42.1:57.9 | 29.8 |
| 1990 | 42 | 63 | 105 | 40.0:60.0 | 52.5 | 11 | 24 | 35 | 31.4:68.6 | 17.5 | 8 | 52 | 60 | 13.3:86.7 | 30.0 |
| 1991 | 56 | 74 | 130 | 43.1:56.9 | 68.1 | 1 | 13 | 14 | 7.1:92.9 | 7.3 | 8 | 39 | 47 | 17.0:83.0 | 24.6 |
| 1992 | 27 | 57 | 84 | 32.1:67.9 | 51.9 | 13 | 23 | 36 | 36.1:63.9 | 22.2 | 10 | 32 | 42 | 23.8:76.2 | 25.9 |
| 1993 | 40 | 51 | 91 | 44.0:56.0 | 62.3 | 6 | 17 | 23 | 26.1:73.9 | 15.8 | 6 | 26 | 32 | 18.8:81.3 | 21.9 |
| 1994 | 22 | 25 | 47 | 46.8:53.2 | 72.3 | 4 | 8 | 12 | 33.3:66.7 | 18.5 | 2 | 4 | 6 | 33.3:66.7 | 9.2 |
| 1995 | 6 | 9 | 15 | 40.0:60.0 | 60.0 | 0 | 3 | 3 | 0.0:100.0 | 12.0 | 1 | 6 | 7 | 14.3:85.7 | 28.0 |
| 1996 | 14 | 20 | 34 | 41.2:58.8 | 63.0 | 5 | 3 | 8 | 62.5:37.5 | 14.8 | 5 | 7 | 12 | 41.7:58.3 | 22.2 |
| 1997 | 21 | 15 | 36 | 58.3:41.7 | 65.5 | 1 | 6 | 7 | 14.3:85.7 | 12.7 | 2 | 10 | 12 | 16.7:83.3 | 21.8 |
| 1998 | 17 | 26 | 43 | 39.5:60.5 | 45.7 | 9 | 13 | 22 | 40.9:59.1 | 23.4 | 7 | 22 | 29 | 24.1:75.9 | 30.9 |
| Average | 32 | 39 | 65 | 45.1:54.9 | 59.6 | 7 | 13 | 18 | 35.0:65.0 | 16.5 | 6 | 23 | 26 | 20.7:79.3 | 23.9 |

**Appendix A8.** Age and gender composition of the greater sage-grouse harvest, Eastern Moffat and Northwestern Routt counties, Colorado, 1976–1998. The season was closed in 1998 but some wings were received. There were no wings received in 1995.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1976 | 10 | 15 | 25 | 40.0:60.0 | 46.3 | 11 | 7 | 18 | 61.1:38.9 | 33.3 | 3 | 8 | 11 | 27.3:72.7 | 20.4 |
| 1977 | 14 | 22 | 36 | 38.9:61.1 | 39.6 | 4 | 14 | 18 | 22.2:77.8 | 19.8 | 13 | 24 | 37 | 35.1:64.9 | 40.7 |
| 1978 | 99 | 108 | 207 | 47.8:52.2 | 77.8 | 8 | 17 | 25 | 32.0:68.0 | 9.4 | 10 | 24 | 34 | 29.4:70.6 | 12.8 |
| 1979 | 112 | 103 | 215 | 52.1:47.9 | 57.5 | 27 | 84 | 111 | 24.3:75.7 | 29.7 | 3 | 45 | 48 | 6.3:93.8 | 12.8 |
| 1980 | 69 | 81 | 150 | 46.0:54.0 | 50.8 | 18 | 48 | 66 | 27.3:72.7 | 22.4 | 26 | 53 | 79 | 32.9:67.1 | 26.8 |
| 1981 | 83 | 107 | 190 | 43.7:56.3 | 42.7 | 43 | 85 | 128 | 33.6:66.4 | 28.8 | 28 | 99 | 127 | 22.0:78.0 | 28.5 |
| 1982 | 52 | 35 | 87 | 59.8:40.2 | 46.3 | 14 | 36 | 50 | 28.0:72.0 | 26.6 | 17 | 34 | 51 | 33.3:66.7 | 27.1 |
| 1983 | 42 | 54 | 96 | 43.8:56.3 | 47.5 | 21 | 23 | 44 | 47.7:52.3 | 21.8 | 18 | 44 | 62 | 29.0:71.0 | 30.7 |
| 1984 | 15 | 21 | 36 | 41.7:58.3 | 62.1 | 1 | 9 | 10 | 10.0:90.0 | 17.2 | 4 | 8 | 12 | 33.3:66.7 | 20.7 |
| 1985 | 34 | 50 | 84 | 40.5:59.5 | 65.1 | 6 | 22 | 28 | 21.4:78.6 | 21.7 | 3 | 14 | 17 | 17.6:82.4 | 13.2 |
| 1986 | 52 | 58 | 110 | 47.3:52.7 | 70.1 | 15 | 14 | 29 | 51.7:48.3 | 18.5 | 5 | 13 | 18 | 27.8:72.2 | 11.5 |
| 1987 | 53 | 44 | 97 | 54.6:45.4 | 65.1 | 6 | 22 | 28 | 21.4:78.6 | 18.8 | 4 | 20 | 24 | 16.7:83.3 | 16.1 |
| 1988 | 36 | 40 | 76 | 47.4:52.6 | 50.7 | 12 | 24 | 36 | 33.3:66.7 | 24.0 | 8 | 30 | 38 | 21.1:78.9 | 25.3 |
| 1989 | 79 | 68 | 147 | 53.7:46.3 | 59.8 | 19 | 30 | 49 | 38.8:61.2 | 19.9 | 4 | 46 | 50 | 8.0:92.0 | 20.3 |
| 1990 | 82 | 81 | 163 | 50.3:49.7 | 49.8 | 40 | 49 | 89 | 44.9:55.1 | 27.2 | 26 | 49 | 75 | 34.7:65.3 | 22.9 |
| 1991 | 28 | 33 | 61 | 45.9:54.1 | 42.1 | 15 | 24 | 39 | 38.5:61.5 | 26.9 | 14 | 31 | 45 | 31.1:68.9 | 31.0 |
| 1992 | 12 | 15 | 27 | 44.4:55.6 | 34.2 | 9 | 9 | 18 | 50.0:50.0 | 22.8 | 7 | 27 | 34 | 20.6:79.4 | 43.0 |
| 1993 | 11 | 13 | 24 | 45.8:54.2 | 32.4 | 3 | 7 | 10 | 30.0:70.0 | 13.5 | 8 | 32 | 40 | 20.0:80.0 | 54.1 |
| 1994 | 20 | 24 | 44 | 45.5:54.5 | 62.0 | 1 | 13 | 14 | 7.1:92.9 | 19.7 | 1 | 12 | 13 | 7.7:92.3 | 18.3 |
| 1995 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 1996 | 5 | 6 | 11 | 45.5:54.5 | 47.8 | 0 | 5 | 5 | 0.0:100.0 | 21.7 | 1 | 6 | 7 | 14.3:85.7 | 30.4 |
| 1997 | 2 | 0 | 2 | 100.0:0.0 | 100.0 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 |
| 1998 | 0 | 2 | 2 | 0.0:100.0 | 14.3 | 0 | 4 | 4 | 0.0:100.0 | 28.6 | 0 | 8 | 8 | 0.0:100.0 | 57.1 |
| Average | 40 | 43 | 82 | 48.2:51.8 | 53.2 | 12 | 24 | 36 | 33.3:66.7 | 23.4 | 9 | 27 | 36 | 25.0:75.0 | 23.4 |

**Appendix A9.** Age and gender composition of the greater sage-grouse harvest, Northcentral Moffat County, Colorado, 1976–1998.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1976 | 143 | 202 | 345 | 41.4:58.6 | 65.1 | 21 | 55 | 76 | 27.6:72.4 | 14.3 | 18 | 91 | 109 | 16.5:83.5 | 20.6 |
| 1977 | 50 | 71 | 121 | 41.3:58.7 | 33.3 | 51 | 54 | 105 | 48.6:51.4 | 28.9 | 56 | 81 | 137 | 40.9:59.1 | 37.7 |
| 1978 | 419 | 460 | 879 | 47.7:52.3 | 71.7 | 18 | 43 | 61 | 29.5:70.5 | 5.0 | 73 | 213 | 286 | 25.5:74.5 | 23.3 |
| 1979 | 495 | 612 | 1107 | 44.7:55.3 | 57.1 | 250 | 291 | 541 | 46.2:53.8 | 27.9 | 91 | 200 | 291 | 31.3:68.7 | 15.0 |
| 1980 | 371 | 464 | 835 | 44.4:55.6 | 53.0 | 118 | 142 | 260 | 45.4:54.6 | 16.5 | 206 | 275 | 481 | 42.8:57.2 | 30.5 |
| 1981 | 264 | 370 | 634 | 41.6:58.4 | 54.8 | 50 | 121 | 171 | 29.2:70.8 | 14.8 | 97 | 255 | 352 | 27.6:72.4 | 30.4 |
| 1982 | 174 | 232 | 406 | 42.9:57.1 | 61.4 | 25 | 63 | 88 | 28.4:71.6 | 13.3 | 34 | 133 | 167 | 20.4:79.6 | 25.3 |
| 1983 | 312 | 363 | 675 | 46.2:53.8 | 57.1 | 95 | 130 | 225 | 42.2:57.8 | 19.0 | 73 | 210 | 283 | 25.8:74.2 | 23.9 |
| 1984 | 148 | 190 | 338 | 43.8:56.2 | 55.7 | 35 | 74 | 109 | 32.1:67.9 | 18.0 | 35 | 125 | 160 | 21.9:78.1 | 26.4 |
| 1985 | 221 | 289 | 510 | 43.3:56.7 | 62.7 | 46 | 80 | 126 | 36.5:63.5 | 15.5 | 53 | 125 | 178 | 29.8:70.2 | 21.9 |
| 1986 | 292 | 317 | 609 | 47.9:52.1 | 58.6 | 80 | 149 | 229 | 34.9:65.1 | 22.0 | 72 | 129 | 201 | 35.8:64.2 | 19.3 |
| 1987 | 358 | 414 | 772 | 46.4:53.6 | 55.9 | 101 | 191 | 292 | 34.6:65.4 | 21.2 | 89 | 227 | 316 | 28.2:71.8 | 22.9 |
| 1988 | 254 | 343 | 597 | 42.5:57.5 | 51.3 | 93 | 158 | 251 | 37.1:62.9 | 21.6 | 101 | 215 | 316 | 32.0:68.0 | 27.1 |
| 1989 | 358 | 474 | 832 | 43.0:57.0 | 53.9 | 126 | 119 | 245 | 51.4:48.6 | 15.9 | 184 | 283 | 467 | 39.4:60.6 | 30.2 |
| 1990 | 295 | 382 | 677 | 43.6:56.4 | 44.5 | 105 | 233 | 338 | 31.1:68.9 | 22.2 | 182 | 326 | 508 | 35.8:64.2 | 33.4 |
| 1991 | 157 | 213 | 370 | 42.4:57.6 | 40.7 | 57 | 109 | 166 | 34.3:65.7 | 18.2 | 109 | 265 | 374 | 29.1:70.9 | 41.1 |
| 1992 | 105 | 150 | 255 | 41.2:58.8 | 41.3 | 48 | 88 | 136 | 35.3:64.7 | 22.0 | 45 | 182 | 227 | 19.8:80.2 | 36.7 |
| 1993 | 96 | 100 | 196 | 49.0:51.0 | 53.1 | 23 | 29 | 52 | 44.2:55.8 | 14.1 | 35 | 86 | 121 | 28.9:71.1 | 32.8 |
| 1994 | 69 | 106 | 175 | 39.4:60.6 | 47.7 | 27 | 35 | 62 | 43.5:56.5 | 16.9 | 19 | 111 | 130 | 14.6:85.4 | 35.4 |
| 1995 | 30 | 33 | 63 | 47.6:52.4 | 64.9 | 5 | 8 | 13 | 38.5:61.5 | 13.4 | 4 | 17 | 21 | 19.0:81.0 | 21.6 |
| 1996 | 23 | 58 | 81 | 28.4:71.6 | 55.9 | 8 | 18 | 26 | 30.8:69.2 | 17.9 | 10 | 28 | 38 | 26.3:73.7 | 26.2 |
| 1997 | 23 | 18 | 41 | 56.1:43.9 | 50.0 | 7 | 9 | 16 | 43.8:56.3 | 19.5 | 7 | 18 | 25 | 28.0:72.0 | 30.5 |
| 1998 | 24 | 24 | 48 | 50.0:50.0 | 60.0 | 10 | 6 | 16 | 62.5:37.5 | 20.0 | 5 | 11 | 16 | 31.3:68.8 | 20.0 |
| Average | 204 | 256 | 459 | 44.3:55.7 | 54.5 | 61 | 96 | 157 | 38.9:61.1 | 18.6 | 69 | 157 | 226 | 30.8:69.2 | 26.8 |

**Appendix A10.** Age and gender composition of the greater sage-grouse harvest, Sumpter, Hunt Unit 51, Oregon, 1993–2013.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1993 | 3 | 2 | 5 | 60.0:40.0 | 83.3 | 0 | 0 | 0 | | 0.0 | 0 | 1 | 1 | 0.0:100.0 | 16.7 |
| 1994 | 1 | 4 | 5 | 20.0:80.0 | 50.0 | 0 | 1 | 1 | 0.0:100.0 | 10.0 | 0 | 4 | 4 | 0.0:100.0 | 40.0 |
| 1995 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 2 | 1 | 3 | 66.7:33.3 | 100.0 |
| 1996 | 0 | 2 | 2 | 0.0:100.0 | 33.3 | 0 | 0 | 0 | | 0.0 | 3 | 1 | 4 | 75.0:25.0 | 66.7 |
| 1997 | 1 | 0 | 1 | 100.0:0.0 | 25.0 | 0 | 0 | 0 | | 0.0 | 2 | 1 | 3 | 66.7:33.3 | 75.0 |
| 1998 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 1999 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 1 | 1 | 2 | 50.0:50.0 | 100.0 |
| 2000 | 0 | 1 | 1 | 0.0:100.0 | 33.3 | 0 | 1 | 1 | 0.0:100.0 | 33.3 | 0 | 1 | 1 | 0.0:100.0 | 33.3 |
| 2001 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 0 | 2 | 2 | 0.0:100.0 | 100.0 |
| 2002 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 2003 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 2 | 2 | 4 | 50.0:50.0 | 100.0 |
| 2004 | 1 | 0 | 1 | 100.0:0.0 | 100.0 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 |
| 2005 | 1 | 1 | 2 | 50.0:50.0 | 100.0 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 |
| 2006 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 2007 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 2008 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 0 | 2 | 2 | 0.0:100.0 | 100.0 |
| 2009 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 2 | 0 | 2 | 100.0:0.0 | 100.0 |
| 2010 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 2011 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 2012 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 2013 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| Average | 0 | 1 | 1 | 41.2:58.8 | 36.2 | 0 | 0 | 0 | 0.0:100.0 | 4.3 | 1 | 1 | 1 | 42.9:57.1 | 59.6 |

**Appendix A11.** Age and gender composition of the greater sage-grouse harvest, Lookout Mountain, Hunt Unit 64, Oregon, 1993–2013.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1993 | 2 | 3 | 5 | 40.0:60.0 | 62.5 | 0 | 0 | 0 | | 0.0 | 1 | 2 | 3 | 33.3:66.7 | 37.5 |
| 1994 | 0 | 1 | 1 | 0.0:100.0 | 25.0 | 0 | 0 | 0 | | 0.0 | 1 | 2 | 3 | 33.3:66.7 | 75.0 |
| 1995 | 3 | 1 | 4 | 75.0:25.0 | 50.0 | 0 | 2 | 2 | 0.0:100.0 | 25.0 | 1 | 1 | 2 | 50.0:50.0 | 25.0 |
| 1996 | 0 | 3 | 3 | 0.0:100.0 | 100.0 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 |
| 1997 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 3 | 0 | 3 | 100.0:0.0 | 100.0 |
| 1998 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 4 | 0 | 4 | 100.0:0.0 | 100.0 |
| 1999 | 3 | 0 | 3 | 100.0:0.0 | 25.0 | 0 | 0 | 0 | | 0.0 | 5 | 4 | 9 | 55.6:44.4 | 75.0 |
| 2000 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 2 | 0 | 2 | 100.0:0.0 | 100.0 |
| 2001 | 1 | 2 | 3 | 33.3:66.7 | 60.0 | 0 | 0 | 0 | | 0.0 | 1 | 1 | 2 | 50.0:50.0 | 40.0 |
| 2002 | 1 | 1 | 2 | 50.0:50.0 | 66.7 | 0 | 0 | 0 | | 0.0 | 1 | 0 | 1 | 100.0:0.0 | 33.3 |
| 2003 | 3 | 3 | 6 | 50.0:50.0 | 66.7 | 0 | 1 | 1 | 0.0:100.0 | 11.1 | 0 | 2 | 2 | 0.0:100.0 | 22.2 |
| 2004 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 2 | 1 | 3 | 66.7:33.3 | 100.0 |
| 2005 | 2 | 2 | 4 | 50.0:50.0 | 50.0 | 0 | 0 | 0 | | 0.0 | 2 | 2 | 4 | 50.0:50.0 | 50.0 |
| 2006 | 2 | 1 | 3 | 66.7:33.3 | 33.3 | 0 | 0 | 0 | | 0.0 | 5 | 1 | 6 | 83.3:16.7 | 66.7 |
| 2007 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 3 | 1 | 4 | 75.0:25.0 | 100.0 |
| 2008 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 0 | 2 | 2 | 0.0:100.0 | 100.0 |
| 2009 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 2010 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 2011 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 0 | 1 | 1 | 0.0:100.0 | 100.0 |
| 2012 | 1 | 0 | 1 | 100.0:0.0 | 25.0 | 0 | 1 | 1 | 0.0:100.0 | 25.0 | 1 | 1 | 2 | 50.0:50.0 | 50.0 |
| 2013 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| Average | 1 | 1 | 2 | 51.4:48.6 | 38.0 | 0 | 0 | 0 | 0.0:100.0 | 4.3 | 2 | 1 | 3 | 60.4:39.6 | 60.0 |

**Appendix A12.** Age and gender composition of the greater sage-grouse harvest, Beulah, Hunt Unit 65, Oregon, 1993–2013.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1993 | 6 | 1 | 7 | 85.7:14.3 | 38.9 | 0 | 1 | 1 | 0.0:100.0 | 5.6 | 3 | 7 | 10 | 30.0:70.0 | 55.6 |
| 1994 | 21 | 6 | 27 | 77.8:22.2 | 52.9 | 0 | 4 | 4 | 0.0:100.0 | 7.8 | 7 | 13 | 20 | 35.0:65.0 | 39.2 |
| 1995 | 3 | 6 | 9 | 33.3:66.7 | 31.0 | 0 | 1 | 1 | 0.0:100.0 | 3.4 | 11 | 8 | 19 | 57.9:42.1 | 65.5 |
| 1996 | 9 | 5 | 14 | 64.3:35.7 | 50.0 | 0 | 1 | 1 | 0.0:100.0 | 3.6 | 5 | 8 | 13 | 38.5:61.5 | 46.4 |
| 1997 | 14 | 17 | 31 | 45.2:54.8 | 45.6 | 1 | 5 | 6 | 16.7:83.3 | 8.8 | 10 | 21 | 31 | 32.3:67.7 | 45.6 |
| 1998 | 17 | 8 | 25 | 68.0:32.0 | 47.2 | 0 | 2 | 2 | 0.0:100.0 | 3.8 | 10 | 16 | 26 | 38.5:61.5 | 49.1 |
| 1999 | 13 | 21 | 34 | 38.2:61.8 | 47.9 | 0 | 3 | 3 | 0.0:100.0 | 4.2 | 19 | 15 | 34 | 55.9:44.1 | 47.9 |
| 2000 | 19 | 12 | 31 | 61.3:38.7 | 47.0 | 0 | 1 | 1 | 0.0:100.0 | 1.5 | 15 | 19 | 34 | 44.1:55.9 | 51.5 |
| 2001 | 14 | 15 | 29 | 48.3:51.7 | 55.8 | 0 | 3 | 3 | 0.0:100.0 | 5.8 | 5 | 15 | 20 | 25.0:75.0 | 38.5 |
| 2002 | 18 | 11 | 29 | 62.1:37.9 | 49.2 | 0 | 2 | 2 | 0.0:100.0 | 3.4 | 8 | 20 | 28 | 28.6:71.4 | 47.5 |
| 2003 | 12 | 11 | 23 | 52.2:47.8 | 39.7 | 0 | 4 | 4 | 0.0:100.0 | 6.9 | 15 | 16 | 31 | 48.4:51.6 | 53.4 |
| 2004 | 17 | 21 | 38 | 44.7:55.3 | 62.3 | 0 | 3 | 3 | 0.0:100.0 | 4.9 | 1 | 19 | 20 | 5.0:95.0 | 32.8 |
| 2005 | 19 | 28 | 47 | 40.4:59.6 | 51.1 | 0 | 2 | 2 | 0.0:100.0 | 2.2 | 18 | 25 | 43 | 41.9:58.1 | 46.7 |
| 2006 | 19 | 19 | 38 | 50.0:50.0 | 63.3 | 0 | 0 | 0 | | 0.0 | 5 | 17 | 22 | 22.7:77.3 | 36.7 |
| 2007 | 4 | 2 | 6 | 66.7:33.3 | 25.0 | 0 | 1 | 1 | 0.0:100.0 | 4.2 | 3 | 14 | 17 | 17.6:82.4 | 70.8 |
| 2008 | 6 | 8 | 14 | 42.9:57.1 | 60.9 | 0 | 1 | 1 | 0.0:100.0 | 4.3 | 0 | 8 | 8 | 0.0:100.0 | 34.8 |
| 2009 | 18 | 15 | 33 | 54.5:45.5 | 57.9 | 0 | 0 | 0 | | 0.0 | 8 | 16 | 24 | 33.3:66.7 | 42.1 |
| 2010 | 11 | 17 | 28 | 39.3:60.7 | 49.1 | 0 | 4 | 4 | 0.0:100.0 | 7.0 | 8 | 17 | 25 | 32.0:68.0 | 43.9 |
| 2011 | 2 | 8 | 10 | 20.0:80.0 | 37.0 | 1 | 2 | 3 | 33.3:66.7 | 11.1 | 8 | 6 | 14 | 57.1:42.9 | 51.9 |
| 2012 | 7 | 5 | 12 | 58.3:41.7 | 38.7 | 0 | 4 | 4 | 0.0:100.0 | 12.9 | 6 | 9 | 15 | 40.0:60.0 | 48.4 |
| 2013 | 3 | 1 | 4 | 75.0:25:0 | 80.0 | 0 | 0 | 0 | | 0 | 1 | 0 | 1 | 100.0:0.0 | 20.0 |
| Average | 12 | 11 | 23 | 51.5:48.5 | 49.4 | 0 | 2 | 2 | 0.0:100.0 | 4.3 | 8 | 14 | 22 | 36.5:63.5 | 46.0 |

**Appendix A13.** Age and gender composition of the greater sage-grouse harvest, Malheur River, Hunt Unit 66, Oregon, 1993–2013.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1993 | 9 | 14 | 23 | 39.1:60.9 | 71.9 | 0 | 1 | 1 | 0.0:100.0 | 3.1 | 2 | 6 | 8 | 25.0:75.0 | 25.0 |
| 1994 | 17 | 23 | 40 | 42.5:57.5 | 46.0 | 3 | 3 | 6 | 50.0:50.0 | 6.9 | 13 | 28 | 41 | 31.7:68.3 | 47.1 |
| 1995 | 5 | 9 | 14 | 35.7:64.3 | 50.0 | 0 | 2 | 2 | 0.0:100.0 | 7.1 | 6 | 6 | 12 | 50.0:50.0 | 42.9 |
| 1996 | 7 | 13 | 20 | 35.0:65.0 | 60.6 | 0 | 1 | 1 | 0.0:100.0 | 3.0 | 2 | 10 | 12 | 16.7:83.3 | 36.4 |
| 1997 | 2 | 10 | 12 | 16.7:83.3 | 52.2 | 0 | 1 | 1 | 0.0:100.0 | 4.3 | 5 | 5 | 10 | 50.0:50.0 | 43.5 |
| 1998 | 5 | 7 | 12 | 41.7:58.3 | 36.4 | 0 | 3 | 3 | 0.0:100.0 | 9.1 | 8 | 10 | 18 | 44.4:55.6 | 54.5 |
| 1999 | 13 | 16 | 29 | 44.8:55.2 | 56.9 | 0 | 3 | 3 | 0.0:100.0 | 5.9 | 7 | 12 | 19 | 36.8:63.2 | 37.3 |
| 2000 | 8 | 12 | 20 | 40.0:60.0 | 41.7 | 1 | 3 | 4 | 25.0:75.0 | 8.3 | 10 | 14 | 24 | 41.7:58.3 | 50.0 |
| 2001 | 13 | 16 | 29 | 44.8:55.2 | 45.3 | 2 | 7 | 9 | 22.2:77.8 | 14.1 | 17 | 9 | 26 | 65.4:34.6 | 40.6 |
| 2002 | 16 | 10 | 26 | 61.5:38.5 | 56.5 | 0 | 3 | 3 | 0.0:100.0 | 6.5 | 6 | 11 | 17 | 35.3:64.7 | 37.0 |
| 2003 | 10 | 19 | 29 | 34.5:65.5 | 54.7 | 1 | 4 | 5 | 20.0:80.0 | 9.4 | 5 | 14 | 19 | 26.3:73.7 | 35.8 |
| 2004 | 14 | 20 | 34 | 41.2:58.8 | 59.6 | 1 | 1 | 2 | 50.0:50.0 | 3.5 | 8 | 13 | 21 | 38.1:61.9 | 36.8 |
| 2005 | 17 | 10 | 27 | 63.0:37.0 | 37.0 | 0 | 3 | 3 | 0.0:100.0 | 4.1 | 24 | 19 | 43 | 55.8:44.2 | 58.9 |
| 2006 | 13 | 5 | 18 | 72.2:27.8 | 46.2 | 0 | 2 | 2 | 0.0:100.0 | 5.1 | 7 | 12 | 19 | 36.8:63.2 | 48.7 |
| 2007 | 2 | 5 | 7 | 28.6:71.4 | 31.8 | 1 | 4 | 5 | 20.0:80.0 | 22.7 | 4 | 6 | 10 | 40.0:60.0 | 45.5 |
| 2008 | 7 | 10 | 17 | 41.2:58.8 | 50.0 | 0 | 2 | 2 | 0.0:100.0 | 5.9 | 6 | 9 | 15 | 40.0:60.0 | 44.1 |
| 2009 | 5 | 2 | 7 | 71.4:28.6 | 43.8 | 0 | 2 | 2 | 0.0:100.0 | 12.5 | 3 | 4 | 7 | 42.9:57.1 | 43.8 |
| 2010 | 9 | 11 | 20 | 45.0:55.0 | 66.7 | 0 | 1 | 1 | 0.0:100.0 | 3.3 | 2 | 7 | 9 | 22.2:77.8 | 30.0 |
| 2011 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 0 | 5 | 5 | 0.0:100.0 | 100.0 |
| 2012 | 1 | 0 | 1 | 100.0:0.0 | 33.3 | 0 | 0 | 0 | | 0.0 | 2 | 0 | 2 | 100.0:0.0 | 66.7 |
| 2013 | 0 | 1 | 1 | 0.0:100.0 | 33.3 | 0 | 1 | 1 | 0.0:100.0 | 33.3 | 0 | 1 | 1 | 0.0:100.0 | 33.3 |
| Average | 8 | 10 | 18 | 44.8.0:55.2 | 49.5 | 0 | 2 | 3 | 16.1:83.9 | 7.2 | 7 | 10 | 17 | 40.5:59.5 | 43.3 |

**Appendix A14.** Age and gender composition of the greater sage-grouse harvest, Owyhee, Hunt Unit 67, Oregon, 1993–2013.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1993 | 1 | 3 | 4 | 25.0:75.0 | 25.0 | 0 | 0 | 0 | | 0.0 | 0 | 12 | 12 | 0.0:100.0 | 75.0 |
| 1994 | 7 | 5 | 12 | 58.3:41.7 | 40.0 | 0 | 0 | 0 | | 0.0 | 2 | 16 | 18 | 11.1:88.9 | 60.0 |
| 1995 | 1 | 5 | 6 | 16.7:83.3 | 37.5 | 0 | 1 | 1 | 0.0:100.0 | 6.3 | 3 | 6 | 9 | 33.3:66.7 | 56.3 |
| 1996 | 8 | 12 | 20 | 40.0:60.0 | 62.5 | 0 | 3 | 3 | 0.0:100.0 | 9.4 | 2 | 7 | 9 | 22.2:77.8 | 28.1 |
| 1997 | 3 | 4 | 7 | 42.9:57.1 | 36.8 | 0 | 0 | 0 | | 0.0 | 5 | 7 | 12 | 41.7:58.3 | 63.2 |
| 1998 | 4 | 2 | 6 | 66.7:33.3 | 18.8 | 0 | 1 | 1 | 0.0:100.0 | 3.1 | 14 | 11 | 25 | 56.0:44.0 | 78.1 |
| 1999 | 12 | 11 | 23 | 52.2:47.8 | 47.9 | 0 | 3 | 3 | 0.0:100.0 | 6.3 | 9 | 13 | 22 | 40.9:59.1 | 45.8 |
| 2000 | 15 | 13 | 28 | 53.6:46.4 | 53.8 | 0 | 2 | 2 | 0.0:100.0 | 3.8 | 12 | 10 | 22 | 54.5:45.5 | 42.3 |
| 2001 | 24 | 21 | 45 | 53.3:46.7 | 66.2 | 1 | 3 | 4 | 25.0:75.0 | 5.9 | 7 | 12 | 19 | 36.8:63.2 | 27.9 |
| 2002 | 6 | 13 | 19 | 31.6:68.4 | 47.5 | 0 | 3 | 3 | 0.0:100.0 | 7.5 | 6 | 12 | 18 | 33.3:66.7 | 45.0 |
| 2003 | 6 | 4 | 10 | 60.0:40.0 | 25.6 | 0 | 2 | 2 | 0.0:100.0 | 5.1 | 12 | 15 | 27 | 44.4:55.6 | 69.2 |
| 2004 | 13 | 15 | 28 | 46.4:53.6 | 52.8 | 0 | 1 | 1 | 0.0:100.0 | 1.9 | 8 | 16 | 24 | 33.3:66.7 | 45.3 |
| 2005 | 10 | 8 | 18 | 55.6:44.4 | 32.1 | 0 | 3 | 3 | 0.0:100.0 | 5.4 | 14 | 21 | 35 | 40.0:60.0 | 62.5 |
| 2006 | 5 | 5 | 10 | 50.0:50.0 | 22.2 | 0 | 1 | 1 | 0.0:100.0 | 2.2 | 21 | 13 | 34 | 61.8:38.2 | 75.6 |
| 2007 | 4 | 1 | 5 | 80.0:20.0 | 20.8 | 1 | 1 | 2 | 50.0:50.0 | 8.3 | 5 | 12 | 17 | 29.4:70.6 | 70.8 |
| 2008 | 5 | 3 | 8 | 62.5:37.5 | 50.0 | 0 | 0 | 0 | | 0.0 | 2 | 6 | 8 | 25.0:75.0 | 50.0 |
| 2009 | 9 | 3 | 12 | 75.0:25.0 | 54.5 | 0 | 0 | 0 | | 0.0 | 1 | 9 | 10 | 10.0:90.0 | 45.5 |
| 2010 | 4 | 2 | 6 | 66.7:33.3 | 37.5 | 0 | 1 | 1 | 0.0:100.0 | 6.3 | 6 | 3 | 9 | 66.7:33.3 | 56.3 |
| 2011 | 1 | 1 | 2 | 50.0:50.0 | 13.3 | 0 | 0 | 0 | | 0.0 | 7 | 6 | 13 | 53.8:46.2 | 86.7 |
| 2012 | 7 | 11 | 18 | 38.9:61.1 | 43.9 | 0 | 2 | 2 | 0.0:100.0 | 4.9 | 10 | 11 | 21 | 47.6:52.4 | 51.2 |
| 2013 | 3 | 3 | 6 | 50.0:50.0 | 46.2 | 0 | 0 | 0 | | 0 | 4 | 3 | 7 | 57.1:42.9 | 53.8 |
| Average | 7 | 7 | 14 | 50.5:49.5 | 42.3 | 0 | 1 | 1 | 6.9:93.1 | 4.2 | 7 | 11 | 18 | 40.4:59.6 | 53.5 |

**Appendix A15.** Age and gender composition of the greater sage-grouse harvest, Whitehorse, Hunt Unit 68, Oregon, 1993–2013. The season was closed in 2012.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1993 | 27 | 30 | 57 | 47.4:52.6 | 44.9 | 0 | 3 | 3 | 0.0:100.0 | 2.4 | 29 | 38 | 67 | 43.3:56.7 | 52.8 |
| 1994 | 38 | 53 | 91 | 41.8:58.2 | 54.5 | 0 | 8 | 8 | 0.0:100.0 | 4.8 | 23 | 45 | 68 | 33.8:66.2 | 40.7 |
| 1995 | 25 | 33 | 58 | 43.1:56.9 | 48.7 | 1 | 7 | 8 | 12.5:87.5 | 6.7 | 13 | 40 | 53 | 24.5:75.5 | 44.5 |
| 1996 | 32 | 37 | 69 | 46.4:53.6 | 51.1 | 0 | 8 | 8 | 0.0:100.0 | 5.9 | 18 | 40 | 58 | 31.0:69.0 | 43.0 |
| 1997 | 39 | 36 | 75 | 52.0:48.0 | 58.1 | 1 | 15 | 16 | 6.3:93.8 | 12.4 | 16 | 22 | 38 | 42.1:57.9 | 29.5 |
| 1998 | 23 | 32 | 55 | 41.8:58.2 | 56.7 | 0 | 2 | 2 | 0.0:100.0 | 2.1 | 14 | 26 | 40 | 35.0:65.0 | 41.2 |
| 1999 | 43 | 46 | 89 | 48.3:51.7 | 64.5 | 0 | 6 | 6 | 0.0:100.0 | 4.3 | 14 | 29 | 43 | 32.6:67.4 | 31.2 |
| 2000 | 18 | 31 | 49 | 36.7:63.3 | 35.8 | 7 | 15 | 22 | 31.8:68.2 | 16.1 | 34 | 32 | 66 | 51.5:48.5 | 48.2 |
| 2001 | 44 | 39 | 83 | 53.0:47.0 | 55.3 | 0 | 9 | 9 | 0.0:100.0 | 6.0 | 25 | 33 | 58 | 43.1:56.9 | 38.7 |
| 2002 | 58 | 42 | 100 | 58.0:42.0 | 63.3 | 1 | 11 | 12 | 8.3:91.7 | 7.6 | 22 | 24 | 46 | 47.8:52.2 | 29.1 |
| 2003 | 37 | 37 | 74 | 50.0:50.0 | 51.4 | 0 | 6 | 6 | 0.0:100.0 | 4.2 | 34 | 30 | 64 | 53.1:46.9 | 44.4 |
| 2004 | 52 | 61 | 113 | 46.0:54.0 | 52.8 | 0 | 11 | 11 | 0.0:100.0 | 5.1 | 44 | 46 | 90 | 48.9:51.1 | 42.1 |
| 2005 | 47 | 52 | 99 | 47.5:52.5 | 44.4 | 0 | 14 | 14 | 0.0:100.0 | 6.3 | 43 | 67 | 110 | 39.1:60.9 | 49.3 |
| 2006 | 42 | 44 | 86 | 48.8:51.2 | 48.0 | 1 | 7 | 8 | 12.5:87.5 | 4.5 | 49 | 36 | 85 | 57.6:42.4 | 47.5 |
| 2007 | 12 | 9 | 21 | 57.1:42.9 | 18.8 | 0 | 3 | 3 | 0.0:100.0 | 2.7 | 36 | 52 | 88 | 40.9:59.1 | 78.6 |
| 2008 | 27 | 38 | 65 | 41.5:58.5 | 63.7 | 0 | 3 | 3 | 0.0:100.0 | 2.9 | 7 | 27 | 34 | 20.6:79.4 | 33.3 |
| 2009 | 28 | 35 | 63 | 44.4:55.6 | 56.8 | 0 | 5 | 5 | 0.0:100.0 | 4.5 | 25 | 18 | 43 | 58.1:41.9 | 38.7 |
| 2010 | 28 | 41 | 69 | 40.6:59.4 | 52.7 | 0 | 7 | 7 | 0.0:100.0 | 5.3 | 14 | 41 | 55 | 25.5:74.5 | 42.0 |
| 2011 | 24 | 37 | 61 | 39.3:60.7 | 48.0 | 0 | 10 | 10 | 0.0:100.0 | 7.9 | 22 | 34 | 56 | 39.3:60.7 | 44.1 |
| 2012 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 2013 | 7 | 3 | 10 | 70.0:30.0 | 47.6 | 0 | 1 | 1 | 0.0:100.0 | 4.8 | 5 | 5 | 10 | 50.0:50.0 | 47.6 |
| Average | 33 | 37 | 69 | 46.9:53.1 | 51.0 | 1 | 8 | 8 | 6.8:93.2 | 6.0 | 24 | 34 | 59 | 41.6:58.4 | 43.1 |

**Appendix A16.** Age and gender composition of the greater sage-grouse harvest, Steens Mountain, Hunt Unit 69, Oregon, 1993–2013.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1993 | 13 | 11 | 24 | 54.2:45.8 | 29.3 | 4 | 4 | 8 | 50.0:50.0 | 9.8 | 23 | 27 | 50 | 46.0:54.0 | 61.0 |
| 1994 | 28 | 23 | 51 | 54.9:45.1 | 45.5 | 0 | 5 | 5 | 0.0:100.0 | 4.5 | 17 | 39 | 56 | 30.4:69.6 | 50.0 |
| 1995 | 7 | 8 | 15 | 46.7:53.3 | 23.4 | 0 | 2 | 2 | 0.0:100.0 | 3.1 | 24 | 23 | 47 | 51.1:48.9 | 73.4 |
| 1996 | 9 | 20 | 29 | 31.0:69.0 | 42.0 | 1 | 4 | 5 | 20.0:80.0 | 7.2 | 14 | 21 | 35 | 40.0:60.0 | 50.7 |
| 1997 | 16 | 18 | 34 | 47.1:52.9 | 51.5 | 4 | 3 | 7 | 57.1:42.9 | 10.6 | 12 | 13 | 25 | 48.0:52.0 | 37.9 |
| 1998 | 6 | 5 | 11 | 54.5:45.5 | 24.4 | 1 | 1 | 2 | 50.0:50.0 | 4.4 | 14 | 18 | 32 | 43.8:56.3 | 71.1 |
| 1999 | 12 | 12 | 24 | 50.0:50.0 | 50.0 | 1 | 3 | 4 | 25.0:75.0 | 8.3 | 6 | 14 | 20 | 30.0:70.0 | 41.7 |
| 2000 | 11 | 11 | 22 | 50.0:50.0 | 57.9 | 0 | 3 | 3 | 0.0:100.0 | 7.9 | 8 | 5 | 13 | 61.5:38.5 | 34.2 |
| 2001 | 12 | 10 | 22 | 54.5:45.5 | 52.4 | 1 | 2 | 3 | 33.3:66.7 | 7.1 | 11 | 6 | 17 | 64.7:35.3 | 40.5 |
| 2002 | 17 | 13 | 30 | 56.7:43.3 | 43.5 | 1 | 12 | 13 | 7.7:92.3 | 18.8 | 14 | 12 | 26 | 53.8:46.2 | 37.7 |
| 2003 | 11 | 19 | 30 | 36.7:63.3 | 53.6 | 1 | 3 | 4 | 25.0:75.0 | 7.1 | 12 | 10 | 22 | 54.5:45.5 | 39.3 |
| 2004 | 9 | 16 | 25 | 36.0:64.0 | 31.6 | 1 | 5 | 6 | 16.7:83.3 | 7.6 | 21 | 27 | 48 | 43.8:56.3 | 60.8 |
| 2005 | 14 | 22 | 36 | 38.9:61.1 | 50.7 | 0 | 1 | 1 | 0.0:100.0 | 1.4 | 25 | 9 | 34 | 73.5:26.5 | 47.9 |
| 2006 | 10 | 18 | 28 | 35.7:64.3 | 41.2 | 3 | 1 | 4 | 75.0:25.0 | 5.9 | 22 | 14 | 36 | 61.1:38.9 | 52.9 |
| 2007 | 6 | 14 | 20 | 30.0:70.0 | 26.0 | 1 | 5 | 6 | 16.7:83.3 | 7.8 | 24 | 27 | 51 | 47.1:52.9 | 66.2 |
| 2008 | 13 | 4 | 17 | 76.5:23.5 | 56.7 | 0 | 1 | 1 | 0.0:100.0 | 3.3 | 7 | 5 | 12 | 58.3:41.7 | 40.0 |
| 2009 | 3 | 12 | 15 | 20.0:80.0 | 46.9 | 0 | 1 | 1 | 0.0:100.0 | 3.1 | 13 | 3 | 16 | 81.3:18.8 | 50.0 |
| 2010 | 5 | 1 | 6 | 83.3:16.7 | 17.6 | 0 | 2 | 2 | 0.0:100.0 | 5.9 | 19 | 7 | 26 | 73.1:26.9 | 76.5 |
| 2011 | 5 | 3 | 8 | 62.5:37.5 | 25.8 | 0 | 0 | 0 | | 0.0 | 15 | 8 | 23 | 65.2:34.8 | 74.2 |
| 2012 | 6 | 6 | 12 | 50.0:50.0 | 25.0 | 2 | 1 | 3 | 66.7:33.3 | 6.3 | 23 | 10 | 33 | 69.7:30.3 | 68.8 |
| 2013 | 7 | 7 | 14 | 50.0:50.0 | 43.8 | 0 | 4 | 4 | 0.0:100.0 | 12.5 | 5 | 9 | 14 | 35.7:64.3 | 43.8 |
| Average | 10 | 12 | 23 | 46.5:53.5 | 39.6 | 1 | 3 | 4 | 17.0:83.0 | 7.0 | 16 | 15 | 30 | 51.7:48.3 | 53.3 |

**Appendix A17.** Age and gender composition of the greater sage-grouse harvest, Beatys Butte, Hunt Unit 70, Oregon, 1993–2013.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1993 | 23 | 23 | 46 | 50.0:50.0 | 59.7 | 1 | 2 | 3 | 33.3:66.7 | 3.9 | 13 | 15 | 28 | 46.4:53.6 | 36.4 |
| 1994 | 13 | 21 | 34 | 38.2:61.8 | 30.1 | 2 | 14 | 16 | 12.5:87.5 | 14.2 | 26 | 37 | 63 | 41.3:58.7 | 55.8 |
| 1995 | 14 | 18 | 32 | 43.8:56.3 | 31.7 | 0 | 1 | 1 | 0.0:100.0 | 1.0 | 16 | 52 | 68 | 23.5:76.5 | 67.3 |
| 1996 | 14 | 16 | 30 | 46.7:53.3 | 43.5 | 0 | 3 | 3 | 0.0:100.0 | 4.3 | 11 | 25 | 36 | 30.6:69.4 | 52.2 |
| 1997 | 42 | 32 | 74 | 56.8:43.2 | 56.1 | 1 | 9 | 10 | 10.0:90.0 | 7.6 | 18 | 30 | 48 | 37.5:62.5 | 36.4 |
| 1998 | 22 | 27 | 49 | 44.9:55.1 | 67.1 | 0 | 2 | 2 | 0.0:100.0 | 2.7 | 6 | 16 | 22 | 27.3:72.7 | 30.1 |
| 1999 | 28 | 37 | 65 | 43.1:56.9 | 55.1 | 3 | 4 | 7 | 42.9:57.1 | 5.9 | 21 | 25 | 46 | 45.7:54.3 | 39.0 |
| 2000 | 16 | 25 | 41 | 39.0:61.0 | 43.2 | 2 | 9 | 11 | 18.2:81.8 | 11.6 | 18 | 25 | 43 | 41.9:58.1 | 45.3 |
| 2001 | 18 | 20 | 38 | 47.4:52.6 | 45.2 | 1 | 3 | 4 | 25.0:75.0 | 4.8 | 23 | 19 | 42 | 54.8:45.2 | 50.0 |
| 2002 | 29 | 26 | 55 | 52.7:47.3 | 58.5 | 0 | 2 | 2 | 0.0:100.0 | 2.1 | 21 | 16 | 37 | 56.8:43.2 | 39.4 |
| 2003 | 27 | 30 | 57 | 47.4:52.6 | 52.8 | 0 | 3 | 3 | 0.0:100.0 | 2.8 | 31 | 17 | 48 | 64.6:35.4 | 44.4 |
| 2004 | 32 | 38 | 70 | 45.7:54.3 | 52.2 | 0 | 9 | 9 | 0.0:100.0 | 6.7 | 17 | 38 | 55 | 30.9:69.1 | 41.0 |
| 2005 | 27 | 29 | 56 | 48.2:51.8 | 44.1 | 0 | 8 | 8 | 0.0:100.0 | 6.3 | 37 | 26 | 63 | 58.7:41.3 | 49.6 |
| 2006 | 21 | 33 | 54 | 38.9:61.1 | 51.9 | 3 | 5 | 8 | 37.5:62.5 | 7.7 | 19 | 23 | 42 | 45.2:54.8 | 40.4 |
| 2007 | 6 | 10 | 16 | 37.5:62.5 | 21.9 | 0 | 6 | 6 | 0.0:100.0 | 8.2 | 20 | 31 | 51 | 39.2:60.8 | 69.9 |
| 2008 | 18 | 21 | 39 | 46.2:53.8 | 60.0 | 0 | 2 | 2 | 0.0:100.0 | 3.1 | 8 | 16 | 24 | 33.3:66.7 | 36.9 |
| 2009 | 31 | 27 | 58 | 53.4:46.6 | 58.0 | 0 | 9 | 9 | 0.0:100.0 | 9.0 | 14 | 19 | 33 | 42.4:57.6 | 33.0 |
| 2010 | 12 | 13 | 25 | 48.0:52.0 | 45.5 | 0 | 1 | 1 | 0.0:100.0 | 1.8 | 8 | 21 | 29 | 27.6:72.4 | 52.7 |
| 2011 | 24 | 27 | 51 | 47.1:52.9 | 51.5 | 0 | 3 | 3 | 0.0:100.0 | 3.0 | 30 | 15 | 45 | 66.7:33.3 | 45.5 |
| 2012 | 3 | 12 | 15 | 20.0:80.0 | 17.6 | 12 | 12 | 24 | 50.0:50.0 | 28.2 | 20 | 26 | 46 | 43.5:56.5 | 54.1 |
| 2013 | 23 | 31 | 54 | 42.6:57.4 | 58.1 | 2 | 5 | 7 | 28.6:71.4 | 7.5 | 14 | 18 | 32 | 43.8:56.2 | 34.4 |
| Average | 21 | 25 | 46 | 46.2:53.8 | 48.0 | 1 | 5 | 7 | 19.4:80.6 | 7.0 | 19 | 24 | 43 | 43.4:56.6 | 45.1 |

**Appendix A18.** Age and gender composition of the greater sage-grouse harvest, Juniper, Hunt Unit 71, Oregon, 1993–2013.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1993 | 9 | 6 | 15 | 60.0:40.0 | 53.6 | 0 | 0 | 0 | | 0.0 | 7 | 6 | 13 | 53.8:46.2 | 46.4 |
| 1994 | 2 | 8 | 10 | 20.0:80.0 | 18.5 | 1 | 6 | 7 | 14.3:85.7 | 13.0 | 6 | 31 | 37 | 16.2:83.8 | 68.5 |
| 1995 | 3 | 4 | 7 | 42.9:57.1 | 23.3 | 0 | 0 | 0 | | 0.0 | 5 | 18 | 23 | 21.7:78.3 | 76.7 |
| 1996 | 10 | 12 | 22 | 45.5:54.5 | 47.8 | 0 | 3 | 3 | 0.0:100.0 | 6.5 | 4 | 17 | 21 | 19.0:81.0 | 45.7 |
| 1997 | 12 | 20 | 32 | 37.5:62.5 | 61.5 | 0 | 1 | 1 | 0.0:100.0 | 1.9 | 7 | 12 | 19 | 36.8:63.2 | 36.5 |
| 1998 | 5 | 9 | 14 | 35.7:64.3 | 50.0 | 0 | 0 | 0 | | 0.0 | 3 | 11 | 14 | 21.4:78.6 | 50.0 |
| 1999 | 16 | 14 | 30 | 53.3:46.7 | 47.6 | 0 | 2 | 2 | 0.0:100.0 | 3.2 | 12 | 19 | 31 | 38.7:61.3 | 49.2 |
| 2000 | 13 | 11 | 24 | 54.2:45.8 | 47.1 | 1 | 0 | 1 | 100.0:0.0 | 2.0 | 13 | 13 | 26 | 50.0:50.0 | 51.0 |
| 2001 | 14 | 22 | 36 | 38.9:61.1 | 59.0 | 0 | 2 | 2 | 0.0:100.0 | 3.3 | 6 | 17 | 23 | 26.1:73.9 | 37.7 |
| 2002 | 14 | 22 | 36 | 38.9:61.1 | 60.0 | 1 | 3 | 4 | 25.0:75.0 | 6.7 | 11 | 9 | 20 | 55.0:45.0 | 33.3 |
| 2003 | 7 | 13 | 20 | 35.0:65.0 | 39.2 | 0 | 2 | 2 | 0.0:100.0 | 3.9 | 10 | 19 | 29 | 34.5:65.5 | 56.9 |
| 2004 | 11 | 11 | 22 | 50.0:50.0 | 48.9 | 0 | 1 | 1 | 0.0:100.0 | 2.2 | 10 | 12 | 22 | 45.5:54.5 | 48.9 |
| 2005 | 10 | 13 | 23 | 43.5:56.5 | 39.0 | 0 | 3 | 3 | 0.0:100.0 | 5.1 | 13 | 20 | 33 | 39.4:60.6 | 55.9 |
| 2006 | 5 | 11 | 16 | 31.3:68.8 | 32.0 | 0 | 0 | 0 | | 0.0 | 14 | 20 | 34 | 41.2:58.8 | 68.0 |
| 2007 | 0 | 4 | 4 | 0.0:100.0 | 13.8 | 0 | 1 | 1 | 0.0:100.0 | 3.4 | 8 | 16 | 24 | 33.3:66.7 | 82.8 |
| 2008 | 13 | 7 | 20 | 65.0:35.0 | 51.3 | 0 | 0 | 0 | | 0.0 | 6 | 13 | 19 | 31.6:68.4 | 48.7 |
| 2009 | 10 | 12 | 22 | 45.5:54.5 | 56.4 | 0 | 1 | 1 | 0.0:100.0 | 2.6 | 6 | 10 | 16 | 37.5:62.5 | 41.0 |
| 2010 | 4 | 9 | 13 | 30.8:69.2 | 44.8 | 0 | 2 | 2 | 0.0:100.0 | 6.9 | 8 | 6 | 14 | 57.1:42.9 | 48.3 |
| 2011 | 8 | 4 | 12 | 66.7:33.3 | 48.0 | 0 | 0 | 0 | | 0.0 | 6 | 7 | 13 | 46.2:53.8 | 52.0 |
| 2012 | 0 | 1 | 1 | 0.0:100.0 | 4.8 | 0 | 3 | 3 | 0.0:100.0 | 14.3 | 8 | 9 | 17 | 47.1:52.9 | 81.0 |
| 2013 | 2 | 2 | 4 | 50.0:50.0 | 50 | 0 | 2 | 2 | 0.0:100.0 | 25 | 0 | 2 | 2 | 0.0:100.0 | 25 |
| Average | 8 | 10 | 18 | 43.9:56.1 | 44.1 | 0 | 2 | 2 | 8.6:91.4 | 4.0 | 8 | 14 | 21 | 36.2:63.8 | 51.8 |

**Appendix A19.** Age and gender composition of the greater sage-grouse harvest, Silvies, Hunt Unit 72, Oregon, 1993–2013.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1993 | 8 | 4 | 12 | 66.7:33.3 | 85.7 | 0 | 1 | 1 | 0.0:100.0 | 7.1 | 0 | 1 | 1 | 0.0:100.0 | 7.1 |
| 1994 | 3 | 6 | 9 | 33.3:66.7 | 47.4 | 0 | 1 | 1 | 0.0:100.0 | 5.3 | 0 | 9 | 9 | 0.0:100.0 | 47.4 |
| 1995 | 3 | 0 | 3 | 100.0:0.0 | 75.0 | 0 | 0 | 0 | | 0.0 | 0 | 1 | 1 | 0.0:100.0 | 25.0 |
| 1996 | 0 | 4 | 4 | 0.0:100.0 | 50.0 | 0 | 0 | 0 | | 0.0 | 0 | 4 | 4 | 0.0:100.0 | 50.0 |
| 1997 | 0 | 7 | 7 | 0.0:100.0 | 63.6 | 0 | 0 | 0 | | 0.0 | 0 | 4 | 4 | 0.0:100.0 | 36.4 |
| 1998 | 0 | 3 | 3 | 0.0:100.0 | 27.3 | 0 | 0 | 0 | | 0.0 | 0 | 8 | 8 | 0.0:100.0 | 72.7 |
| 1999 | 9 | 2 | 11 | 81.8:18.2 | 91.7 | 0 | 0 | 0 | | 0.0 | 0 | 1 | 1 | 0.0:100.0 | 8.3 |
| 2000 | 0 | 1 | 1 | 0.0:100.0 | 20.0 | 0 | 0 | 0 | | 0.0 | 4 | 0 | 4 | 100.0:0.0 | 80.0 |
| 2001 | 2 | 1 | 3 | 66.7:33.3 | 33.3 | 0 | 1 | 1 | 0.0:100.0 | 11.1 | 2 | 3 | 5 | 40.0:60.0 | 55.6 |
| 2002 | 3 | 5 | 8 | 37.5:62.5 | 80.0 | 0 | 1 | 1 | 0.0:100.0 | 10.0 | 0 | 1 | 1 | 0.0:100.0 | 10.0 |
| 2003 | 2 | 1 | 3 | 66.7:33.3 | 25.0 | 0 | 0 | 0 | | 0.0 | 1 | 8 | 9 | 11.1:88.9 | 75.0 |
| 2004 | 0 | 0 | 0 | | | 0 | 0 | 0 | | | 0 | 0 | 0 | | |
| 2005 | 0 | 3 | 3 | 0.0:100.0 | 37.5 | 1 | 0 | 1 | 100.0:0.0 | 12.5 | 2 | 2 | 4 | 50.0:50.0 | 50.0 |
| 2006 | 2 | 6 | 8 | 25.0:75.0 | 61.5 | 0 | 1 | 1 | 0.0:100.0 | 7.7 | 1 | 3 | 4 | 25.0:75.0 | 30.8 |
| 2007 | 4 | 4 | 8 | 50.0:50.0 | 50.0 | 0 | 1 | 1 | 0.0:100.0 | 6.3 | 3 | 4 | 7 | 42.9:57.1 | 43.8 |
| 2008 | 2 | 1 | 3 | 66.7:33.3 | 21.4 | 0 | 0 | 0 | | 0.0 | 4 | 7 | 11 | 36.4:63.6 | 78.6 |
| 2009 | 1 | 3 | 4 | 25.0:75.0 | 36.4 | 0 | 1 | 1 | 0.0:100.0 | 9.1 | 3 | 3 | 6 | 50.0:50.0 | 54.5 |
| 2010 | 0 | 2 | 2 | 0.0:100.0 | 25.0 | 0 | 0 | 0 | | 0.0 | 1 | 5 | 6 | 16.7:83.3 | 75.0 |
| 2011 | 0 | 3 | 3 | 0.0:100.0 | 50.0 | 0 | 0 | 0 | | 0.0 | 2 | 1 | 3 | 66.7:33.3 | 50.0 |
| 2012 | 2 | 1 | 3 | 66.7:33.3 | 75.0 | 0 | 1 | 1 | 0.0:100.0 | 25.0 | 0 | 0 | 0 | | 0.0 |
| 2013 | 3 | 2 | 5 | 60.0:40.0 | 71.4 | 0 | 1 | 1 | 0.0:100.0 | 14.3 | 0 | 1 | 1 | 0.0:100.0 | 14.3 |
| Average | 2 | 3 | 5 | 42.7:57.3 | 51.0 | 0 | 0 | 0 | 10.0:90.0 | 5.0 | 1 | 3 | 4 | 25.8:74.2 | 44.1 |

**Appendix A20.** Age and gender composition of the greater sage-grouse harvest, Wagontire, Hunt Unit 73, Oregon, 1993–2013.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n* ) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1993 | 0 | 0 | 0 | | 0.0 | 0 | 0 | 0 | | 0.0 | 1 | 4 | 5 | 20.0:80.0 | 100.0 |
| 1994 | 6 | 4 | 10 | 60.0:40.0 | 35.7 | 0 | 1 | 1 | 0.0:100.0 | 3.6 | 7 | 10 | 17 | 41.2:58.8 | 60.7 |
| 1995 | 1 | 3 | 4 | 25.0:75.0 | 23.5 | 0 | 2 | 2 | 0.0:100.0 | 11.8 | 2 | 9 | 11 | 18.2:81.8 | 64.7 |
| 1996 | 5 | 11 | 16 | 31.3:68.8 | 64.0 | 0 | 0 | 0 | | 0.0 | 1 | 8 | 9 | 11.1:88.9 | 36.0 |
| 1997 | 8 | 7 | 15 | 53.3:46.7 | 53.6 | 0 | 1 | 1 | 0.0:100.0 | 3.6 | 3 | 9 | 12 | 25.0:75.0 | 42.9 |
| 1998 | 12 | 14 | 26 | 46.2:53.8 | 57.8 | 0 | 2 | 2 | 0.0:100.0 | 4.4 | 7 | 10 | 17 | 41.2:58.8 | 37.8 |
| 1999 | 4 | 3 | 7 | 57.1:42.9 | 33.3 | 0 | 1 | 1 | 0.0:100.0 | 4.8 | 5 | 8 | 13 | 38.5:61.5 | 61.9 |
| 2000 | 10 | 10 | 20 | 50.0:50.0 | 41.7 | 0 | 3 | 3 | 0.0:100.0 | 6.3 | 9 | 16 | 25 | 36.0:64.0 | 52.1 |
| 2001 | 14 | 18 | 32 | 43.8:56.3 | 60.4 | 0 | 5 | 5 | 0.0:100.0 | 9.4 | 7 | 9 | 16 | 43.8:56.3 | 30.2 |
| 2002 | 3 | 13 | 16 | 18.8:81.3 | 55.2 | 1 | 1 | 2 | 50.0:50.0 | 6.9 | 3 | 8 | 11 | 27.3:72.7 | 37.9 |
| 2003 | 4 | 6 | 10 | 40.0:60.0 | 34.5 | 1 | 2 | 3 | 33.3:66.7 | 10.3 | 6 | 10 | 16 | 37.5:62.5 | 55.2 |
| 2004 | 6 | 5 | 11 | 54.5:45.5 | 55.0 | 1 | 1 | 2 | 50.0:50.0 | 10.0 | 1 | 6 | 7 | 14.3:85.7 | 35.0 |
| 2005 | 6 | 8 | 14 | 42.9:57.1 | 60.9 | 1 | 2 | 3 | 33.3:66.7 | 13.0 | 1 | 5 | 6 | 16.7:83.3 | 26.1 |
| 2006 | 10 | 4 | 14 | 71.4:28.6 | 53.8 | 2 | 1 | 3 | 66.7:33.3 | 11.5 | 4 | 5 | 9 | 44.4:55.6 | 34.6 |
| 2007 | 5 | 7 | 12 | 41.7:58.3 | 40.0 | 0 | 0 | 0 | | 0.0 | 4 | 14 | 18 | 22.2:77.8 | 60.0 |
| 2008 | 2 | 2 | 4 | 50.0:50.0 | 25.0 | 0 | 0 | 0 | | 0.0 | 6 | 6 | 12 | 50.0:50.0 | 75.0 |
| 2009 | 7 | 10 | 17 | 41.2:58.8 | 73.9 | 0 | 0 | 0 | | 0.0 | 2 | 4 | 6 | 33.3:66.7 | 26.1 |
| 2010 | 3 | 4 | 7 | 42.9:57.1 | 35.0 | 0 | 0 | 0 | | 0.0 | 2 | 11 | 13 | 15.4:84.6 | 65.0 |
| 2011 | 5 | 4 | 9 | 55.6:44.4 | 56.3 | 0 | 2 | 2 | 0.0:100.0 | 12.5 | 1 | 4 | 5 | 20.0:80.0 | 31.3 |
| 2012 | 4 | 4 | 8 | 50.0:50.0 | 32.0 | 0 | 1 | 1 | 0.0:100.0 | 4.0 | 6 | 10 | 16 | 37.5:62.5 | 64.0 |
| 2013 | 7 | 5 | 12 | 58.3:41.7 | 63.2 | 0 | 0 | 0 | | 0 | 0 | 7 | 7 | 0.0:100.0 | 36.8 |
| Average | 6 | 7 | 13 | 46.2:53.8 | 48.4 | 0 | 1 | 1 | 19.4:80.6 | 5.7 | 4 | 8 | 12 | 31.1:68.9 | 46.0 |

**Appendix A21.** Age and gender composition of the greater sage-grouse harvest, Warner, Hunt Unit 74, Oregon, 1993–2013.

| | Juveniles | | | | | Yearlings | | | | | Adults | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest | Males (*n*) | Females (*n*) | Total (*n*) | Male:female sex ratio | % in harvest |
| 1993 | 2 | 2 | 4 | 50.0:50.0 | 30.8 | 0 | 2 | 2 | 0.0:100.0 | 15.4 | 1 | 6 | 7 | 14.3:85.7 | 53.8 |
| 1994 | 9 | 14 | 23 | 39.1:60.9 | 39.7 | 0 | 2 | 2 | 0.0:100.0 | 3.4 | 14 | 19 | 33 | 42.4:57.6 | 56.9 |
| 1995 | 3 | 6 | 9 | 33.3:66.7 | 26.5 | 0 | 2 | 2 | 0.0:100.0 | 5.9 | 3 | 20 | 23 | 13.0:87.0 | 67.6 |
| 1996 | 11 | 13 | 24 | 45.8:54.2 | 61.5 | 0 | 0 | 0 | | 0.0 | 8 | 7 | 15 | 53.3:46.7 | 38.5 |
| 1997 | 10 | 18 | 28 | 35.7:64.3 | 54.9 | 0 | 2 | 2 | 0.0:100.0 | 3.9 | 7 | 14 | 21 | 33.3:66.7 | 41.2 |
| 1998 | 16 | 12 | 28 | 57.1:42.9 | 62.2 | 0 | 4 | 4 | 0.0:100.0 | 8.9 | 6 | 7 | 13 | 46.2:53.8 | 28.9 |
| 1999 | 20 | 39 | 59 | 33.9:66.1 | 67.8 | 1 | 6 | 7 | 14.3:85.7 | 8.0 | 9 | 12 | 21 | 42.9:57.1 | 24.1 |
| 2000 | 10 | 12 | 22 | 45.5:54.5 | 56.4 | 0 | 1 | 1 | 0.0:100.0 | 2.6 | 6 | 10 | 16 | 37.5:62.5 | 41.0 |
| 2001 | 25 | 15 | 40 | 62.5:37.5 | 51.9 | 0 | 10 | 10 | 0.0:100.0 | 13.0 | 9 | 18 | 27 | 33.3:66.7 | 35.1 |
| 2002 | 27 | 25 | 52 | 51.9:48.1 | 65.0 | 0 | 1 | 1 | 0.0:100.0 | 1.3 | 14 | 13 | 27 | 51.9:48.1 | 33.8 |
| 2003 | 26 | 28 | 54 | 48.1:51.9 | 59.3 | 1 | 3 | 4 | 25.0:75.0 | 4.4 | 14 | 19 | 33 | 42.4:57.6 | 36.3 |
| 2004 | 23 | 35 | 58 | 39.7:60.3 | 53.2 | 1 | 11 | 12 | 8.3:91.7 | 11.0 | 18 | 21 | 39 | 46.2:53.8 | 35.8 |
| 2005 | 18 | 25 | 43 | 41.9:58.1 | 50.0 | 0 | 2 | 2 | 0.0:100.0 | 2.3 | 10 | 31 | 41 | 24.4:75.6 | 47.7 |
| 2006 | 18 | 23 | 41 | 43.9:56.1 | 55.4 | 0 | 2 | 2 | 0.0:100.0 | 2.7 | 10 | 21 | 31 | 32.3:67.7 | 41.9 |
| 2007 | 15 | 18 | 33 | 45.5:54.5 | 46.5 | 0 | 6 | 6 | 0.0:100.0 | 8.5 | 11 | 21 | 32 | 34.4:65.6 | 45.1 |
| 2008 | 24 | 30 | 54 | 44.4:55.6 | 54.0 | 0 | 8 | 8 | 0.0:100.0 | 8.0 | 10 | 28 | 38 | 26.3:73.7 | 38.0 |
| 2009 | 19 | 29 | 48 | 39.6:60.4 | 60.8 | 0 | 5 | 5 | 0.0:100.0 | 6.3 | 15 | 11 | 26 | 57.7:42.3 | 32.9 |
| 2010 | 20 | 25 | 45 | 44.4:55.6 | 54.2 | 1 | 4 | 5 | 20.0:80.0 | 6.0 | 11 | 22 | 33 | 33.3:66.7 | 39.8 |
| 2011 | 9 | 15 | 24 | 37.5:62.5 | 34.3 | 1 | 3 | 4 | 25.0:75.0 | 5.7 | 14 | 28 | 42 | 33.3:66.7 | 60.0 |
| 2012 | 8 | 16 | 24 | 33.3:66.7 | 38.1 | 0 | 8 | 8 | 0.0:100.0 | 12.7 | 13 | 18 | 31 | 41.9:58.1 | 49.2 |
| 2013 | 19 | 18 | 37 | 51.4:48.6 | 69.8 | 0 | 2 | 2 | 0.0:100.0 | 3.8 | 3 | 11 | 14 | 21.4:78.6 | 26.4 |
| Average | 16 | 20 | 36 | 44.3:55.7 | 53.5 | 0 | 4 | 4 | 5.6:94.4 | 6.3 | 10 | 17 | 27 | 36.6:63.4 | 40.2 |

**Appendix B1.** Greater sage-grouse productivity data, North Park, Colorado, 1974–1998.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1974 | 64.8 | 165 | 46.1 | 89 | 58.3 | 254 | 50.1 | 1.4 | 2.4 |
| 1975 | 52.8 | 127 | 39.0 | 59 | 48.4 | 186 | 42.0 | 1.1 | 2.4 |
| 1976 | 52.9 | 121 | 26.8 | 71 | 43.2 | 192 | 42.3 | 1.1 | 2.5 |
| 1977 | 59.1 | 171 | 32.9 | 76 | 51.0 | 247 | 45.9 | 1.2 | 2.3 |
| 1978 | 59.7 | 129 | 38.3 | 81 | 51.4 | 210 | 53.2 | 1.8 | 3.6 |
| 1979 | 65.1 | 129 | 55.8 | 154 | 60.1 | 283 | 57.7 | 2.2 | 3.7 |
| 1980 | 55.7 | 158 | 30.6 | 170 | 42.7 | 328 | 49.1 | 1.4 | 3.3 |
| 1981 | 37.4 | 227 | 21.9 | 151 | 31.2 | 378 | 47.4 | 1.3 | 4.1 |
| 1982 | 58.8 | 170 | 37.5 | 80 | 52.0 | 250 | 50.6 | 1.6 | 3.0 |
| 1983 | 65.6 | 183 | 50.6 | 164 | 58.5 | 347 | 57.4 | 1.9 | 3.3 |
| 1984 | 74.6 | 126 | 53.3 | 137 | 63.5 | 263 | 57.0 | 1.9 | 2.9 |
| 1985 | 54.9 | 113 | 43.8 | 112 | 49.3 | 225 | 53.6 | 1.6 | 3.2 |
| 1986 | 61.0 | 105 | 47.3 | 93 | 54.5 | 198 | 61.8 | 2.0 | 3.7 |
| 1987 | 50.4 | 115 | 36.0 | 114 | 43.2 | 229 | 54.2 | 1.6 | 3.7 |
| 1988 | 61.1 | 90 | 38.3 | 81 | 50.3 | 171 | 42.9 | 1.1 | 2.1 |
| 1989 | 49.4 | 85 | 19.6 | 92 | 33.9 | 177 | 46.1 | 1.1 | 3.1 |
| 1990 | 45.9 | 109 | 32.2 | 59 | 41.1 | 168 | 38.7 | 0.8 | 2.0 |
| 1991 | 53.0 | 83 | 28.6 | 28 | 46.8 | 111 | 43.0 | 1.0 | 2.1 |
| 1992 | 33.3 | 63 | 35.0 | 20 | 33.7 | 83 | 36.7 | 0.9 | 2.6 |
| 1993 | 69.2 | 78 | 40.0 | 20 | 63.3 | 98 | 45.1 | 1.1 | 1.7 |
| 1994 | 62.1 | 58 | 43.8 | 16 | 58.1 | 74 | 56.1 | 1.8 | 3.1 |
| 1995 | 63.6 | 11 | 60.0 | 15 | 61.5 | 26 | 36.5 | 0.9 | 1.4 |
| 1996 | 67.7 | 31 | 40.0 | 15 | 58.7 | 46 | 54.7 | 1.5 | 2.6 |
| 1997 | 53.6 | 28 | 44.4 | 18 | 50.0 | 46 | 51.4 | 1.6 | 3.1 |
| 1998 | 47.1 | 34 | 17.6 | 34 | 32.4 | 68 | 37.2 | 0.7 | 2.2 |
| Totals | 56.6 | 2709 | 38.8 | 1949 | 49.1 | 4658 | 50.7 | 1.5 | 3.0 |

**Appendix B2.** Greater sage-grouse productivity data, Middle Park, Colorado, 1975–1998.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1975 | 85.7 | 14 | 37.5 | 8 | 68.2 | 22 | 66.7 | 2.5 | 3.6 |
| 1976 | 64.3 | 14 | 64.3 | 14 | 64.3 | 28 | 63.9 | 2.5 | 3.8 |
| 1977 | 51.9 | 27 | 25.0 | 20 | 40.4 | 47 | 57.1 | 1.9 | 4.7 |
| 1978 | 68.4 | 38 | 44.4 | 27 | 58.5 | 65 | 45.9 | 1.4 | 2.3 |
| 1979 | 80.0 | 30 | 42.9 | 21 | 64.7 | 51 | 50.0 | 1.6 | 2.5 |
| 1980 | 53.3 | 15 | 70.6 | 17 | 62.5 | 32 | 51.6 | 1.5 | 2.5 |
| 1981 | 33.3 | 9 | 33.3 | 9 | 33.3 | 18 | 22.0 | 0.5 | 1.5 |
| 1982 | 77.8 | 9 | 25.0 | 4 | 61.5 | 13 | 75.8 | 3.6 | 5.9 |
| 1983 | 71.4 | 21 | 27.8 | 18 | 51.3 | 39 | 51.6 | 1.7 | 3.2 |
| 1984 | 92.3 | 13 | 40.0 | 15 | 64.3 | 28 | 56.0 | 2.2 | 3.4 |
| 1985 | 71.4 | 14 | 50.0 | 14 | 60.7 | 28 | 38.7 | 0.9 | 1.4 |
| 1986 | 65.2 | 23 | 37.5 | 16 | 53.8 | 39 | 58.6 | 1.7 | 3.1 |
| 1987 | 83.3 | 18 | 20.0 | 10 | 60.7 | 28 | 66.4 | 2.7 | 4.4 |
| 1988 | 75.0 | 16 | 50.0 | 10 | 65.4 | 26 | 54.3 | 1.9 | 2.9 |
| 1989 | 66.7 | 15 | 71.4 | 7 | 68.2 | 22 | 38.2 | 1.2 | 1.7 |
| 1990 | 60.0 | 10 | 33.3 | 9 | 47.4 | 19 | 38.6 | 1.4 | 3.0 |
| 1991 | 66.7 | 18 | 71.4 | 7 | 68.0 | 25 | 47.9 | 1.4 | 2.1 |
| 1992 | 23.8 | 21 | 28.6 | 7 | 25.0 | 28 | 45.3 | 1.2 | 4.9 |
| 1993 | 40.0 | 10 | 33.3 | 12 | 36.4 | 22 | 54.7 | 1.3 | 3.6 |
| 1994 | | 0 | | 0 | | 0 | 100.0 | | |
| 1995 | 75.0 | 4 | 100.0 | 1 | 80.0 | 5 | 30.8 | 0.8 | 1.0 |
| 1996 | 50.0 | 2 | 66.7 | 3 | 60.0 | 5 | 68.4 | 2.6 | 4.3 |
| 1997 | 100.0 | 3 | 33.3 | 3 | 66.7 | 6 | 30.0 | 0.5 | 0.7 |
| 1998 | 0.0 | 1 | 0.0 | 1 | 0.0 | 2 | 0.0 | 0.0 | |
| Totals | 65.5 | 345 | 42.7 | 253 | 55.9 | 598 | 52.6 | 1.6 | 2.9 |

**Appendix B3.** Greater sage-grouse productivity data, Eagle, Colorado, 1977–1998. Wings of only juveniles were reported in 1982 and no wings were received in 1995 and 1996.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1977 | 50.0 | 4 | 50.0 | 8 | 50.0 | 12 | 65.7 | 1.9 | 3.8 |
| 1978 | 57.9 | 19 | 100.0 | 3 | 63.6 | 22 | 59.5 | 2.1 | 3.4 |
| 1979 | 62.5 | 8 | 83.3 | 6 | 71.4 | 14 | 48.6 | 2.6 | 3.6 |
| 1980 | 60.0 | 10 | 42.9 | 7 | 52.9 | 17 | 69.1 | 2.8 | 5.2 |
| 1981 | 100.0 | 1 | 0.0 | 1 | 50.0 | 2 | 76.9 | 5.0 | 10.0 |
| 1982 | | 0 | | 0 | | 0 | 100.0 | | |
| 1983 | 75.0 | 12 | 50.0 | 16 | 60.7 | 28 | 56.7 | 1.8 | 3.0 |
| 1984 | 100.0 | 3 | 83.3 | 6 | 88.9 | 9 | 42.3 | 1.2 | 1.4 |
| 1985 | 71.4 | 7 | 50.0 | 2 | 66.7 | 9 | 58.8 | 2.2 | 3.3 |
| 1986 | 50.0 | 8 | 50.0 | 4 | 50.0 | 12 | 69.2 | 2.3 | 4.5 |
| 1987 | 75.0 | 8 | 40.0 | 10 | 55.6 | 18 | 55.6 | 1.9 | 3.5 |
| 1988 | 83.3 | 6 | 33.3 | 6 | 58.3 | 12 | 54.1 | 1.7 | 2.9 |
| 1989 | 100.0 | 1 | 100.0 | 1 | 100.0 | 2 | 75.0 | 3.0 | 3.0 |
| 1990 | 75.0 | 8 | | 0 | 75.0 | 8 | 61.5 | 2.0 | 2.7 |
| 1991 | 100.0 | 2 | 80.0 | 5 | 85.7 | 7 | 63.6 | 4.0 | 4.7 |
| 1992 | 33.3 | 3 | 0.0 | 1 | 25.0 | 4 | 45.5 | 2.5 | 10.0 |
| 1993 | 100.0 | 2 | | 0 | 100.0 | 2 | 25.0 | 0.5 | 0.5 |
| 1994 | 100.0 | 2 | | 0 | 100.0 | 2 | 36.4 | 2.0 | 2.0 |
| 1995 | | 0 | | 0 | | 0 | 0.0 | | |
| 1996 | | 0 | | 0 | | 0 | 0.0 | | |
| 1997 | | 0 | 100.0 | 1 | 100.0 | 1 | 50.0 | 1.0 | 1.0 |
| 1998 | 100.0 | 1 | | 0 | 100.0 | 1 | 80.0 | 4.0 | 4.0 |
| Totals | 68.6 | 105 | 55.8 | 77 | 63.2 | 182 | 59.3 | 2.3 | 3.6 |

**Appendix B4.** Greater sage-grouse productivity data, Yampa, Colorado, 1977–1998.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1977 | 45.5 | 11 | 25.0 | 16 | 33.3 | 27 | 58.6 | 2.1 | 6.5 |
| 1978 | 50.0 | 32 | 50.0 | 14 | 50.0 | 46 | 45.5 | 1.2 | 2.4 |
| 1979 | 68.4 | 19 | 39.3 | 28 | 51.1 | 47 | 37.0 | 1.1 | 2.1 |
| 1980 | 48.1 | 27 | 52.6 | 19 | 50.0 | 46 | 42.4 | 1.3 | 2.7 |
| 1981 | 50.0 | 18 | 20.0 | 25 | 32.6 | 43 | 21.3 | 0.4 | 1.2 |
| 1982 | 60.0 | 5 | 25.0 | 4 | 44.4 | 9 | 57.6 | 2.1 | 4.8 |
| 1983 | 83.3 | 6 | 57.1 | 7 | 69.2 | 13 | 57.1 | 1.8 | 2.7 |
| 1984 | 100.0 | 3 | 33.3 | 3 | 66.7 | 6 | 51.9 | 2.3 | 3.5 |
| 1985 | 42.9 | 7 | 0.0 | 3 | 30.0 | 10 | 34.8 | 0.8 | 2.7 |
| 1986 | 100.0 | 2 | 0.0 | 2 | 50.0 | 4 | 63.6 | 1.8 | 3.5 |
| 1987 | 0.0 | 3 | 66.7 | 3 | 33.3 | 6 | 33.3 | 0.7 | 2.0 |
| 1988 | 75.0 | 4 | 50.0 | 2 | 66.7 | 6 | 16.7 | 0.8 | 1.2 |
| 1989 | 0.0 | 2 | 33.3 | 3 | 20.0 | 5 | 43.2 | 3.2 | 16.0 |
| 1990 | 50.0 | 4 | 50.0 | 2 | 50.0 | 6 | 47.1 | 1.3 | 2.7 |
| 1991 | 60.0 | 5 | 80.0 | 5 | 70.0 | 10 | 48.1 | 1.3 | 1.9 |
| 1992 | 66.7 | 3 | | 0 | 66.7 | 3 | 25.0 | 1.0 | 1.5 |
| 1993 | 42.9 | 14 | 100.0 | 2 | 50.0 | 16 | 54.8 | 1.4 | 2.9 |
| 1994 | 100.0 | 1 | 0.0 | 1 | 50.0 | 2 | 18.2 | 1.0 | 2.0 |
| 1995 | 100.0 | 4 | | 0 | 100.0 | 4 | 50.0 | 1.0 | 1.0 |
| 1996 | | 0 | | 0 | | 0 | 100.0 | | |
| 1997 | | 0 | 100.0 | 1 | 100.0 | 1 | 0.0 | | |
| 1998 | 100.0 | 1 | | 0 | 100.0 | 1 | 100.0 | | |
| Totals | 55.0 | 171 | 39.3 | 140 | 47.9 | 311 | 43.2 | 1.2 | 2.6 |

**Appendix B5.** Greater sage-grouse productivity data, Piceance Basin, Colorado, 1977–1994.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1977 | 73.3 | 15 | 55.6 | 9 | 66.7 | 24 | 49.2 | 1.3 | 2.0 |
| 1978 | 76.5 | 17 | 50.0 | 12 | 65.5 | 29 | 65.8 | 2.6 | 3.9 |
| 1979 | 100.0 | 10 | 100.0 | 4 | 100.0 | 14 | 54.9 | 2.8 | 2.8 |
| 1980 | 66.7 | 6 | 33.3 | 6 | 50.0 | 12 | 67.9 | 4.4 | 8.8 |
| 1981 | 0.0 | 2 | 100.0 | 1 | 33.3 | 3 | 83.3 | 6.7 | 20.0 |
| 1982 | 66.7 | 9 | 50.0 | 6 | 60.0 | 15 | 69.5 | 2.7 | 4.6 |
| 1983 | 50.0 | 4 | 77.8 | 9 | 69.2 | 13 | 62.7 | 2.5 | 3.6 |
| 1984 | 71.4 | 7 | 60.0 | 5 | 66.7 | 12 | 61.9 | 2.2 | 3.2 |
| 1985 | 50.0 | 6 | 50.0 | 2 | 50.0 | 8 | 69.4 | 3.1 | 6.3 |
| 1986 | 45.5 | 11 | 41.7 | 12 | 43.5 | 23 | 37.9 | 1.1 | 2.5 |
| 1987 | 50.0 | 4 | 40.0 | 10 | 42.9 | 14 | 63.0 | 2.4 | 5.7 |
| 1988 | 60.0 | 5 | 80.0 | 5 | 70.0 | 10 | 55.6 | 1.5 | 2.1 |
| 1989 | 20.0 | 5 | 37.5 | 8 | 30.8 | 13 | 36.7 | 1.4 | 4.5 |
| 1990 | 33.3 | 3 | 0.0 | 2 | 20.0 | 5 | 37.5 | 1.8 | 9.0 |
| 1991 | 0.0 | 3 | 0.0 | 1 | 0.0 | 4 | 14.3 | 0.3 | |
| 1992 | 50.0 | 4 | 20.0 | 5 | 33.3 | 9 | 47.4 | 1.0 | 3.0 |
| 1993 | 75.0 | 4 | 0.0 | 1 | 60.0 | 5 | 57.1 | 1.6 | 2.7 |
| 1994 | 100.0 | 4 | | 0 | 100.0 | 4 | 70.6 | 3.0 | 3.0 |
| Totals | 63.0 | 119 | 50.0 | 98 | 57.1 | 217 | 57.6 | 2.1 | 3.7 |

**Appendix B6.** Greater sage-grouse productivity data, Blue Mountain, Colorado, 1976–1998.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1976 | 50.0 | 22 | 20.0 | 10 | 40.6 | 32 | 61.6 | 2.2 | 5.3 |
| 1977 | 35.7 | 14 | 28.6 | 7 | 33.3 | 21 | 60.4 | 3.0 | 9.2 |
| 1978 | 51.4 | 74 | 36.8 | 68 | 44.4 | 142 | 62.1 | 2.3 | 5.2 |
| 1979 | 54.3 | 70 | 36.5 | 74 | 45.1 | 144 | 45.0 | 1.4 | 3.1 |
| 1980 | 56.6 | 53 | 25.8 | 31 | 45.2 | 84 | 68.8 | 2.8 | 6.3 |
| 1981 | 41.7 | 12 | 52.6 | 19 | 48.4 | 31 | 54.9 | 2.2 | 4.5 |
| 1982 | 55.6 | 18 | 33.3 | 21 | 43.6 | 39 | 70.5 | 4.1 | 9.3 |
| 1983 | 69.2 | 26 | 29.4 | 17 | 53.5 | 43 | 63.2 | 2.1 | 4.0 |
| 1984 | 60.7 | 28 | 46.4 | 28 | 53.6 | 56 | 63.1 | 2.8 | 5.3 |
| 1985 | 86.2 | 29 | 41.7 | 36 | 61.5 | 65 | 67.4 | 3.4 | 5.6 |
| 1986 | 55.1 | 49 | 36.0 | 50 | 45.5 | 99 | 59.5 | 2.3 | 5.1 |
| 1987 | 48.2 | 56 | 41.5 | 41 | 45.4 | 97 | 66.3 | 3.1 | 6.8 |
| 1988 | 61.1 | 36 | 20.8 | 48 | 38.1 | 84 | 50.0 | 1.8 | 4.6 |
| 1989 | 49.2 | 61 | 29.3 | 58 | 39.5 | 119 | 41.3 | 1.3 | 3.2 |
| 1990 | 41.5 | 53 | 15.8 | 38 | 30.8 | 91 | 55.4 | 1.7 | 5.7 |
| 1991 | 55.3 | 38 | 31.4 | 35 | 43.8 | 73 | 54.0 | 1.7 | 3.8 |
| 1992 | 36.4 | 33 | 13.0 | 23 | 26.8 | 56 | 45.9 | 1.3 | 4.9 |
| 1993 | 75.8 | 33 | 54.5 | 11 | 70.5 | 44 | 65.2 | 2.3 | 3.3 |
| 1994 | 66.7 | 18 | 45.5 | 22 | 55.0 | 40 | 48.7 | 1.4 | 2.5 |
| 1995 | 77.8 | 9 | 46.2 | 13 | 59.1 | 22 | 74.5 | 3.2 | 5.4 |
| 1996 | 61.5 | 26 | 31.3 | 16 | 50.0 | 42 | 56.6 | 2.0 | 3.9 |
| 1997 | 50.0 | 8 | 55.6 | 9 | 52.9 | 17 | 50.0 | 2.0 | 3.8 |
| 1998 | 57.1 | 7 | 16.7 | 6 | 38.5 | 13 | 50.0 | 1.5 | 4.0 |
| Totals | 55.1 | 773 | 33.6 | 681 | 45.0 | 1454 | 58.3 | 2.2 | 4.8 |

**Appendix B7.** Greater sage-grouse productivity data, Cold Spring Mountain, Colorado, 1976–1998. Wings were not identifiable to specific hunting area in 1978–1979.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1976 | 80.0 | 10 | 0.0 | 2 | 66.7 | 12 | 73.1 | 3.2 | 4.7 |
| 1977 | 80.0 | 20 | 25.0 | 12 | 59.4 | 32 | 59.8 | 1.9 | 3.2 |
| 1978 | | 0 | | 0 | | 0 | 0.0 | | |
| 1979 | | 0 | | 0 | | 0 | 0.0 | | |
| 1980 | 61.9 | 21 | 50.0 | 4 | 60.0 | 25 | 60.3 | 1.9 | 3.1 |
| 1981 | 47.6 | 42 | 21.4 | 28 | 37.1 | 70 | 61.7 | 2.2 | 6.0 |
| 1982 | 53.8 | 13 | 12.5 | 8 | 38.1 | 21 | 64.6 | 2.4 | 6.4 |
| 1983 | 73.2 | 41 | 54.2 | 24 | 66.2 | 65 | 68.0 | 2.7 | 4.1 |
| 1984 | 61.5 | 13 | 37.5 | 8 | 52.4 | 21 | 39.1 | 0.9 | 1.6 |
| 1985 | 63.2 | 38 | 31.8 | 22 | 51.7 | 60 | 62.1 | 2.1 | 4.0 |
| 1986 | 77.3 | 22 | 33.3 | 12 | 61.8 | 34 | 61.4 | 2.1 | 3.3 |
| 1987 | 63.6 | 11 | 33.3 | 12 | 47.8 | 23 | 49.3 | 1.5 | 3.2 |
| 1988 | 64.3 | 14 | 15.4 | 13 | 40.7 | 27 | 54.1 | 1.7 | 4.2 |
| 1989 | 60.6 | 33 | 20.8 | 24 | 43.9 | 57 | 51.3 | 1.7 | 3.9 |
| 1990 | 57.7 | 52 | 16.7 | 24 | 44.7 | 76 | 52.5 | 1.4 | 3.1 |
| 1991 | 59.0 | 39 | 53.8 | 13 | 57.7 | 52 | 68.1 | 2.5 | 4.3 |
| 1992 | 62.5 | 32 | 56.5 | 23 | 60.0 | 55 | 51.9 | 1.5 | 2.5 |
| 1993 | 88.5 | 26 | 70.6 | 17 | 81.4 | 43 | 62.3 | 2.1 | 2.6 |
| 1994 | 100.0 | 4 | 87.5 | 8 | 91.7 | 12 | 72.3 | 3.9 | 4.3 |
| 1995 | 83.3 | 6 | 33.3 | 3 | 66.7 | 9 | 60.0 | 1.7 | 2.5 |
| 1996 | 71.4 | 7 | 66.7 | 3 | 70.0 | 10 | 63.0 | 3.4 | 4.9 |
| 1997 | 60.0 | 10 | 33.3 | 6 | 50.0 | 16 | 65.5 | 2.3 | 4.5 |
| 1998 | 54.5 | 22 | 15.4 | 13 | 40.0 | 35 | 45.7 | 1.2 | 3.1 |
| Totals | 64.5 | 476 | 35.8 | 279 | 53.9 | 755 | 59.4 | 1.8 | 3.4 |

**Appendix B8.** Greater sage-grouse productivity data, Eastern Moffat and Northwestern Routt counties, Colorado, 1976–1998. Season closed in 1998 but some wings were received. No wings were received in 1995.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1976 | 50.0 | 8 | 28.6 | 7 | 40.0 | 15 | 46.3 | 1.7 | 4.2 |
| 1977 | 58.3 | 24 | 28.6 | 14 | 47.4 | 38 | 39.6 | 0.9 | 2.0 |
| 1978 | 70.8 | 24 | 76.5 | 17 | 73.2 | 41 | 77.8 | 5.0 | 6.9 |
| 1979 | 48.9 | 45 | 35.7 | 84 | 40.3 | 129 | 57.5 | 1.7 | 4.1 |
| 1980 | 47.2 | 53 | 29.2 | 48 | 38.6 | 101 | 50.8 | 1.5 | 3.8 |
| 1981 | 31.3 | 99 | 18.8 | 85 | 25.5 | 184 | 42.7 | 1.0 | 4.0 |
| 1982 | 52.9 | 34 | 27.8 | 36 | 40.0 | 70 | 46.3 | 1.2 | 3.1 |
| 1983 | 59.1 | 44 | 34.8 | 23 | 50.7 | 67 | 47.5 | 1.4 | 2.8 |
| 1984 | 62.5 | 8 | 77.8 | 9 | 70.6 | 17 | 62.1 | 2.1 | 3.0 |
| 1985 | 64.3 | 14 | 31.8 | 22 | 44.4 | 36 | 65.1 | 2.3 | 5.3 |
| 1986 | 69.2 | 13 | 57.1 | 14 | 63.0 | 27 | 70.1 | 4.1 | 6.5 |
| 1987 | 55.0 | 20 | 27.3 | 22 | 40.5 | 42 | 65.1 | 2.3 | 5.7 |
| 1988 | 50.0 | 30 | 12.5 | 24 | 33.3 | 54 | 50.7 | 1.4 | 4.2 |
| 1989 | 50.0 | 46 | 16.7 | 30 | 36.8 | 76 | 59.8 | 1.9 | 5.3 |
| 1990 | 49.0 | 49 | 16.3 | 49 | 32.7 | 98 | 49.8 | 1.7 | 5.1 |
| 1991 | 38.7 | 31 | 33.3 | 24 | 36.4 | 55 | 42.1 | 1.1 | 3.0 |
| 1992 | 33.3 | 27 | 33.3 | 9 | 33.3 | 36 | 34.2 | 0.8 | 2.3 |
| 1993 | 53.1 | 32 | 0.0 | 7 | 43.6 | 39 | 32.4 | 0.6 | 1.4 |
| 1994 | 75.0 | 12 | 30.8 | 13 | 52.0 | 25 | 62.0 | 1.8 | 3.4 |
| 1995 | | 0 | | 0 | | 0 | 0.0 | | |
| 1996 | 66.7 | 6 | 20.0 | 5 | 45.5 | 11 | 47.8 | 1.0 | 2.2 |
| 1997 | | 0 | | 0 | | 0 | 100.0 | | |
| 1998 | 25.0 | 8 | 50.0 | 4 | 33.3 | 12 | 14.3 | 0.2 | 0.5 |
| Totals | 48.8 | 627 | 29.1 | 546 | 39.6 | 1173 | 53.5 | 1.6 | 4.1 |

**Appendix B9.** Greater sage-grouse productivity data, Northcentral Moffat County, Colorado, 1976–1998.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1976 | 54.9 | 91 | 40.0 | 55 | 49.3 | 146 | 65.1 | 2.4 | 4.8 |
| 1977 | 25.9 | 81 | 7.4 | 54 | 18.5 | 135 | 33.3 | 0.9 | 4.8 |
| 1978 | 74.2 | 213 | 60.5 | 43 | 71.9 | 256 | 71.7 | 3.4 | 4.8 |
| 1979 | 62.0 | 200 | 49.5 | 291 | 54.6 | 491 | 57.1 | 2.3 | 4.1 |
| 1980 | 45.1 | 275 | 33.8 | 142 | 41.2 | 417 | 53.0 | 2.0 | 4.9 |
| 1981 | 47.5 | 255 | 41.3 | 121 | 45.5 | 376 | 54.8 | 1.7 | 3.7 |
| 1982 | 43.6 | 133 | 27.0 | 63 | 38.3 | 196 | 61.4 | 2.1 | 5.4 |
| 1983 | 56.2 | 210 | 40.0 | 130 | 50.0 | 340 | 57.1 | 2.0 | 4.0 |
| 1984 | 57.6 | 125 | 44.6 | 74 | 52.8 | 199 | 55.7 | 1.7 | 3.2 |
| 1985 | 62.4 | 125 | 42.5 | 80 | 54.6 | 205 | 62.7 | 2.5 | 4.6 |
| 1986 | 50.4 | 129 | 38.3 | 149 | 43.9 | 278 | 58.6 | 2.2 | 5.0 |
| 1987 | 48.0 | 227 | 36.1 | 191 | 42.6 | 418 | 55.9 | 1.8 | 4.3 |
| 1988 | 39.5 | 215 | 29.7 | 158 | 35.4 | 373 | 51.3 | 1.6 | 4.5 |
| 1989 | 45.2 | 283 | 37.8 | 119 | 43.0 | 402 | 53.9 | 2.1 | 4.8 |
| 1990 | 41.1 | 326 | 16.7 | 233 | 30.9 | 559 | 44.5 | 1.2 | 3.9 |
| 1991 | 46.8 | 265 | 23.9 | 109 | 40.1 | 374 | 40.7 | 1.0 | 2.5 |
| 1992 | 42.3 | 182 | 13.6 | 88 | 33.0 | 270 | 41.3 | 0.9 | 2.9 |
| 1993 | 65.1 | 86 | 37.9 | 29 | 58.3 | 115 | 53.1 | 1.7 | 2.9 |
| 1994 | 54.1 | 111 | 25.7 | 35 | 47.3 | 146 | 47.7 | 1.2 | 2.5 |
| 1995 | 47.1 | 17 | 75.0 | 8 | 56.0 | 25 | 64.9 | 2.5 | 4.5 |
| 1996 | 60.7 | 28 | 33.3 | 18 | 50.0 | 46 | 55.9 | 1.8 | 3.5 |
| 1997 | 55.6 | 18 | 55.6 | 9 | 55.6 | 27 | 50.0 | 1.5 | 2.7 |
| 1998 | 63.6 | 11 | 66.7 | 6 | 64.7 | 17 | 60.0 | 2.8 | 4.4 |
| Totals | 50.0 | 3606 | 34.7 | 2205 | 44.2 | 5811 | 54.6 | 1.8 | 4.1 |

**Appendix B10.** Greater sage-grouse productivity data, Sumpter, Hunt Unit 51, Oregon, 1993–2013.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1993 | 100.0 | 1 | | 0 | 100.0 | 1 | 83.3 | 5.0 | 5.0 |
| 1994 | 25.0 | 4 | 100.0 | 1 | 40.0 | 5 | 50.0 | 1.0 | 2.5 |
| 1995 | 100.0 | 1 | | 0 | 100.0 | 1 | 0.0 | 0.0 | 0.0 |
| 1996 | 100.0 | 1 | | 0 | 100.0 | 1 | 33.3 | 2.0 | 2.0 |
| 1997 | 0.0 | 1 | | 0 | 0.0 | 1 | 25.0 | 1.0 | |
| 1998 | | 0 | | 0 | | 0 | 0.0 | | |
| 1999 | 100.0 | 1 | | 0 | 100.0 | 1 | 0.0 | 0.0 | 0.0 |
| 2000 | 0.0 | 1 | 0.0 | 1 | 0.0 | 2 | 33.3 | 0.5 | |
| 2001 | 0.0 | 2 | | 0 | 0.0 | 2 | 0.0 | 0.0 | |
| 2002 | | 0 | | 0 | | 0 | 0.0 | | |
| 2003 | 0.0 | 2 | | 0 | 0.0 | 2 | 0.0 | 0.0 | |
| 2004 | | 0 | | 0 | | 0 | 100.0 | | |
| 2005 | | 0 | | 0 | | 0 | 100.0 | | |
| 2006 | | 0 | | 0 | | 0 | 0.0 | | |
| 2007 | | 0 | | 0 | | 0 | 0.0 | | |
| 2008 | 0.0 | 2 | | 0 | 0.0 | 2 | 0.0 | 0.0 | |
| 2009 | | 0 | | 0 | | 0 | 0.0 | | |
| 2010 | | 0 | | 0 | | 0 | 0.0 | | |
| 2011 | | 0 | | 0 | | 0 | 0.0 | | |
| 2012 | | 0 | | 0 | | 0 | 0.0 | | |
| 2013 | | 0 | | 0 | | 0 | 0.0 | | |
| Totals | 31.3 | 16 | 50.0 | 2 | 33.3 | 18 | 50.0 | 0.9 | 2.8 |

**Appendix B11.** Greater sage-grouse productivity data, Lookout Mountain, Hunt Unit 64, Oregon, 1993–2013.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1993 | 0.0 | 2 | | 0 | 0.0 | 2 | 62.5 | 2.5 | |
| 1994 | 0.0 | 2 | | 0 | 0.0 | 2 | 25.0 | 0.5 | |
| 1995 | 0.0 | 1 | 50.0 | 2 | 33.3 | 3 | 50.0 | 1.3 | 4.0 |
| 1996 | | 0 | | 0 | | 0 | 100.0 | | |
| 1997 | | 0 | | 0 | | 0 | 0.0 | | |
| 1998 | | 0 | | 0 | | 0 | 0.0 | | |
| 1999 | 0.0 | 4 | | 0 | 0.0 | 4 | 25.0 | 0.8 | |
| 2000 | | 0 | | 0 | | 0 | 0.0 | | |
| 2001 | 0.0 | 1 | | 0 | 0.0 | 1 | 60.0 | 3.0 | |
| 2002 | | 0 | | 0 | | 0 | 66.7 | | |
| 2003 | 100.0 | 2 | 100.0 | 1 | 100.0 | 3 | 66.7 | 2.0 | 2.0 |
| 2004 | 0.0 | 1 | | 0 | 0.0 | 1 | 0.0 | 0.0 | |
| 2005 | 0.0 | 2 | | 0 | 0.0 | 2 | 50.0 | 2.0 | |
| 2006 | 0.0 | 1 | | 0 | 0.0 | 1 | 33.3 | 3.0 | |
| 2007 | 0.0 | 1 | | 0 | 0.0 | 1 | 0.0 | 0.0 | |
| 2008 | 50.0 | 2 | | 0 | 50.0 | 2 | 0.0 | 0.0 | 0.0 |
| 2009 | | 0 | | 0 | | 0 | 0.0 | | |
| 2010 | | 0 | | 0 | | 0 | 0.0 | | |
| 2011 | 0.0 | 1 | | 0 | 0.0 | 1 | 0.0 | 0.0 | |
| 2012 | 0.0 | 1 | 0.0 | 1 | 0.0 | 2 | 25.0 | 0.5 | |
| 2013 | | 0 | | 0 | | 0 | 0.0 | | |
| Totals | 14.3 | 21 | 50.0 | 4 | 20.0 | 25 | 40.0 | 1.4 | 7.0 |

**Appendix B12.** Greater sage-grouse productivity data, Beulah, Hunt Unit 65, Oregon, 1993–2013.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1993 | 71.4 | 7 | 100.0 | 1 | 75.0 | 8 | 38.9 | 0.9 | 1.2 |
| 1994 | 30.8 | 13 | 50.0 | 4 | 35.3 | 17 | 52.9 | 1.6 | 4.5 |
| 1995 | 12.5 | 8 | 100.0 | 1 | 22.2 | 9 | 31.0 | 1.0 | 4.5 |
| 1996 | 25.0 | 8 | 0.0 | 1 | 22.2 | 9 | 50.0 | 1.6 | 7.0 |
| 1997 | 28.6 | 21 | 40.0 | 5 | 30.8 | 26 | 45.6 | 1.2 | 3.9 |
| 1998 | 50.0 | 16 | 100.0 | 2 | 55.6 | 18 | 47.2 | 1.4 | 2.5 |
| 1999 | 60.0 | 15 | 100.0 | 3 | 66.7 | 18 | 47.9 | 1.9 | 2.8 |
| 2000 | 31.6 | 19 | 100.0 | 1 | 35.0 | 20 | 47.0 | 1.6 | 4.4 |
| 2001 | 53.3 | 15 | 33.3 | 3 | 50.0 | 18 | 55.8 | 1.6 | 3.2 |
| 2002 | 60.0 | 20 | 100.0 | 2 | 63.6 | 22 | 49.2 | 1.3 | 2.1 |
| 2003 | 25.0 | 16 | 0.0 | 4 | 20.0 | 20 | 39.7 | 1.2 | 5.8 |
| 2004 | 31.6 | 19 | 100.0 | 3 | 40.9 | 22 | 62.3 | 1.7 | 4.2 |
| 2005 | 56.0 | 25 | 100.0 | 2 | 59.3 | 27 | 51.1 | 1.7 | 2.9 |
| 2006 | 23.5 | 17 | | 0 | 23.5 | 17 | 63.3 | 2.2 | 9.5 |
| 2007 | 14.3 | 14 | 100.0 | 1 | 20.0 | 15 | 25.0 | 0.4 | 2.0 |
| 2008 | 37.5 | 8 | 100.0 | 1 | 44.4 | 9 | 60.9 | 1.6 | 3.5 |
| 2009 | 25.0 | 16 | | 0 | 25.0 | 16 | 57.9 | 2.1 | 8.3 |
| 2010 | 47.1 | 17 | 0.0 | 4 | 38.1 | 21 | 49.1 | 1.3 | 3.5 |
| 2011 | 33.3 | 6 | 50.0 | 2 | 37.5 | 8 | 37.0 | 1.3 | 3.3 |
| 2012 | 11.1 | 9 | 0.0 | 4 | 7.7 | 13 | 38.7 | 0.9 | 12.0 |
| 2013 | | 0 | | 0 | | 0 | 80.0 | - | - |
| Totals | 37.7 | 289 | 52.3 | 44 | 39.6 | 333 | 49.0 | 1.5 | 3.7 |

**Appendix B13.** Greater sage-grouse productivity data, Malheur River, Hunt Unit 66, Oregon, 1993–2013.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1993 | 66.7 | 6 | 100.0 | 1 | 71.4 | 7 | 71.9 | 3.3 | 4.6 |
| 1994 | 42.9 | 28 | 33.3 | 3 | 41.9 | 31 | 46.0 | 1.3 | 3.1 |
| 1995 | 16.7 | 6 | 0.0 | 2 | 12.5 | 8 | 50.0 | 1.8 | 14.0 |
| 1996 | 20.0 | 10 | 100.0 | 1 | 27.3 | 11 | 60.6 | 1.8 | 6.7 |
| 1997 | 0.0 | 5 | 0.0 | 1 | 0.0 | 6 | 52.2 | 2.0 | |
| 1998 | 40.0 | 10 | 100.0 | 3 | 53.8 | 13 | 36.4 | 0.9 | 1.7 |
| 1999 | 50.0 | 12 | 100.0 | 3 | 60.0 | 15 | 56.9 | 1.9 | 3.2 |
| 2000 | 42.9 | 14 | 66.7 | 3 | 47.1 | 17 | 41.7 | 1.2 | 2.5 |
| 2001 | 44.4 | 9 | 42.9 | 7 | 43.8 | 16 | 45.3 | 1.8 | 4.1 |
| 2002 | 36.4 | 11 | 100.0 | 3 | 50.0 | 14 | 56.5 | 1.9 | 3.7 |
| 2003 | 35.7 | 14 | 25.0 | 4 | 33.3 | 18 | 54.7 | 1.6 | 4.8 |
| 2004 | 76.9 | 13 | 100.0 | 1 | 78.6 | 14 | 59.6 | 2.4 | 3.1 |
| 2005 | 42.1 | 19 | 100.0 | 3 | 50.0 | 22 | 37.0 | 1.2 | 2.5 |
| 2006 | 25.0 | 12 | 50.0 | 2 | 28.6 | 14 | 46.2 | 1.3 | 4.5 |
| 2007 | 16.7 | 6 | 50.0 | 4 | 30.0 | 10 | 31.8 | 0.7 | 2.3 |
| 2008 | 22.2 | 9 | 50.0 | 2 | 27.3 | 11 | 50.0 | 1.5 | 5.7 |
| 2009 | 25.0 | 4 | 50.0 | 2 | 33.3 | 6 | 43.8 | 1.2 | 3.5 |
| 2010 | 57.1 | 7 | 0.0 | 1 | 50.0 | 8 | 66.7 | 2.5 | 5.0 |
| 2011 | 20.0 | 5 | | 0 | 20.0 | 5 | 0.0 | 0.0 | 0.0 |
| 2012 | | 0 | | 0 | | 0 | 33.3 | | |
| 2013 | 100 | 1 | 100 | 1 | 100 | 2 | 33.3 | 0.5 | 0.5 |
| Totals | 39.3 | 201 | 59.6 | 47 | 43.1 | 248 | 46.4 | 1.6 | 3.6 |

**Appendix B14.** Greater sage-grouse productivity data, Owyhee, Hunt Unit 67, Oregon, 1993–2013.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1993 | 50.0 | 12 | | 0 | 50.0 | 12 | 25.0 | 0.3 | 0.7 |
| 1994 | 18.8 | 16 | | 0 | 18.8 | 16 | 40.0 | 0.8 | 4.0 |
| 1995 | 50.0 | 6 | 0.0 | 1 | 42.9 | 7 | 37.5 | 0.9 | 2.0 |
| 1996 | 42.9 | 7 | 66.7 | 3 | 50.0 | 10 | 62.5 | 2.0 | 4.0 |
| 1997 | 28.6 | 7 | | 0 | 28.6 | 7 | 36.8 | 1.0 | 3.5 |
| 1998 | 36.4 | 11 | 100.0 | 1 | 41.7 | 12 | 18.8 | 0.5 | 1.2 |
| 1999 | 38.5 | 13 | 100.0 | 3 | 50.0 | 16 | 47.9 | 1.4 | 2.9 |
| 2000 | 20.0 | 10 | 0.0 | 2 | 16.7 | 12 | 53.8 | 2.3 | 14.0 |
| 2001 | 33.3 | 12 | 66.7 | 3 | 40.0 | 15 | 66.2 | 3.0 | 7.5 |
| 2002 | 66.7 | 12 | 100.0 | 3 | 73.3 | 15 | 47.5 | 1.3 | 1.7 |
| 2003 | 26.7 | 15 | 50.0 | 2 | 29.4 | 17 | 25.6 | 0.6 | 2.0 |
| 2004 | 37.5 | 16 | 100.0 | 1 | 41.2 | 17 | 52.8 | 1.6 | 4.0 |
| 2005 | 38.1 | 21 | 100.0 | 3 | 45.8 | 24 | 32.1 | 0.8 | 1.6 |
| 2006 | 23.1 | 13 | 100.0 | 1 | 28.6 | 14 | 22.2 | 0.7 | 2.5 |
| 2007 | 16.7 | 12 | 0.0 | 1 | 15.4 | 13 | 20.8 | 0.4 | 2.5 |
| 2008 | 16.7 | 6 | | 0 | 16.7 | 6 | 50.0 | 1.3 | 8.0 |
| 2009 | 33.3 | 9 | | 0 | 33.3 | 9 | 54.5 | 1.3 | 4.0 |
| 2010 | 0.0 | 3 | 0.0 | 1 | 0.0 | 4 | 37.5 | 1.5 | |
| 2011 | 0.0 | 6 | | 0 | 0.0 | 6 | 13.3 | 0.3 | |
| 2012 | 36.4 | 11 | 0.0 | 2 | 30.8 | 13 | 43.9 | 1.4 | 4.5 |
| 2013 | 33 | 3 | 0 | 0 | 33.3 | 3 | 46.2 | 1.7 | 5 |
| Totals | 32.6 | 221 | 63.0 | 27 | 35.9 | 248 | 42.3 | 1.2 | 3.3 |

**Appendix B15.** Greater sage-grouse productivity data, Whitehorse, Hunt Unit 68, Oregon, 1993–2013. The Whitehorse Unit was closed to hunting in 2012.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1993 | 42.1 | 38 | 100.0 | 3 | 46.3 | 41 | 44.9 | 1.4 | 3.0 |
| 1994 | 35.6 | 45 | 50.0 | 8 | 37.7 | 53 | 54.5 | 1.7 | 4.6 |
| 1995 | 50.0 | 40 | 42.9 | 7 | 48.9 | 47 | 48.7 | 1.2 | 2.5 |
| 1996 | 62.5 | 40 | 37.5 | 8 | 58.3 | 48 | 51.1 | 1.4 | 2.5 |
| 1997 | 54.5 | 22 | 86.7 | 15 | 67.6 | 37 | 58.1 | 2.0 | 3.0 |
| 1998 | 30.8 | 26 | 100.0 | 2 | 35.7 | 28 | 56.7 | 2.0 | 5.5 |
| 1999 | 75.9 | 29 | 100.0 | 6 | 80.0 | 35 | 64.5 | 2.5 | 3.2 |
| 2000 | 28.1 | 32 | 53.3 | 15 | 36.2 | 47 | 35.8 | 1.0 | 2.9 |
| 2001 | 34.4 | 32 | 77.8 | 9 | 43.9 | 41 | 55.3 | 2.0 | 4.5 |
| 2002 | 45.8 | 24 | 100.0 | 11 | 62.9 | 35 | 63.3 | 2.9 | 4.5 |
| 2003 | 60.0 | 30 | 83.3 | 6 | 63.9 | 36 | 51.4 | 2.1 | 3.2 |
| 2004 | 41.3 | 46 | 100.0 | 11 | 52.6 | 57 | 52.8 | 2.0 | 3.8 |
| 2005 | 46.3 | 67 | 100.0 | 14 | 55.6 | 81 | 44.4 | 1.2 | 2.2 |
| 2006 | 52.8 | 36 | 57.1 | 7 | 53.5 | 43 | 48.0 | 2.0 | 3.7 |
| 2007 | 21.2 | 52 | 33.3 | 3 | 21.8 | 55 | 18.8 | 0.4 | 1.8 |
| 2008 | 51.9 | 27 | 100.0 | 3 | 56.7 | 30 | 63.7 | 2.2 | 3.8 |
| 2009 | 38.9 | 18 | 60.0 | 5 | 43.5 | 23 | 56.8 | 2.7 | 6.3 |
| 2010 | 26.8 | 41 | 57.1 | 7 | 31.3 | 48 | 52.7 | 1.4 | 4.6 |
| 2011 | 29.4 | 34 | 70.0 | 10 | 38.6 | 44 | 48.0 | 1.4 | 3.6 |
| 2012 | | 0 | | 0 | | 0 | | | |
| 2013 | 60 | 5 | 0 | 1 | 50.0 | 6 | 47.6 | 1.7 | 3.3 |
| Totals | 42.8 | 684 | 74.2 | 151 | 48.5 | 835 | 51.1 | 1.7 | 3.4 |

**Appendix B16.** Greater sage-grouse productivity data, Steens Mountain, Hunt Unit 69, Oregon, 1993–2013.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1993 | 66.7 | 27 | 100.0 | 4 | 71.0 | 31 | 29.3 | 0.8 | 1.1 |
| 1994 | 33.3 | 39 | 20.0 | 5 | 31.8 | 44 | 45.5 | 1.2 | 3.6 |
| 1995 | 34.8 | 23 | 0.0 | 2 | 32.0 | 25 | 23.4 | 0.6 | 1.9 |
| 1996 | 33.3 | 21 | 100.0 | 4 | 44.0 | 25 | 42.0 | 1.2 | 2.6 |
| 1997 | 61.5 | 13 | 100.0 | 3 | 68.8 | 16 | 51.5 | 2.1 | 3.1 |
| 1998 | 44.4 | 18 | 100.0 | 1 | 47.4 | 19 | 24.4 | 0.6 | 1.2 |
| 1999 | 71.4 | 14 | 100.0 | 3 | 76.5 | 17 | 50.0 | 1.4 | 1.8 |
| 2000 | 20.0 | 5 | 66.7 | 3 | 37.5 | 8 | 57.9 | 2.8 | 7.3 |
| 2001 | 16.7 | 6 | 0.0 | 2 | 12.5 | 8 | 52.4 | 2.8 | 22.0 |
| 2002 | 50.0 | 12 | 100.0 | 12 | 75.0 | 24 | 43.5 | 1.3 | 1.7 |
| 2003 | 70.0 | 10 | 100.0 | 3 | 76.9 | 13 | 53.6 | 2.3 | 3.0 |
| 2004 | 29.6 | 27 | 100.0 | 5 | 40.6 | 32 | 31.6 | 0.8 | 1.9 |
| 2005 | 33.3 | 9 | 100.0 | 1 | 40.0 | 10 | 50.7 | 3.6 | 9.0 |
| 2006 | 57.1 | 14 | 0.0 | 1 | 53.3 | 15 | 41.2 | 1.9 | 3.5 |
| 2007 | 44.4 | 27 | 100.0 | 5 | 53.1 | 32 | 26.0 | 0.6 | 1.2 |
| 2008 | 80.0 | 5 | 100.0 | 1 | 83.3 | 6 | 56.7 | 2.8 | 3.4 |
| 2009 | 33.3 | 3 | 100.0 | 1 | 50.0 | 4 | 46.9 | 3.8 | 7.5 |
| 2010 | 57.1 | 7 | 100.0 | 2 | 66.7 | 9 | 17.6 | 0.7 | 1.0 |
| 2011 | 37.5 | 8 | | 0 | 37.5 | 8 | 25.8 | 1.0 | 2.7 |
| 2012 | 20.0 | 10 | 0.0 | 1 | 18.2 | 11 | 25.0 | 1.1 | 6.0 |
| 2013 | 55.6 | 9 | 50.0 | 4 | 53.8 | 13 | 43.8 | 1.1 | 2.0 |
| Totals | 44.6 | 307 | 79.4 | 63 | 50.5 | 370 | 39.6 | 1.3 | 2.5 |

**Appendix B17.** Greater sage-grouse productivity data, Beatys Butte, Hunt Unit 70, Oregon, 1993–2013.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1993 | 66.7 | 15 | 100.0 | 2 | 70.6 | 17 | 59.7 | 2.7 | 3.8 |
| 1994 | 59.5 | 37 | 35.7 | 14 | 52.9 | 51 | 30.1 | 0.7 | 1.3 |
| 1995 | 42.3 | 52 | 0.0 | 1 | 41.5 | 53 | 31.7 | 0.6 | 1.5 |
| 1996 | 44.0 | 25 | 0.0 | 3 | 39.3 | 28 | 43.5 | 1.1 | 2.7 |
| 1997 | 70.0 | 30 | 100.0 | 9 | 76.9 | 39 | 56.1 | 1.9 | 2.5 |
| 1998 | 50.0 | 16 | 100.0 | 2 | 55.6 | 18 | 67.1 | 2.7 | 4.9 |
| 1999 | 68.0 | 25 | 100.0 | 4 | 72.4 | 29 | 55.1 | 2.2 | 3.1 |
| 2000 | 64.0 | 25 | 44.4 | 9 | 58.8 | 34 | 43.2 | 1.2 | 2.1 |
| 2001 | 47.4 | 19 | 100.0 | 3 | 54.5 | 22 | 45.2 | 1.7 | 3.2 |
| 2002 | 68.8 | 16 | 100.0 | 2 | 72.2 | 18 | 58.5 | 3.1 | 4.2 |
| 2003 | 76.5 | 17 | 100.0 | 3 | 80.0 | 20 | 52.8 | 2.9 | 3.6 |
| 2004 | 47.4 | 38 | 100.0 | 9 | 57.4 | 47 | 52.2 | 1.5 | 2.6 |
| 2005 | 34.6 | 26 | 100.0 | 8 | 50.0 | 34 | 44.1 | 1.6 | 3.3 |
| 2006 | 52.2 | 23 | 60.0 | 5 | 53.6 | 28 | 51.9 | 1.9 | 3.6 |
| 2007 | 45.2 | 31 | 33.3 | 6 | 43.2 | 37 | 21.9 | 0.4 | 1.0 |
| 2008 | 56.3 | 16 | 100.0 | 2 | 61.1 | 18 | 60.0 | 2.2 | 3.5 |
| 2009 | 52.6 | 19 | 66.7 | 9 | 57.1 | 28 | 58.0 | 2.1 | 3.6 |
| 2010 | 42.9 | 21 | 100.0 | 1 | 45.5 | 22 | 45.5 | 1.1 | 2.5 |
| 2011 | 60.0 | 15 | 33.3 | 3 | 55.6 | 18 | 51.5 | 2.8 | 5.1 |
| 2012 | 46.2 | 26 | 41.7 | 12 | 44.7 | 38 | 17.6 | 0.4 | 0.9 |
| 2013 | 27.8 | 18 | 60 | 5 | 34.8 | 23 | 58.1 | 2.4 | 6.8 |
| Totals | 52.4 | 510 | 66.1 | 112 | 54.8 | 622 | 48.0 | 1.5 | 2.8 |

**Appendix B18.** Greater sage-grouse productivity data, Juniper, Hunt Unit 71, Oregon, 1993–2013.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1993 | 33.3 | 6 | | 0 | 33.3 | 6 | 53.6 | 2.5 | 7.5 |
| 1994 | 58.1 | 31 | 50.0 | 6 | 56.8 | 37 | 18.5 | 0.3 | 0.5 |
| 1995 | 11.1 | 18 | | 0 | 11.1 | 18 | 23.3 | 0.4 | 3.5 |
| 1996 | 64.7 | 17 | 33.3 | 3 | 60.0 | 20 | 47.8 | 1.1 | 1.8 |
| 1997 | 75.0 | 12 | 100.0 | 1 | 76.9 | 13 | 61.5 | 2.5 | 3.2 |
| 1998 | 45.5 | 11 | | 0 | 45.5 | 11 | 50.0 | 1.3 | 2.8 |
| 1999 | 68.4 | 19 | 100.0 | 2 | 71.4 | 21 | 47.6 | 1.4 | 2.0 |
| 2000 | 46.2 | 13 | | 0 | 46.2 | 13 | 47.1 | 1.8 | 4.0 |
| 2001 | 29.4 | 17 | 100.0 | 2 | 36.8 | 19 | 59.0 | 1.9 | 5.1 |
| 2002 | 66.7 | 9 | 100.0 | 3 | 75.0 | 12 | 60.0 | 3.0 | 4.0 |
| 2003 | 73.7 | 19 | 50.0 | 2 | 71.4 | 21 | 39.2 | 1.0 | 1.3 |
| 2004 | 33.3 | 12 | 100.0 | 1 | 38.5 | 13 | 48.9 | 1.7 | 4.4 |
| 2005 | 65.0 | 20 | 100.0 | 3 | 69.6 | 23 | 39.0 | 1.0 | 1.4 |
| 2006 | 80.0 | 20 | | 0 | 80.0 | 20 | 32.0 | 0.8 | 1.0 |
| 2007 | 31.3 | 16 | 0.0 | 1 | 29.4 | 17 | 13.8 | 0.2 | 0.8 |
| 2008 | 46.2 | 13 | | 0 | 46.2 | 13 | 51.3 | 1.5 | 3.3 |
| 2009 | 80.0 | 10 | 100.0 | 1 | 81.8 | 11 | 56.4 | 2.0 | 2.4 |
| 2010 | 33.3 | 6 | 100.0 | 2 | 50.0 | 8 | 44.8 | 1.6 | 3.3 |
| 2011 | 42.9 | 7 | | 0 | 42.9 | 7 | 48.0 | 1.7 | 4.0 |
| 2012 | 33.3 | 9 | 0.0 | 3 | 25.0 | 12 | 4.8 | 0.1 | 0.3 |
| 2013 | 0 | 2 | 100 | 2 | 50 | 4 | 50 | 1 | 2 |
| Totals | 52.6 | 287 | 68.7 | 32 | 54.2 | 319 | 44.1 | 1.2 | 2.2 |

**Appendix B19.** Greater sage-grouse productivity data, Silvies, Hunt Unit 72, Oregon, 1993–2013.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1993 | 100.0 | 1 | 100.0 | 1 | 100.0 | 2 | 85.7 | 6.0 | 6.0 |
| 1994 | 22.2 | 9 | 0.0 | 1 | 20.0 | 10 | 47.4 | 0.9 | 4.5 |
| 1995 | 0.0 | 1 | | 0 | 0.0 | 1 | 75.0 | 3.0 | |
| 1996 | 75.0 | 4 | | 0 | 75.0 | 4 | 50.0 | 1.0 | 1.3 |
| 1997 | 75.0 | 4 | | 0 | 75.0 | 4 | 63.6 | 1.8 | 2.3 |
| 1998 | 87.5 | 8 | | 0 | 87.5 | 8 | 27.3 | 0.4 | 0.4 |
| 1999 | 100.0 | 1 | | 0 | 100.0 | 1 | 91.7 | 11.0 | 11.0 |
| 2000 | | 0 | | 0 | | 0 | 20.0 | | |
| 2001 | 66.7 | 3 | 100.0 | 1 | 75.0 | 4 | 33.3 | 0.8 | 1.0 |
| 2002 | 100.0 | 1 | 100.0 | 1 | 100.0 | 2 | 80.0 | 4.0 | 4.0 |
| 2003 | 12.5 | 8 | | 0 | 12.5 | 8 | 25.0 | 0.4 | 3.0 |
| 2004 | | 0 | | 0 | | 0 | 0.0 | | |
| 2005 | 100.0 | 2 | | 0 | 100.0 | 2 | 37.5 | 1.5 | 1.5 |
| 2006 | 66.7 | 3 | 100.0 | 1 | 75.0 | 4 | 61.5 | 2.0 | 2.7 |
| 2007 | 0.0 | 4 | 100.0 | 1 | 20.0 | 5 | 50.0 | 1.6 | 8.0 |
| 2008 | 28.6 | 7 | | 0 | 28.6 | 7 | 21.4 | 0.4 | 1.5 |
| 2009 | 33.3 | 3 | 0.0 | 1 | 25.0 | 4 | 36.4 | 1.0 | 4.0 |
| 2010 | 60.0 | 5 | | 0 | 60.0 | 5 | 25.0 | 0.4 | 0.7 |
| 2011 | 0.0 | 1 | | 0 | 0.0 | 1 | 50.0 | 3.0 | |
| 2012 | | 0 | 0.0 | 1 | 0.0 | 1 | 75.0 | 3.0 | |
| 2013 | 100 | 1 | 0 | 1 | 50 | 2 | 71.4 | 2.5 | 5 |
| Totals | 48.5 | 66 | 55.6 | 9 | 49.3 | 75 | 51 | 1.4 | 2.8 |

**Appendix B20.** Greater sage-grouse productivity data, Wagontire, Hunt Unit 73, Oregon, 1993–2013.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1993 | 50.0 | 4 | | 0 | 50.0 | 4 | 0.0 | 0.0 | 0.0 |
| 1994 | 30.0 | 10 | 0.0 | 1 | 27.3 | 11 | 35.7 | 0.9 | 3.3 |
| 1995 | 33.3 | 9 | 0.0 | 2 | 27.3 | 11 | 23.5 | 0.4 | 1.3 |
| 1996 | 62.5 | 8 | | 0 | 62.5 | 8 | 64.0 | 2.0 | 3.2 |
| 1997 | 44.4 | 9 | 100.0 | 1 | 50.0 | 10 | 53.6 | 1.5 | 3.0 |
| 1998 | 70.0 | 10 | 100.0 | 2 | 75.0 | 12 | 57.8 | 2.2 | 2.9 |
| 1999 | 87.5 | 8 | 100.0 | 1 | 88.9 | 9 | 33.3 | 0.8 | 0.9 |
| 2000 | 62.5 | 16 | 100.0 | 3 | 68.4 | 19 | 41.7 | 1.1 | 1.5 |
| 2001 | 44.4 | 9 | 60.0 | 5 | 50.0 | 14 | 60.4 | 2.3 | 4.6 |
| 2002 | 50.0 | 8 | 100.0 | 1 | 55.6 | 9 | 55.2 | 1.8 | 3.2 |
| 2003 | 10.0 | 10 | 100.0 | 2 | 25.0 | 12 | 34.5 | 0.8 | 3.3 |
| 2004 | 66.7 | 6 | 100.0 | 1 | 71.4 | 7 | 55.0 | 1.6 | 2.2 |
| 2005 | 80.0 | 5 | 100.0 | 2 | 85.7 | 7 | 60.9 | 2.0 | 2.3 |
| 2006 | 40.0 | 5 | 0.0 | 1 | 33.3 | 6 | 53.8 | 2.3 | 7.0 |
| 2007 | 42.9 | 14 | | 0 | 42.9 | 14 | 40.0 | 0.9 | 2.0 |
| 2008 | 33.3 | 6 | | 0 | 33.3 | 6 | 25.0 | 0.7 | 2.0 |
| 2009 | 50.0 | 4 | | 0 | 50.0 | 4 | 73.9 | 4.3 | 8.5 |
| 2010 | 45.5 | 11 | | 0 | 45.5 | 11 | 35.0 | 0.6 | 1.4 |
| 2011 | 75.0 | 4 | 100.0 | 2 | 83.3 | 6 | 56.3 | 1.5 | 1.8 |
| 2012 | 50.0 | 10 | 0.0 | 1 | 45.5 | 11 | 32.0 | 0.7 | 1.6 |
| 2013 | 57.1 | 7 | | 0 | 57.1 | 7 | 63.2 | 1.7 | 3 |
| Totals | 50.3 | 173 | 72.0 | 25 | 53.0 | 198 | 48.4 | 1.3 | 2.5 |

**Appendix B21.** Greater sage-grouse productivity data, Warner, Hunt Unit 74, Oregon, 1993–2013.

| Year | Estimated annual reproductive success | | | | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult | | Yearling | | All females | | In harvest (%) | Per hen | Per successful hen |
| | % | *n* | % | *n* | % | *n* | | | |
| 1993 | 66.7 | 6 | 100.0 | 2 | 75.0 | 8 | 30.8 | 0.5 | 0.7 |
| 1994 | 42.1 | 19 | 0.0 | 2 | 38.1 | 21 | 39.7 | 1.1 | 2.9 |
| 1995 | 25.0 | 20 | 50.0 | 2 | 27.3 | 22 | 26.5 | 0.4 | 1.5 |
| 1996 | 85.7 | 7 | | 0 | 85.7 | 7 | 61.5 | 3.4 | 4.0 |
| 1997 | 71.4 | 14 | 50.0 | 2 | 68.8 | 16 | 54.9 | 1.8 | 2.5 |
| 1998 | 14.3 | 7 | 100.0 | 4 | 45.5 | 11 | 62.2 | 2.5 | 5.6 |
| 1999 | 83.3 | 12 | 100.0 | 6 | 88.9 | 18 | 67.8 | 3.3 | 3.7 |
| 2000 | 50.0 | 10 | 100.0 | 1 | 54.5 | 11 | 56.4 | 2.0 | 3.7 |
| 2001 | 66.7 | 18 | 70.0 | 10 | 67.9 | 28 | 51.9 | 1.4 | 2.1 |
| 2002 | 69.2 | 13 | 100.0 | 1 | 71.4 | 14 | 65.0 | 3.7 | 5.2 |
| 2003 | 84.2 | 19 | 66.7 | 3 | 81.8 | 22 | 59.3 | 2.5 | 3.0 |
| 2004 | 47.6 | 21 | 100.0 | 11 | 65.6 | 32 | 53.2 | 1.8 | 2.8 |
| 2005 | 35.5 | 31 | 100.0 | 2 | 39.4 | 33 | 50.0 | 1.3 | 3.3 |
| 2006 | 57.1 | 21 | 50.0 | 2 | 56.5 | 23 | 55.4 | 1.8 | 3.2 |
| 2007 | 52.4 | 21 | 50.0 | 6 | 51.9 | 27 | 46.5 | 1.2 | 2.4 |
| 2008 | 60.7 | 28 | 62.5 | 8 | 61.1 | 36 | 54.0 | 1.5 | 2.5 |
| 2009 | 54.5 | 11 | 80.0 | 5 | 62.5 | 16 | 60.8 | 3.0 | 4.8 |
| 2010 | 13.6 | 22 | 50.0 | 4 | 19.2 | 26 | 54.2 | 1.7 | 9.0 |
| 2011 | 53.6 | 28 | 33.3 | 3 | 51.6 | 31 | 34.3 | 0.8 | 1.5 |
| 2012 | 16.7 | 18 | 0.0 | 8 | 11.5 | 26 | 38.1 | 0.9 | 8.0 |
| 2013 | 54.5 | 11 | 50 | 2 | 53.8 | 13 | 69.8 | 2.9 | 5.3 |
| Totals | 50.4 | 357 | 65.5 | 84 | 53.3 | 441 | 53.5 | 1.7 | 3.2 |



Bureau of Land Management and Oregon Dept. of Fish and Wildlife biologists examine greater sage-grouse wings mailed in by hunters in 2004, Hines, Oregon.

# Wildlife Technical Report Series

001 – 2008 “The Effectiveness of Tetracycline as a Marker to Estimate Black Bear Numbers in Oregon.”
002 – 2013 “Population Ecology of Black Bears in the Starkey Wildlife Management Unit of Northeastern Oregon, 1993-2000.”
003 – 2013 “Age Structure of Harvested Black-tailed Deer in Southwest Oregon Based on Voluntary Contributions from Successful Hunters.”
004 – 2014 “Comparison of Mule Deer Distributions During Winter and Hunting Seasons in South-central Oregon.”
005 – 2015 “Fall Population Structure of Sage-grouse in Colorado and Oregon”

OREGON DEPARTMENT OF FISH AND WILDLIFE

BioOne RESEARCH EVOLVED

# Sage-Grouse Habitat Selection During Winter in Alberta

Author(s): Jennifer Carpenter, Cameron Aldridge, and Mark S. Boyce
Source: Journal of Wildlife Management, 74(8):1806-1814. 2010.
Published By: The Wildlife Society-2
DOI: 10.2193/2009-368
URL: http://www.bioone.org/doi/full/10.2193/2009-368

BioOne (www.bioone.org) is an electronic aggregator of bioscience research content, and the online home to over 160 journals and books published by not-for-profit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Journal of Wildlife Management 74(8):1806–1814; 2010; DOI: 10.2193/2009-368

*Management and Conservation Article*

# Sage-Grouse Habitat Selection During Winter in Alberta

**JENNIFER CARPENTER,**[1] *Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada*
**CAMERON ALDRIDGE,**[2] *Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada*
**MARK S. BOYCE,**[3] *Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada*

**ABSTRACT** Greater sage-grouse (*Centrocercus urophasianus*) are dependent on sagebrush (*Artemisia* spp.) for food and shelter during winter, yet few studies have assessed winter habitat selection, particularly at scales applicable to conservation planning. Small changes to availability of winter habitats have caused drastic reductions in some sage-grouse populations. We modeled winter habitat selection by sage-grouse in Alberta, Canada, by using a resource selection function. Our purpose was to 1) generate a robust winter habitat-selection model for Alberta sage-grouse; 2) spatially depict habitat suitability in a Geographic Information System to identify areas with a high probability of selection and thus, conservation importance; and 3) assess the relative influence of human development, including oil and gas wells, in landscape models of winter habitat selection. Terrain and vegetation characteristics, sagebrush cover, anthropogenic landscape features, and energy development were important in top Akaike's Information Criterion–selected models. During winter, sage-grouse selected dense sagebrush cover and homogenous less rugged areas, and avoided energy development and 2-track truck trails. Sage-grouse avoidance of energy development highlights the need for comprehensive management strategies that maintain suitable habitats across all seasons.

**KEY WORDS** *Centrocercus urophasianus*, critical habitat, energy development, greater sage-grouse, resource selection functions, winter habitats.

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is an endangered species in Canada (Committee on the Status of Endangered Wildlife in Canada 2004). Range-wide sage-grouse have lost approximately 44% of their presettlement range (Schroeder et al. 2004), and populations have continued to decline by 2% per year since 1965 (Connelly and Braun 1997, Connelly et al. 2004), with local declines as high as 92% (Connelly et al. 2000, Aldridge and Brigham 2003). As a result, sage-grouse are the focus of intensive research and management efforts across their range. Population declines are thought to be driven by reductions in habitat quality during 3 critical life stages: nesting, brood rearing, and wintering (Connelly et al. 2000, 2004; Moynahan et al. 2006; Aldridge and Boyce 2007; Hagen et al. 2007). Aldridge and Boyce (2007) identified and mapped critical habitats for sage-grouse nesting and brood rearing in Alberta, Canada, but Doherty et al. (2008) noted the lack information on landscape-level winter habitat needs for sage-grouse. Winter habitats are generally not considered a research priority because winter survival of sage-grouse is typically high (Connelly et al. 2004), but winter habitats may be of greater importance in declining populations. For example, in northern Colorado, USA, 80% of winter sites used by sage-grouse occurred in <7% of the total area of sagebrush (*Artemisia* spp.; Beck 1977), and small changes to the quality and availability of winter habitats have resulted in severe reductions in sage-grouse populations (Swenson et al. 1987). Furthermore, severe winters can contribute to reduced annual survival (Moynahan et al. 2006).

[1] *Present address: Alberta Conservation Association, 1609-3 Avenue South, Lethbridge, AB T1J 2J8, Canada*
[2] *Present address: NREL, Colorado State University and United States Geological Survey, 2150 Centre Avenue, Building C, Fort Collins, CO 80526-8118, USA*
[3] *E-mail: boyce@ualberta.ca*

Most studies of sage-grouse winter habitats focused on site-specific features such as height, canopy cover, or crude protein levels in sagebrush and clearly identified the importance of moderate-to-dense sagebrush cover during winter (e.g., Eng and Schladweiler 1972, Beck 1977, Connelly et al. 2000, Crawford et al. 2004, Sauls 2006). Although important in understanding habitat use, such local studies do not present managers an understanding of habitat selection at a scale useful to identify and prioritize landscapes for conservation. An exception is in the Powder River Basin of Wyoming and Montana, USA, where a landscape approach was successfully used to determine that landscape factors, including vegetation, topography, and oil and gas development, affected sage-grouse winter habitat selection (Doherty et al. 2008).

Modeling habitat selection using resource selection functions (RSF) offers the ability to rank areas by their relative probability of selection (Manly et al. 2002). Mapping these relative probabilities in a Geographic Information System (GIS) can identify regions with high-quality habitats and can provide managers with a meaningful tool for prioritizing areas of conservation importance (Aldridge and Boyce 2007). Testing a habitat-selection model with independent data ensures inferences regarding habitat selection are robust and a competing-models framework can be used to evaluate alternative models of habitat selection (Burnham and Anderson 2002, Manly et al. 2002).

We investigated winter habitat selection by sage-grouse in southeastern Alberta. Our objectives were to 1) generate a robust winter habitat selection model for sage-grouse; 2) spatially depict habitat suitability to identify areas with a high probability of selection and thus, conservation importance; and 3) assess the relative influence of human development in landscape models, including intensive

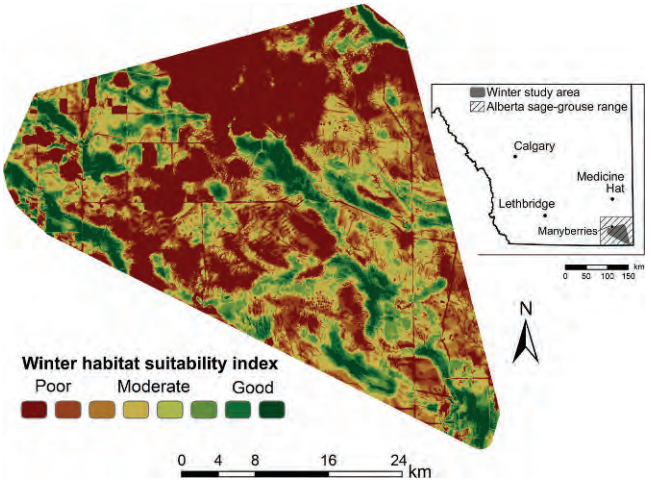



**Figure 1.** Winter habitat suitability for greater sage-grouse as determined by a resource selection function that incorporated terrain and vegetation, sagebrush, energy development, and anthropogenic feature variables. Good index values indicate increased probability of habitat selection by sage-grouse during winter. Inset depicts range of greater sage-grouse and location of study area within southeastern Alberta, Canada, 2002–2004.

energy development, on winter habitat selection. We hypothesized that sage-grouse select habitats containing greater abundance of sagebrush in landscapes that are free of snow throughout winter and that sage-grouse avoid landscapes with anthropogenic disturbances, such as those associated with energy development (i.e., well sites).

## STUDY AREA

In the dry mixed grass prairie of southern Alberta, sage-grouse are found within an approximately 4,000-km$^2$ area. Cattle graze most of this area and approximately 30% of this area is influenced by oil and gas development (Aldridge and Boyce 2007). Our study area (49°24′N, 110°42′W, ~900-m elevation) encompassed the core of the winter range (1,400 km$^2$; Fig. 1, inset). Snowfall between November and March averaged 73 cm, and approximately 30 days per year were $<-20^{\circ}$ C (Environment Canada 2009). Silver sagebrush (*Artemisia cana*) was the predominant shrub and no other species grows in this area. Grass was dominated by native grasses such as needle-and-thread grass (*Stipa comata*), June grass (*Koeleria macrantha*), and western wheatgrass (*Agropyron smithii*; Coupland 1961, Aldridge and Brigham 2003).

## METHODS

We captured female sage-grouse on 5 of 8 active leks (breeding sites) in southeastern Alberta from 1999 to 2003 by using walk-in traps (Schroeder and Braun 1991). In August and September 2003, we captured additional juvenile females by on foot nightlighting of flocks containing adult females with radiocollars (Connelly et al. 2003). We fit females with 14-g necklace-style radio-transmitters (RI-2BM transmitters; Holohil Systems Ltd., Carp, ON, Canada). We located birds with a 3-element Yagi antenna and an R-1000 scanning telemetry receiver (Communications Specialists, Inc., Orange, CA). When we could not locate signals from the ground, we searched for signals from a fixed-wing aircraft. We located and flushed females approximately once per week during winter from 1 November to 15 March in 2002–2003 and 2003–2004 (hereafter winter 1 and winter 2, respectively). If a flock of birds flushed and we could not determine the exact location of the radiocollared bird, we recorded the approximate center of the flock as the use location. In this case, if we flushed multiple marked birds from the same flock, we considered a location for each bird in model development.

### Geographic Information System Predictor Variables

Following Aldridge and Boyce (2007), we developed a suite of variables in a GIS that are probably important predictors of sage-grouse winter habitat selection. Following our hypotheses that sage-grouse select habitats with sagebrush and avoid landscapes with anthropogenic disturbances, we grouped variables into 4 classes: 1) terrain and vegetation; 2) sagebrush; 3) energy development; and 4) anthropogenic features, encompassing 86 variables (Table 1).

To analyze terrain and vegetation variables, we used Landsat Thematic Mapper satellite images from July 2000 to generate brightness (*brit_30*), greenness (*gren_30*), and normalized difference vegetation index (*ndvi*) by using a tasselled-cap transformation (Crist and Cicone 1984, Sellers 1985) in the program PCI Geomatica Prime 8.2 (PCI Geomatics, Richmond Hill, ON, Canada). We used a soil moisture index, referred to as compound topographic index (*cti*), that is correlated with soil moisture and nutrients and derived from a digital elevation model (Evans 2004). We also used a terrain ruggedness index (*tri*) derived from the amount of elevation difference between adjacent cells of a digital elevation model (Riley et al. 1999). We also estimated the mean of *ndvi*, *cti*, and *tri* and standard deviation of *ndvi* and *cti* values within a 1-km$^2$ moving window (*av_ndvi*, *sd_ndvi*, *cti_mean*, *cti_sd*, *tri_km$^2$*). We interpreted higher standard deviation values as representative of increasingly variable (heterogeneous) patches. Finally, we used a dry mixed grass plant community guide primarily based on soil types (Adams et al. 2005) to assign plant communities to ecosite categories (B. W. Adams, Alberta Sustainable Resource Development, personal communication) and estimated the proportion of each ecosite within a 1-km$^2$ moving window (*pec1*…*pec7*).

Sagebrush is an important habitat component for sage-grouse across all life stages at local scales (Beck 1977, Connelly et al. 2000, Crawford et al. 2004, Sauls 2006, Hagen et al. 2007) and also across landscapes (Aldridge and Boyce 2007, Doherty et al. 2008). Following Aldridge and Boyce (2007), we estimated sagebrush cover at both the pixel (*sbcov*) and 1-km$^2$ moving-window (*sbmean*) by using the results of Jones et al. (2005). Because sage-grouse seem to select intermediate sagebrush cover (Aldridge and Boyce 2007), we assessed quadratic functions for all sagebrush-cover metrics to identify potential nonlinearities in selection. We developed 2 measures (*sb_patch1*, *sb_patch2*) of patchy or heterogeneous sagebrush distribution (Aldridge and Boyce 2007) based on sagebrush distribution patterns described by

**Table 1.** Explanatory Geographic Information System (GIS) variables used within an information-theoretic approach to model winter habitat of sage-grouse in Alberta, Canada, 2002–2004. Data are 10-m resolution except where indicated. Decay function is in the form of (−exp[dist]/decay distance), where dist is the distance to the variable and decay distance is the specified decay distance value that shapes the function.

| Variable name | Description |
|---|---|
| Landscape features | |
| *crop_dst* | Distance to nearest cultivated lands in km |
| *crop_den* | Proportion of land that is cultivated within a 1-km$^2$ moving window |
| *crop_dst1000/500/250/50* | Decay function for distance to *crop* |
| *urban_dst* | Distance to nearest urban development in km |
| *urban_den* | Proportion of land that is urban within a 1-km$^2$ moving window |
| *urban_dst1000/500/250/50* | Decay function for distance to *urban* |
| *human_dst* | Distance to any human habitat (roads, wells, urban) in km |
| *human_den* | Proportion of land that is human habitats within a 1-km$^2$ moving window |
| *human_dst1000/500/250/50* | Decay function for distance to *human* |
| *edge_dst* | Distance to habitat that creates an anthropogenic edge (*human* and *crop*) in km |
| *edge_den* | Proportion of land that is edge habitat within 1-km$^2$ moving window |
| *edge_dst1000/500/250/50* | Decay function for distance to *edge* |
| *water_dst* | Distance to nearest natural water body in km |
| *water_dst1000/500/250/50* | Decay function for distance to *water* |
| *imped_dst* | Distance to nearest water impoundment (dam, dugout, canal) in km |
| *imped_den* | Count of number of water impoundments within a 1-km$^2$ moving window |
| *imped_dst1000/500/250/50* | Decay function for distance to water impoundment |
| *trail_dst* | Distance to nearest *trail* (non-paved or graveled 2-track truck road) in km |
| *trail_den* | Linear km per km$^2$ of *trail* (non-paved or graveled 2-track truck road) |
| *trail_dst1000/500/250/50* | Decay function for distance to *trail* (non-paved or graveled 2-track truck road) |
| *road_dst* | Distance to nearest *road* (paved or graveled) in km |
| *road_den* | Linear km per km$^2$ of *roads* (paved or graveled) |
| *road_dst1000/500/250/50* | Decay function for distance to *road* |
| Energy development | |
| *well_dst* | Distance to nearest standing energy well site in km |
| *well_den* | Count of energy well sites within a 1-km$^2$ moving window |
| *well_dst1000/500/250/50* | Decay function for distance to energy well site |
| Terrain and vegetation | |
| *brit_30* | Brightness generated from Landsat 7 TM satellite imagery[a] |
| *gren_30*[b] | Greenness generated from Landsat 7 TM imagery[a] |
| *wet_30m* | Wetness generated from Landsat 7 TM imagery[a] |
| *ndvi* | Normalized difference vegetation index calculated from TM[c] imagery[a] |
| *av_ndvi*[b] | Mean NDVI[d] value within a 1-km$^2$ moving window[a] |
| *sd_ndvi* | Standard deviation of NDVI within a 1-km$^2$ moving window[a] |
| *cti*[b] | Compound topographic index (CTI; high values = increased moisture)[a] |
| *cti_mean*[b] | Mean CTI values within a 1-km$^2$ moving window[a] |
| *cti_sd* | Standard deviation of CTI values within a 1-km$^2$ moving window[a] |
| *tri_alb*[b] | Terrain ruggedness index (TRI; high values = increased ruggedness)[a] |
| *tri_km$^2$* | Mean TRI within a 1-km$^2$ moving window[a] |
| *eco1* | Thin break range sites, soils vary, characterized by greater shrub cover (1,0; categorical) |
| *eco2* | Loamy upland sites with medium texture soils and needle-and-thread grass, wheatgrass (*Agropyron* spp.), and June grass (1,0; categorical) |
| *eco3* | Blowout and overflow sites, solonetzic soils; varies, but higher density of sagebrush (1,0; categorical) |
| *eco4* | Saline lowlands, swales and depression, sparse low sagebrush (1,0; categorical) |
| *eco5* | Broad, wetland, and shrubby (willow [*Salix* spp.], rose [*Rosa* spp.], snowberry [*Symphoricarpos occidentalis*]) riparian habitats (1,0; categorical) |
| *eco6* | Loamy range site with well drained soils, low sagebrush cover (1,0; categorical) |
| *eco7* | Badlands type habitats with juniper (*Juniperus horizontalis*), needle-and-thread grass, and blue grama (*Bouteloua gracilis*; 1,0; categorical) |
| *eco8* | All anthropogenic altered habitats (urban, crop, wells, roads; 1,0; categorical) |
| *pec1, pec2, … pec7*[b] | Proportion of class within a 1-km$^2$ moving window that is eco1, eco2, …, eco7 |
| Sagebrush | |
| *sbcov* | Sagebrush cover (%) as identified from air photo interpretation |
| *sbcovsq* | Squared term for *sbcov* |
| *sbmean* | Mean sagebrush cover (%) within a 1-km$^2$ moving window |
| *sbmeansq* | Squared term for *sbmean* |
| *sb_patch1,sb_patch2* | Patchy sagebrush distribution 1 (codes 7, 8, 9) or 2 (codes 7, 8, 9, 11) from Jones et al. (2005) |
| *sb_prop_patch1, 2* | Proportion of habitat within a 1-km$^2$ moving window that fits within patchy sagebrush distribution 1 or 2 |

[a] 30-m resolution.
[b] Variables removed from model development due to correlations.
[c] Thematic Mapper.
[d] Normalized difference vegetation index.

Jones et al. (2005). We assessed the proportion of each patch class within a 1-km$^2$ moving-window across the landscape (*sb_prop_patch1*, *sb_prop_patch2*).

Energy developments included distance to the nearest energy well site and the number of well sites within a 1-km$^2$ moving window (*well_dst*, *well_den*). Anthropogenic features included distance to the nearest road (*road_dst*); 2-track truck trail (*trail_dst*); cultivated (crop) land (*crop_dst*); and urban development, including a town, farmstead, or building not at a well site (*urban_dst*). Because anthropogenic variables can change between years, we fixed these variables at their 2003 condition and incorporated them into the landscape for the sagebrush and ecosite variables by replacement where an anthropogenic feature, such as a road or well, existed in 2003. We calculated density metrics for roads and 2-track truck trails as their linear km per km$^2$ or as the proportion of area that was crop or urban within a 1-km$^2$ moving window (*road_den*, *trail_den*, *crop_den*, *urban_den*). We generated additive estimates of human (roads, energy wells, urban) and anthropogenic edge (roads, oil wells, urban, crop) metrics as both distance and density (proportion of area within a 1-km$^2$ moving window) variables (*human_dst*, *human_den*, *edge_dst*, *edge_den*). In addition, we included metrics measuring the distance to nearest water source (*water_dst*) and water impoundment (*imped_dst*, *imped_den*).

For all distance variables, we calculated decay variables (Nielsen et al. 2009) because the response of birds to a given landscape factor typically declines as the distance between them increases. Accordingly, we created 4 decay variables for each distance variable by using the form $e^{-\alpha/d}$, where $d$ was the distance in meters from each pixel to a landscape feature, and we set $\alpha$ at 50, 250, 500, and 1,000. This scaled each distance variable between 0 and 1, with highest values close to the feature of interest.

**Model Development**

We used logistic regression contrasting used versus available pixels to estimate an exponential RSF to identify the relative probability of selection as a function of landscape covariates (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). We generated 5,000 random locations across a 1-km buffer around a 100% minimum convex polygon surrounding 296 winter locations of 23 sage-grouse females. Annual variation can be of vital importance to understanding habitat selection if resource use varies between years (Schooley 1994). However, there was no indication of behavioral differences between winter 1 and winter 2 so to increase sample size, we included bird locations from both years in the same model. To reduce bias associated with the larger sample of available (0) resource units, we used an importance weight that gave full weighting to used resource units, but available resource units received a weighting (down) proportional to the ratio of sampled use (1) points to available points (StataCorp 2007; see Aldridge and Boyce 2007).

With limited large-scale studies on which to base a priori models (Burnham and Anderson 2002), we used a hierarchical information-theoretic method. First, we compared models or metrics and determined a best model to represent each of 4 variable classes (terrain and vegetation, sagebrush, energy developments, and anthropogenic features). Second, we allowed all combinations of the top models from each variable class to compete in an Akaike's Information Criterion (AIC) framework. At all stages, we accepted only models with a change in AIC ($\Delta$AIC) score of $<2$, relative to the best model.

In the terrain and vegetation class, a priori models included variables for ecosite and measures of terrain. In cases of correlated predictors ($|r| > 0.7$), we chose to keep the most explanatory variable based on a univariate comparison. After removing correlated terrain variables, all models included *brit_30*, *wet_30m*, *ndvi*, *sd_ndvi*, and *cti*. We included a measure of landscape ruggedness (*tri_km$^2$*) in 2 of the models based on the importance of gentle topography in winter habitat selection by sage-grouse in Montana and Wyoming (Doherty et al. 2008). Because sagebrush and other shrubs might be important for both food and cover, we created 4 combinations of ecosite classes associated with shrub cover: higher density sagebrush (*pec1*), low sparse sagebrush (*pec4*), riparian shrubs (*pec5*), and low sagebrush cover (*pec6*).

In the sagebrush variable class, a priori models included both univariate and quadratic measures of sagebrush cover and patchiness. Based on Aldridge and Boyce (2007), we also included multi-variable models for sagebrush cover and patchiness (*sbcov*, *sbmean*, *sb_patch1*, *sb_patch2*, *sb_prop_patch1*, *sb_prop_patch2*). For the energy developments variable class, we evaluated univariate metrics for the density and distance to energy well sites by using AIC, and we selected only the best-performing metric to represent the energy variable class. We removed variables for well density and the smallest distance decay because there was no use of habitats within these buffers, causing models with the variables *well_dst50* and *well_den* to not converge. In the anthropogenic features variable class, we selected the best metric or scale for each of *road*, *trail*, *edge*, *urban*, *crop*, *water*, *imped*, and *human*. After removing correlated variables, we combined the best metrics for each of these to represent the anthropogenic variable class because we suspect these metrics all influence sage-grouse habitat selection.

After identifying a final model within each of the 4 variable classes, we allowed all 15 combinations of these top models to compete and accepted only models with a $\Delta$AIC score $<2$ relative to the best model to represent winter sage-grouse habitat selection. At all levels of model selection, we did not allow correlated predictors ($|r| > 0.7$) in the same model. After estimating the final model, we assessed the effect size of anthropogenic features by predicting the relative probability of selection at increasing distances from the feature while holding each other variable at its mean value from the use locations.

We evaluated our top AIC-selected model by predicting it to an independent sample of 54 winter tracking locations made on birds captured between 1998 and 2001. During winters 1998–1999 and 2001–2002, 7 male (1.9 $\pm$ 0.34 locations/bird) and 25 female (1.6 $\pm$ 0.11 locations/bird)

**Table 2.** Akaike's Information Criterion (AIC)–selected models representing terrain and vegetation in winter habitat selection by greater sage-grouse in Alberta, Canada, from 2002 to 2004. We report model log likelihood (LL), number of model parameters (*K*), AIC, change in AIC from lowest model (ΔAIC), and Akaike weights ($w_i$) for 4 a priori candidate models.

| Model[a] | LL | *K* | AIC | ΔAIC | $w_i$ |
|---|---|---|---|---|---|
| *brit_30*, *wet_30m*, *sd_ndvi*, *cti_sd*, *tri_km²*, *pec1*, *pec2*, *pec3*, *pec4*, *pec5*, *pec6*[b] | −202.5 | 12 | 429 | 0 | 1.00 |
| *brit_30*, *wet_30m*, *sd_ndvi*, *cti_sd*, *tri_km²*, *pec3*, *pec4*, *pec5* | −234.8 | 9 | 488 | 59 | 0.00 |
| *brit_30*, *wet_30m*, *sd_ndvi*, *cti_sd*, *tri_km²*, *pec3*, *pec4*, *pec5*, *pec6* | −234.8 | 10 | 490 | 61 | 0.00 |
| *brit_30*, *wet_30m*, *sd_ndvi*, *cti_sd*, *pec1*, *pec2*, *pec3*, *pec4*, *pec5*, *pec6* | −265.4 | 11 | 553 | 124 | 0.00 |

[a] Refer to Table 1 for variable descriptions.
[b] Accepted model for the terrain and vegetation class (ΔAIC < 2).

sage-grouse were flushed or located from a fixed wing aircraft. Although we used data from 9 of these females in subsequent years in model development, we believe that locations from separate years are sufficiently independent for inclusion in the evaluation of model predictive capacity. To evaluate the top AIC-selected model, we grouped the landscape by geometric means into 10 bins. Because some bins contained no data points for evaluation, we combined bins to avoid null cells, resulting in a total of 8 bins. Following Johnson et al. (2006), we converted expected and observed locations within each RSF bin into proportions and assessed the relationship between expected and observed frequencies by using linear regression testing the slope relative to 1 and evaluated overall fit using a chi-square goodness-of-fit test.

## RESULTS

During the 2 winters, we obtained 296 locations for 23 females. We tracked 7 females only during winter 1, 10 only during winter 2, and 6 during both winters. There were 3 mortalities, all in February of either 2003 or 2004. Both years had close to average mean monthly temperatures. Snowfall during winter 1 (74 cm) was typical compared to the Canadian Climate Normal of 73 cm (1971–2000; Environment Canada 2009), but snowfall was greater (104 cm) during winter 2. Flock size of relocated birds was 13.5 ± 0.72 (SE; range 1–100), with many mixed sex flocks. On several occasions, radiomarked birds made long-distance movements of approximately 50 km in <2 days during winter.

Evaluation of the terrain and vegetation variable class model indicated the model combination of brightness; wetness; standard deviation of *ndvi*, *cti*; mean *tri*; and the remaining ecosite classes (*brit_30*, *wet_30m*, *sd_ndvi*, *cti_sd*, *tri_km²*, *pec1 pec2*, *pec3*, *pec4*, *pec5*, *pec6*; Table 1) was the top model with greatest support, and no other models had moderate support (ΔAIC < 2.0; Table 2). The most supported model for the sagebrush variable class (ΔAIC < 2.0; Table 3) included the quadratic form of mean sagebrush cover and patchy distribution 2 (*sbmean*, *sb_prop_patch2*). Among 5 energy feature variable models, the most supported model (ΔAIC < 2.0; Table 4) was distance to well with a decay function of 250 m (*well_dst250*). For the anthropogenic features class, we removed variables for roads, urban, crop, and human (*road*, *urban*, *crop*, *human*) due to correlations with other variables. The most supported models among the impediment, water, edge, and 2-track truck trail variable groups (ΔAIC ≤ 2.0; Table 5) included impediment density (*imped_den*), distance to water (*water_dst50*), distance to edge (*edge_dst50*), and distance to 2-track truck trail (*trail_dst500*), respectively.

Combined evaluation of the best models from all 4 variable classes (Table 6) indicated the most supported model (ΔAIC < 2.0; Table 7) included the terrain and vegetation, sagebrush, energy development, and anthropogenic features. After applying this RSF model spatially to the landscape (Fig. 1), we used validation points to predict a linear regression model of the proportion of expected and observed validation location points. Model fit was high ($r^2 = 0.94$), with a slope different from zero ($P < 0.01$) and an intercept not different from zero ($\beta_0 = 0.02$, $P = 0.29$). A chi-square goodness-of-fit test ($\chi^2_8 = 5.05$, $P > 0.5$) and Spearman rank

**Table 3.** Akaike's Information Criterion (AIC)–selected models representing sagebrush in winter habitat selection by greater sage-grouse in Alberta, Canada, from 2002 to 2004. We report model log likelihood (LL), number of model parameters (*K*), AIC, change in AIC from lowest model (ΔAIC), and Akaike weights ($w_i$) for all 10 candidate models.

| Model[a] | LL | *K* | AIC | ΔAIC | $w_i$ |
|---|---|---|---|---|---|
| *sbmean*, *sbmeansq*, *sb_prop_patch2*[b] | −213 | 4 | 434 | 0 | 0.99 |
| *sbmean*, *sbmeansq* | −219 | 3 | 444 | 10 | 0.01 |
| *sbmean* | −235 | 2 | 474 | 40 | 0.00 |
| *sbcov*, *sbcovsq*, *sb_prop_patch2* | −256 | 4 | 520 | 86 | 0.00 |
| *sbcov*, *sbcovsq* | −274 | 3 | 554 | 120 | 0.00 |
| *sbcov* | −284 | 2 | 572 | 138 | 0.00 |
| *sb_prop_patch2* | −342 | 2 | 688 | 254 | 0.00 |
| *sb_patch2* | −370 | 2 | 744 | 310 | 0.00 |
| *sb_prop_patch1* | −408 | 2 | 820 | 386 | 0.00 |
| *sb_patch1* | −410 | 2 | 824 | 390 | 0.00 |

[a] Refer to Table 1 for variable descriptions.
[b] Accepted model representing sagebrush (ΔAIC < 2).

**Table 4.** Akaike's Information Criterion (AIC)–selected models representing energy development in winter habitat selection by greater sage-grouse in Alberta, Canada, from 2002 to 2004. We report model log likelihood (LL), number of model parameters (*K*), AIC, change in AIC from lowest model (ΔAIC), and Akaike weights ($w_i$) for all 4 candidate models.

| Model[a] | LL | *K* | AIC | ΔAIC | $w_i$ |
|---|---|---|---|---|---|
| *well_dst250*[b] | −386 | 2 | 776 | 0 | 0.95 |
| *well_dst500* | −389 | 2 | 782 | 6 | 0.05 |
| *well_dst1000* | −398 | 2 | 800 | 24 | 0 |
| *well_dst* | −407 | 2 | 818 | 42 | 0 |

[a] Refer to Table 1 for variable descriptions.
[b] Accepted model representing energy development (ΔAIC < 2).

**Table 5.** Akaike's Information Criterion (AIC)–selected models of anthropogenic feature variables for winter habitat selection by greater sage-grouse in Alberta, Canada, from 2002 to 2004. We report model log likelihood (LL), number of model parameters (*K*), AIC, change in AIC from lowest model (ΔAIC), and Akaike weights ($w_i$) for each variable relative to similar variables at different scales. We combined the 4 accepted variables to represent the anthropogenic features variable class.

| Variable[a] | LL | *K* | AIC | ΔAIC | $w_i$ |
|---|---|---|---|---|---|
| *water_dst50*[b] | −408.0 | 2 | 820 | 0 | 0.61 |
| *water_dst250* | −409.5 | 2 | 823 | 3 | 0.14 |
| *water_dst500* | −409.9 | 2 | 824 | 4 | 0.09 |
| *water_dst1000* | −410.0 | 2 | 824 | 4 | 0.08 |
| *water_dst* | −410.0 | 2 | 824 | 4 | 0.08 |
| *trail_dst500*[b] | −391.0 | 2 | 786 | 0 | 0.54 |
| *trail_den* | −392.0 | 2 | 788 | 2 | 0.20 |
| *trail_dst1000* | −392.0 | 2 | 788 | 2 | 0.20 |
| *trail_dst* | −394.0 | 2 | 792 | 6 | 0.03 |
| *trail_dst250* | −394.0 | 2 | 792 | 6 | 0.03 |
| *trail_dst50* | −405.0 | 2 | 814 | 28 | 0.00 |
| *imped_den*[b] | −386.0 | 2 | 776 | 0 | 0.97 |
| *imped_dst1000* | −390.0 | 2 | 784 | 8 | 0.02 |
| *imped_dst500* | −391.0 | 2 | 786 | 10 | 0.01 |
| *imped_dst* | −392.0 | 2 | 788 | 12 | 0.00 |
| *imped_dst250* | −395.0 | 2 | 794 | 18 | 0.00 |
| *imped_dst50* | −408.0 | 2 | 820 | 44 | 0.00 |
| *edge_dst50*[b] | −397.0 | 2 | 798 | 0 | 0.88 |
| *edge_dst* | −399.0 | 2 | 802 | 4 | 0.12 |
| *edge_dst250* | −407.0 | 2 | 818 | 20 | 0.00 |
| *edge_den* | −409.0 | 2 | 822 | 24 | 0.00 |
| *edge_dst1000* | −409.0 | 2 | 822 | 24 | 0.00 |
| *edge_dst500* | −410.0 | 2 | 824 | 26 | 0.00 |

[a] Refer to Table 1 for variable descriptions.
[b] Accepted variables (ΔAIC < 2) included in the anthropogenic features variable class.

correlation ($r_s$ = 0.83) corroborated the ability of our model to predict independent winter sage-grouse locations.

After estimating the final model, we assessed the effect size of the energy development, trail, and edge variables (*well_dst250*, *trail_dst500*, *edge_dst50*) by predicting relative probability of selection at increasing distances from the landscape feature while holding all other variables constant at their mean values (Table 8). We also added or subtracted one standard error from the coefficient of the variable of interest and held all other model variables constant at their mean, to estimate standard errors around predictions. The predicted probability of selection dropped sharply at approximately 1,900 m from energy wells and at 200 m from anthropogenic edges but for trails, the effect was less pronounced (Fig. 2).

## DISCUSSION

Our habitat model was highly predictive and is useful in identifying important winter habitats for wintering sage-grouse. Consistent with findings in Wyoming and Montana (Doherty et al. 2008), and as we hypothesized, the abundance and patchy distribution of sagebrush on the landscape influenced sage-grouse winter habitat selection. Topographic metrics and measures of productivity calculated from satellite imagery also contributed to the model. Again consistent with findings of Doherty et al. (2008), sage-grouse selected less rugged areas at lower elevations. During breeding season, sage-grouse in this population showed avoidance of anthropogenic edge (Aldridge and Boyce 2007). Human impacts also were important predictors of winter habitats. During winter, sage-grouse avoided all anthropogenic edges, regardless of type, although the smallest scale we tested provided the best model fit (*edge_dst50*), and edge was pronounced in our model with no habitats selected within 100 m of edge and limited selection from 100 m to 300 m (Fig. 2).

Models that included energy development (well metrics) performed better in AIC selection than the identical competing model without wells. Furthermore, the response to energy wells was at a large scale in our model, with no habitats selected within 1,200 m and limited selection between 1,200 m and 1,900 m. Doherty et al. (2008) found that density of coal bed natural gas wells was a better measure of sage-grouse avoidance at a large scale than a more local scale. Similarly, our model for sage-grouse in Alberta

**Table 6.** Mean, standard deviation, and range (min. and max. values) for all covariates included in final candidate Akaike's Information Criterion models to predict greater sage-grouse winter habitat selection in Alberta, Canada, from 2002 to 2004.

| Variable category | Variable name[a] | $\bar{x}$ | SD | Min. | Max. |
|---|---|---|---|---|---|
| Energy | *well_dst250* | 0.020 | 0.086 | 0 | 0.95 |
| Sagebrush | *sbmean* | 14.91 | 13.70 | 0 | 86.78 |
| | *sbmeansq* | 409.96 | 795.52 | 0 | 7530 |
| | *sb_prop_patch2* | 0.19 | 0.27 | 0 | 1 |
| Terrain and vegetation | *brit_30* | 217.52 | 20.58 | 54.99 | 360.61 |
| | *wet_30m* | 18.22 | 8.84 | −8.98 | 86.62 |
| | *sd_ndvi* | 0.038 | 0.027 | 0.0091 | 0.19 |
| | *tri_km*$^2$ | 2.37 | 2.63 | 0 | 18.16 |
| | *pec1* | 0.130 | 0.2630 | 0 | 1 |
| | *pec2* | 0.0963 | 0.2542 | 0 | 1 |
| | *pec3* | 0.355 | 0.4002 | 0 | 1 |
| | *pec4* | 0.0898 | 0.2412 | 0 | 1 |
| | *pec5* | 0.144 | 0.2840 | 0 | 1 |
| | *pec6* | 0.0834 | 0.1970 | 0 | 1 |
| Anthropogenic | *imped_den* | 0.42 | 0.66 | 0 | 5 |
| | *water_dst50* | 0.21 | 0.28 | 0 | 1 |
| | *edge_dst50* | 0.064 | 0.21 | 0 | 1 |
| | *trail_dst500* | 0.0032 | 0.048 | 0 | 1 |

[a] Refer to Table 1 for variable descriptions.

**Table 7.** Akaike's Information Criterion (AIC)–selected models for winter habitat selection by greater sage-grouse in Alberta, Canada, from 2002 to 2004. We report model log likelihood (LL), number of model parameters (*K*), AIC, change in AIC from lowest model (ΔAIC), and Akaike weights ($w_i$) for all candidate models. Variable classes include energy development (E), sagebrush (S), anthropogenic features (A), and terrain and vegetation (T).

| Model[a] | LL | *K* | AIC | ΔAIC | $w_i$ |
|---|---|---|---|---|---|
| E, S, A, T[b] | −108 | 20 | 256 | 0 | 0.98 |
| S, A, T | −113 | 19 | 264 | 8 | 0.02 |
| E, S, T | −119 | 16 | 270 | 14 | <0.01 |
| S, T | −126 | 15 | 282 | 26 | <0.01 |
| E, S, A | −172 | 9 | 362 | 106 | <0.01 |
| S, A | −182 | 8 | 380 | 124 | <0.01 |
| E, A, T | −180 | 17 | 393 | 137 | <0.01 |
| T, A | −184 | 16 | 400 | 144 | <0.01 |
| E, S | −202 | 5 | 414 | 158 | <0.01 |
| T, E | −197 | 13 | 420 | 164 | <0.01 |
| T | −202 | 12 | 428 | 172 | <0.01 |
| S | −214 | 4 | 436 | 180 | <0.01 |
| E, A | −337 | 6 | 686 | 430 | <0.01 |
| A | −354 | 5 | 718 | 462 | <0.01 |
| E | −386 | 2 | 776 | 520 | <0.01 |

[a] Refer to Table 6 for covariates included in each variable class.
[b] Accepted model for sage-grouse winter habitat selection.

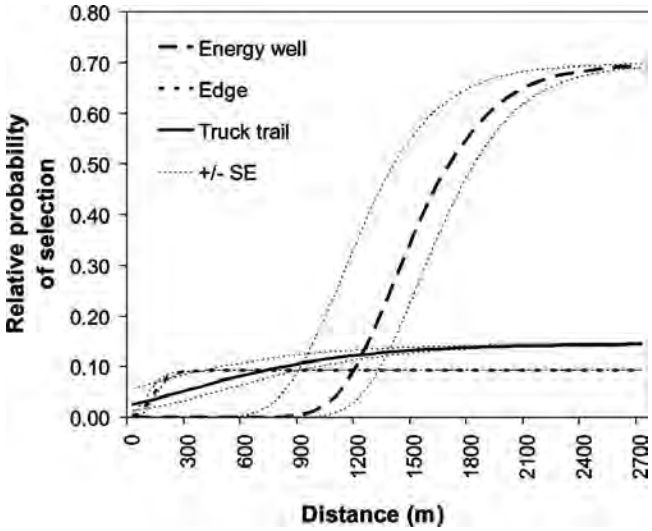



**Figure 2.** Predicted probability of selection by greater sage-grouse in Alberta, Canada, 2002–2004, as determined by a resource selection function. We calculated relative probabilities at different distances for 2-track truck trail, energy well, and edge (*trail_dst500*, *well_dst250*, *edge_dst50*, respectively) while holding all other model variables constant at their mean values. Faint dashed lines represent relative probabilities calculated using plus or minus a standard error to the coefficient of the variable of interest (one of *trail_dst500*, *well_dst250*, or *edge_dst50*) and recalculating the predictions.

predicted that the relative probability of selection drops sharply when habitat is within 1,900 m of an energy well (Fig. 2) and not surprisingly, the closest distance any sage-grouse was located to a well during the study was 1,293 m. Although mean distance from a well was 8,802 m (95% CI, $8{,}589 \leq \bar{x} \leq 9{,}016$), in the third of the winter study area with the highest oil and gas activity (460 km$^2$), mean distance to a well was 1,034 m (95% CI, $1{,}008 \leq \bar{x} \leq 1{,}060$). Thus, avoidance of energy development by sage-grouse in Alberta resulted in substantial loss of functional habitat surrounding wells, similar to other life stages (Aldridge and Boyce 2007).

Aldridge and Boyce (2007) identify the potential importance of habitat connectivity between winter and other life stages (i.e., nest and brood). Despite year-round tracking efforts, the importance of habitat connectivity was difficult to assess. Although summer and winter habitats of some birds were adjacent or overlapping, other birds made seasonal movements of 40–50 km (C. L. Aldridge, Colorado State University, unpublished data). A limited number of tracking locations suggest birds make these long movements following the topography of large valleys, potentially tracking the distribution of sagebrush. However, data collected at more frequent intervals than we obtained during

**Table 8.** Estimated coefficients (β), standard errors, and 95% confidence intervals of covariates included in the accepted model for winter habitat selection by greater sage-grouse in Alberta, Canada, from 2002 to 2004. To characterize habitat availability, we weighted 5,000 random points by using importance weights such that the available sample was effectively 296 points.

| | | | | 95% CI | |
|---|---|---|---|---|---|
| Variable class | Variable[a] | β | SE | Lower | Upper |
| Energy development | *well_dst250* | −173.96 | 119.69 | −408.54 | 60.62 |
| Sagebrush | *sbmean* | 0.24 | 0.041 | 0.16 | 0.32 |
| | *sbmeansq* | −0.0019 | 0.0005 | −0.0029 | −0.0009 |
| | *sb_prop_patch2* | 1.74 | 0.82 | 0.14 | 3.34 |
| Anthropogenic features | *edge_dst50* | −5.86 | 2.43 | −10.62 | −1.099 |
| | *water_dst50* | −2.039 | 0.73 | −3.48 | −0.60 |
| | *imped_den* | 0.70 | 0.28 | 0.15 | 1.26 |
| | *trail_dst500* | −1.65 | 0.77 | −3.16 | −0.14 |
| Terrain and vegetation | *brit_30* | −0.026 | 0.0082 | −0.042 | −0.0097 |
| | *wet_30m* | 0.10 | 0.022 | 0.059 | 0.15 |
| | *sd_ndvi* | 15.84 | 7.90 | 0.35 | 31.32 |
| | *cti_sd* | 1.034 | 0.49 | 0.079 | 1.99 |
| | *tri_km*$^2$ | −1.63 | 0.30 | −2.21 | −1.035 |
| | *pec1* | 4.39 | 2.58 | −0.67 | 9.45 |
| | *pec2* | −0.72 | 2.69 | −6.00 | 4.56 |
| | *pec3* | −1.9664 | 2.4341 | −6.7371 | 2.8043 |
| | *pec4* | −2.3040 | 2.4912 | −7.1867 | 2.5786 |
| | *pec5* | −1.2870 | 2.5303 | −6.2463 | 3.6723 |
| | *pec6* | −3.9847 | 2.7289 | −9.3332 | 1.3637 |

[a] Refer to Table 1 for variable descriptions.

our study, possibly with Global Positioning System technologies, are needed to confirm these movements and to assess how birds travel through disturbed landscapes to reach suitable winter habitats. Threats such as oil and gas development or cultivation of native habitats could reduce connectivity and disrupt migratory patterns, possibly causing bottlenecks between seasonal ranges or populations.

Sage-grouse congregate into groups of varying size during winter. We located a flock estimated at 100 birds on one occasion in 2004. This flock represented a substantial proportion of the population in one location, because the Alberta population was estimated at between 288 and 427 birds during spring 2003 (Lungle and Pruss 2008). Of the validation locations, 72% occurred in the 2 highest RSF bins, which represents just 13% of our study area. Beck (1977) also found winter habitat was limited in northern Colorado where 80% of winter sites used by sage-grouse occurred in $<7\%$ of the total area of sagebrush. Because winter habitats are limited in Alberta, comprehensive management strategies to maintain suitable habitats across all seasons are required, particularly because sage-grouse avoid energy development in otherwise suitable winter habitats.

## MANAGEMENT IMPLICATIONS

Sound management planning requires an understanding of habitat selection at large scales, identifying where priority habitats are located and determining how species respond to relevant disturbances. Our model for sage-grouse winter habitats in Alberta provides one step toward meeting this management challenge. Given the endangered status of sage-grouse in Canada, any loss of crucial winter habitats could be detrimental to population persistence (Beck 1977, Swenson et al. 1987). We recommend that areas identified as crucial to meeting winter habitat needs of sage-grouse be protected from disturbance and degradation and designated as Critical Habitat under the Canadian Species at Risk Act (Species at Risk Act 2002). Moreover, we recommend a setback distance of $\geq$1,900 m for any energy development from all winter habitats identified as Critical Habitat based on our model. Mitigation of disturbances that negatively affect sage-grouse winter habitat quality (energy and anthropogenic development) could be applied in key sagebrush habitats to enhance critical winter habitats for sage-grouse.

Although much past management for prairie grouse has focused around lek sites (Aldridge and Boyce 2007), modeling approaches such as applied here permit more comprehensive conservation planning. Considering spatially explicit models for sage-grouse nest, brood, and wintering habitats, combined with knowledge of lek locations, bird movements, and habitat connectivity, provide a biological foundation for development of an effective conservation strategy for sage-grouse.

## ACKNOWLEDGMENTS

We thank landowners who allowed us to conduct research on their lands. This research was supported financially, logistically, or both by Alberta Conservation Association, Alberta Sport Recreation Parks and Wildlife Foundation, Alberta Sustainable Resource Development, Cactus Communications (Medicine Hat, Alberta), Challenge Grants in Biodiversity, Endangered Species Recovery Fund (World Wildlife Fund Canada and the Canadian Wildlife Service), Esso Imperial Oil (Manyberries Alberta), Murray Chevrolet (Medicine Hat, Alberta), the North American Waterfowl Management Plan, and the University of Alberta. C. L. Aldridge was supported by Andrew Stewart Memorial Graduate Prize, Bill Shostak Wildlife Award, Dorothy J. Killam Memorial Graduate Prize, Edmonton Bird Club Scholarship, Izaak Walton Killam Memorial Scholarship, John and Patricia Schlosser Environment Scholarship, Macnaughton Conservation Scholarship, and a Natural Science and Engineering Research Council Scholarship. C. C. Nielsen and H. L. Beyer provided GIS assistance. R. Penniket, R. McNeil, B. W. Adams, L. Robinson, A. Buhlmann, and D. Eslinger assisted with data compilation and logistics. We thank P. Jones and J. Nicholson for assistance with many aspects of this project. M. Swystun, J. Sanders, and C. Peters assisted with field data collection.

## LITERATURE CITED

Adams, B. W., L. Poulin-Klein, D. Moisey, and R. L. McNeil. 2005. Rangeland plant communities and range health assessment guidelines for the dry mixed grass natural subregion of Alberta. Publication Number T/040, Rangeland Management Branch, Public Lands Division, Alberta Sustainable Resource Development, Lethbridge, Alberta, Canada.

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: a habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

Aldridge, C. L., and R. M. Brigham. 2003. Distribution, abundance, and status of the greater sage-grouse, *Centrocercus urophasianus*, in Canada. Canadian Field-Naturalist 117:25–34.

Beck, T. D. 1977. Sage-grouse flock characteristics and habitat selection in winter. Journal of Wildlife Management 41:18–26.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Committee on the Status of Endangered Wildlife in Canada. 2004. Canadian Species at Risk, November 2004. Committee on the Status of Endangered Wildlife in Canada. <http://www.cosewic.gc.ca/eng/sct0/sar_2004_11_e.cfm>. Accessed 1 Jun 2009.

Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. Wildlife Biology 3:229–234.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA. <http://sagemap.wr.usgs.gov/ConservationAssessment.aspx>. Accessed 1 Jun 2009.

Connelly, J. W., K. P. Reese, M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station; Moscow, Idaho Station Bulletin 80:1–54.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Coupland, R. T. 1961. A reconsideration of grassland classification in the northern Great Plains of North-America. Journal of Ecology 49:135–167.

Crawford, J. A., R. A. Olsen, N. E. West, J. C. Moseley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004.

Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2–19.
Crist, E. P., and R. C. Cicone. 1984. Application of the tasselled cap concept to simulated thematic mapper data. Photogrammetric Engineering and Remote Sensing 50:343–352.
Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187–195.
Eng, R. L., and P. Schladweiler. 1972. Sage grouse winter movements and habitat use in central Montana. Journal of Wildlife Management 36:141–146.
Environment Canada. 2009. Climate data online. <http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html>. Accessed 1 Jun 2009.
Evans, J. 2004. Compound topographic index, AML script. ESRI Support Center Downloads. ESRI, Redlands, California, USA. <http://arcscripts.esri.com/details.asp?dbid=11863>. Accessed 1 Feb 2008.
Hagen, C. A., J. W. Connelly, and M. A. Schroeder. 2007. A meta analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. Wildlife Biology 13(Supplement 1):43–50.
Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.
Jones, P. F., R. Penniket, L. Fent, J. Nicholson, and B. Adams. 2005. Silver sagebrush community associations in southeastern Alberta, Canada. Rangeland Ecology and Management 58:400–405.
Lungle, K., and S. Pruss. 2008. Recovery strategy for the greater sage-grouse (*Centrocercus urophasianus urophasianus*) in Canada. Species at risk act recovery strategy series. Parks Canada Agency, Ottawa, Ontario, Canada.
Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, Dordrecht, The Netherlands.
Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2006. Factors contributing to process variance in annual survival of female greater sage-grouse in north-central Montana. Ecological Applications 16:1529–1538.
Nielsen, S. E., J. Cranston, and G. B. Stenhouse. 2009. Identification of priority areas for grizzly bear conservation and recovery in Alberta, Canada. Journal of Conservation Planning 5:38–60.
Riley, S. J., S. D. Degloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:23–27.
Sauls, H. S. 2006. The role of selective foraging and cecal microflora in sage-grouse nutritional ecology. Thesis, University of Montana, Missoula, USA.
Schooley, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. Journal of Wildlife Management 58:367–374.
Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnel, J. W. Connelly, P. A. Diebert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, and C. W. McCarthy. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.
Schroeder, M. A., and C. E. Braun. 1991. Walk-in traps for capturing greater prairie-chickens on leks. Journal of Field Ornithology 62:378–385.
Sellers, P. J. 1985. Canopy reflectance, photosynthesis and transpiration. International Journal of Remote Sensing 6:1335–1372.
Species at Risk Act. 2002. Statutes of Canada, Canada Gazette Part III 25:3 Chapter 29. Her Majesty the Queen in Right of Canada. <http://www.sararegistry.gc.ca/approach/act/default_e.cfm>. Accessed 1 Jun 2009.
StataCorp. 2007. Stata statistical software: release 10 user's manual. StataCrop LP, College Station, Texas, USA.
Swenson, J. E., C. A. Simmons, and C. D. Eustace. 1987. Decrease of sage grouse *Centrocercus urophasianus* after ploughing of sagebrush steppe. Biological Conservation 41:125–132.

*Associate Editor: Twedt.*

BioOne COMPLETE

# Estimating sightability of greater sage-grouse at leks using an aerial infrared system and N-mixture models

Authors: Coates, Peter S., Wann, Gregory T., Gillette, Gifford L., Ricca, Mark A., Prochazka, Brian G., et al.

Source: Wildlife Biology, 2019(1) : 1-11

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00552

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Jul 2020
Terms of Use: https://bioone.org/terms-of-use

**Wildlife Biology 2019: wlb.00552**
doi: 10.2981/wlb.00552
© 2019 The Authors. This is an Open Access article
Subject Editor: Christian Hagen. Editor-in-Chief: Ilse Storch. Accepted 9 May 2019

# Estimating sightability of greater sage-grouse at leks using an aerial infrared system and *N*-mixture models

**Peter S. Coates, Gregory T. Wann, Gifford L. Gillette, Mark A. Ricca, Brian G. Prochazka, John P. Severson, Katie M. Andrle, Shawn P. Espinosa, Michael L. Casazza and David J. Delehanty**

*P. S. Coates (https://orcid.org/0000-0003-2672-9994) ✉ (pcoates@usgs.gov), G. T. Wann, M. A. Ricca, B. G. Prochazka, J. P. Severson and M. L. Casazza, U.S. Geological Survey, Western Ecological Research Center, Dixon Field Station, Dixon, CA 95620, USA. – G. L. Gillette and D. J. Delehanty, Dept of Biological Sciences, Idaho State Univ., Pocatello, ID, USA. – K. M. Andrle, Nevada Dept of Wildlife, Sagebrush Ecosystem Program, Carson City, NV, USA. – S. P. Espinosa, Nevada Dept of Wildlife, Reno, NV, USA.*

Counts of grouse present at leks (breeding grounds) during spring are widely used to monitor population numbers and assess trends. However, only a proportion of birds available to count are detected resulting in a biased population index. We designed a study using an aerial integrated infrared imaging system (AIRIS) and experimental pseudo-leks to quantify sightability (proportion of birds detected) of conventional ground-based visual (GBV) surveys for greater sage-grouse *Centrocercus urophasianus*. Specifically, we calibrated AIRIS at pseudo-leks composed of known numbers of captively-raised birds, primarily ring-necked pheasant *Phasianus colchicus*. We then carried out AIRIS and GBV surveys, simultaneously, on nearby sage-grouse leks, allowing us to model AIRIS and GBV sightability. AIRIS detected ~93% of birds on pseudo-leks while GBV detected ~86% of sage-grouse on leks. Thus, the ground count observation error was −14% from the 'true' number of male sage-grouse attending the leks. We also found sagebrush cover decreased sightability for GBV counts but did not influence sightability by AIRIS. Because standard GBV protocols typically make repeated counts of sage-grouse in a single morning, we also modeled repeated GBV counts using *N*-mixture models and found an 88% sightability, which was nearly the same as GBV sightability from the AIRIS analysis. This suggests that the use of repeated morning counts can potentially account for imperfect detection in the standard GBV surveys currently implemented. We also provide generalized correction values that could be employed by resource managers using either GBV or AIRIS to better estimate 'true' numbers of sage-grouse attending leks within similar environments to this study. The findings and interpretation presented can help guide effective monitoring protocols that account for observation error and improve accuracy of data used for population trend and abundance estimation.

Keywords: aerial survey, *Centrocercus urophasianus*, detection, greater sage-grouse, infrared, lek counts, *N*-mixture model, observation error, sightability

A primary goal in designing wildlife monitoring surveys is to develop data collection protocols capable of informing managers of changes in population abundance over time (Nichols 1991, Williams et al. 2002). Count data obtained from leks (traditional breeding grounds) of greater sage-grouse *Centrocercus urophasianus* (hereafter sage-grouse) have been a primary source of information used to assess population trends since the 1940s when lek monitoring first began (Patterson 1952, Connelly and Schroeder 2007). Sage-grouse numbers have declined throughout their range since the 1950s averaging an annual decrease of approximately 0.85% per year (Garton et al. 2015, WAFWA 2015). The species currently occupies roughly one half of its historic distribution (Schroeder et al. 2004), and with further habitat losses in the sagebrush biome likely in coming decades (Coates et al. 2016, Smith et al. 2016, Green et al. 2017) and upcoming consideration for protection under the Endangered Species Act, improved information on populations from lek count data will be central to sage-grouse conservation.

Accordingly, accounting for intrinsic biases in count data due to observation error would improve estimation of true demographic patterns resulting from environmental change. Like many types of survey data used as population indices, lek-count data is often scrutinized as a biased representation of true population numbers (Beck and Braun 1980, Applegate 2000). Part of the uncertainty in lek-count data results from imperfect observation rates of individual grouse during conventional ground-based visual (GBV) surveys lead-

This work is licensed under the terms of a Creative Commons Attribution 4.0 International License (CC-BY) <http://creativecommons.org/licenses/by/4.0/>. The license permits use, distribution and reproduction in any medium, provided the original work is properly cited.



Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Jul 2020
Terms of Use: https://bioone.org/terms-of-use

ing to variable and biased estimates. This long-recognized problem has led to several evaluations of lek counts and the factors that affect their accuracy (Fremgen et al. 2016, Baumgardt et al. 2017). Nichols et al. (2009) described four distinct components to detectability in count surveys. The first component is the probability ($p$) that an individual's home range overlaps the sampling unit ($p_s$). Because the sampling unit for sage-grouse is the lek site, home ranges of all sage-grouse within those populations are assumed to intersect the lek. However, not all leks on the landscape are known and counted (Shyvers et al. 2018), so individuals associated with those leks will not be counted. A second component is the probability an individual is present at the sampling unit during the time of survey ($p_p$). For example, individual attendance on leks can vary within mornings (Monroe et al. 2016), throughout the breeding season, and among years (Blomberg et al. 2013, Fremgen et al. 2019, Wann et al. 2019). Given the individual is present at the sampling unit, the third and fourth components are the probability of being available for detection during the count ($p_a$, e.g. not obscured by vegetation) and probability of detection conditional on availability ($p_d$; e.g. accurate count of unobscured individuals), respectively, and are collectively referred to as sightability ($p_a p_d$; Fremgen et al. 2016, Baumgardt et al. 2017). Thus, sightability can also be interpreted as the proportion of available individuals which are observed.

Infrared video-surveying is an emerging technology that is particularly useful for sensing endothermic animals (Havens and Sharp 1998) and shows promise as a tool for monitoring upland gamebird populations. The spectral signatures of these animals in the infrared wavelength (i.e. heat) is generally distinct from their environment. Infrared technology has been applied in wildlife studies for decades but has been limited primarily to uncooled infrared sensors (Gillette et al. 2013). Current systems include a single, gyroscopically-stabilized unit (to reduce motion blur in a moving aircraft) which contains both an infrared camera that is cryogenically-cooled (to improve measurement precision of spectral intensity) and a high-resolution camera in the visible spectra allowing for high-magnification zooming (e.g. to distinguish between male and female sage-grouse). We refer to this combination of technologies into one device operated from fixed-wing aircraft as an aerial integrated infrared imaging system (AIRIS).

Several state agencies have initiated lek surveys using a combination of AIRIS and GBV counts within their monitoring programs. However, without accounting for differences in sightability among survey types, population trend estimates can be confounded by mixed survey methodology which may misinform population performance and ultimately management actions. Rigorous measurement of sightability differences between AIRIS and GBV surveys may provide appropriate adjustment to lek counts and improve accuracy of trend estimates. Furthermore, AIRIS can also be used to assess the accuracy of GBV counts, as we demonstrate in this study. Although past studies have compared similarities between counts recorded with infrared cameras to those collected on the ground for sharp-tailed grouse *Tympanuchus phasianellus* and sage-grouse (Gillette et al. 2013, 2015), sightability of newer AIRIS has not been formally estimated.

Conversely, AIRIS surveys can be relatively expensive and may not be feasible for extensive surveying (Gillette et al. 2015). Therefore, agencies charged with monitoring sage-grouse populations over large areas may be interested in cost-effective alternatives to AIRIS to account for imperfect detection in lek counts. The *N*-mixture model developed by Royle (2004) offers one promising alternative because it only requires repeated counts during a period of population closure (i.e. no movement in and out of survey site during time counts occur), which is a crucial assumption. *N*-mixture models estimate sightability and true population abundance ($N$; i.e. animals available at the survey site for observation). The *N*-mixture model has been used to estimate the male population of sage-grouse at leks using repeated surveys conducted throughout the breeding season (McCaffery and Lukacs 2016). However, those estimates may be difficult to interpret given that the closure assumption is likely violated due to variation in attendance rates across survey days (Fremgen et al. 2019, Wann et al. 2019, Monroe et al. 2019). In contrast, repeated counts that occur across a relatively short period in morning hours should satisfy the closure assumption, although the estimated lek abundance will be specific to the day the counts occurred and will change by survey day given the variability in lek attendance. Nonetheless, estimating the day-specific abundance is analogous to the conventional survey estimate of using the maximum daily count and is precisely of interest in our study.

Sightability can vary considerably among lek surveys (Fremgen et al. 2016, Baumgardt et al. 2017), meaning the error in raw lek counts (i.e. the proportion of the true number of birds missed) may include substantial bias, and there is a lack of consensus on how to account for these errors. In this study, we quantify sightability error through an experimental approach that combined emerging technology with traditional methods, and then offer multiple options to account for error to managers assessing and collecting lek data. Our first objective was to estimate AIRIS sightability by quantifying the proportion of a known number of captively-raised galliform birds serving as proxies for sage-grouse on pseudo-leks. Our second objective was to estimate overall GBV error by combining the sightability of GBV counts relative to simultaneous AIRIS counts with the AIRIS sightability from objective one. We also assessed the effects of environmental factors such as sagebrush cover (serving as an index visual obstruction) and the time since sunrise (serving as an index of degree of daylight) on sightability for GBV and AIRIS counts. We were particularly interested in differences in the effects of environmental predictors and how sightability varied between the two types of survey counts. Our third objective was to derive an alternative estimate of sightability using *N*-mixture models from repeated within-morning GBV counts. We compared the *N*-mixture estimate to the result of objective two and discuss the practical potential of all three methods (i.e. GBV, AIRIS, *N*-mixture GBV) for integrated sage-grouse monitoring designs.



Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Jul 2020
Terms of Use: https://bioone.org/terms-of-use

## Methods

### Study area

We surveyed sage-grouse leks and pseudo-leks located in northeastern California (Lassen County; lattitude: 40°58′ N, 120°27′W), eastern Idaho (Clark, Fremont and Jefferson Counties; 43°99′N, 111°96′W), southwestern Idaho (Owyhee County; 42°98'N, 116°50'W), northeastern Nevada (Elko County; 41°38′N, 115°68′W), and north-central Nevada (Eureka and Lander counties; 40°08′N, −116°36′W) over three breeding seasons during April and May, 2015–2017 (Fig. 1). Vegetation communities in our study areas were typical of the sagebrush ecosystem of the northern Great Basin. Dominant shrubs included several species of sagebrush (primarily *Artemisia arbuscula*, *A. nova* and *A. tridentata*), rabbitbrush *Ericameria nauseosa* and *Chrysothamnus viscidiflorus*, snowberry *Symphoricarpos* spp., western serviceberry *Amelanchier alnifolia*, and antelope bitterbrush *Purshia tridentata*. Forbs and grasses were largely dormant when our surveys occurred, but leks were generally snow free.

### Study design

We surveyed birds at two different location types: 1) active leks consisting of wild sage-grouse and 2) pseudo-leks consisting of captively-raised ring-necked pheasant *Phasianus colchicus* (hereafter, pheasant) or chukar partridges *Alectoris chukar* (hereafter, chukar) which were tethered to the ground. Pseudo-leks contained known numbers of birds which provided a true population size for deriving AIRIS sightability. Pseudo-lek locations were randomly generated (given the following constraints) between 500 and 600 m from a real sage-grouse lek. We chose 500 m as a minimum because leks were clearly distinct from the aircraft at this distance. We chose 600 m as a maximum so general habitat characteristics were similar and flight time for the aircraft between locations was minimized, allowing for similar levels of ambient infrared radiation between both survey types. We targeted areas with percent shrub cover ≤20% within the boundaries of the pseudo-lek, which was similar to our real sage-grouse leks. Additionally, pseudo-leks had to be relatively close to an unimproved or two-track road (≤100 m) to facilitate transportation and placement of pheasant and chukar.

We placed a known number of captively-raised pheasant or chukar at pseudo-leks as a proxy for sage-grouse to estimate a proportion of birds observed by AIRIS. We chose these morphologically different galliform species to create size variation and to avoid unknown idiosyncrasies of a single species. We rationalized that lack of difference in AIRIS sightability between pheasant and chukar would indicate that sage-grouse share similarities in sightability. AIRIS at sage-grouse leks and their paired pseudo-leks occurred on the same mornings so weather and visibility conditions

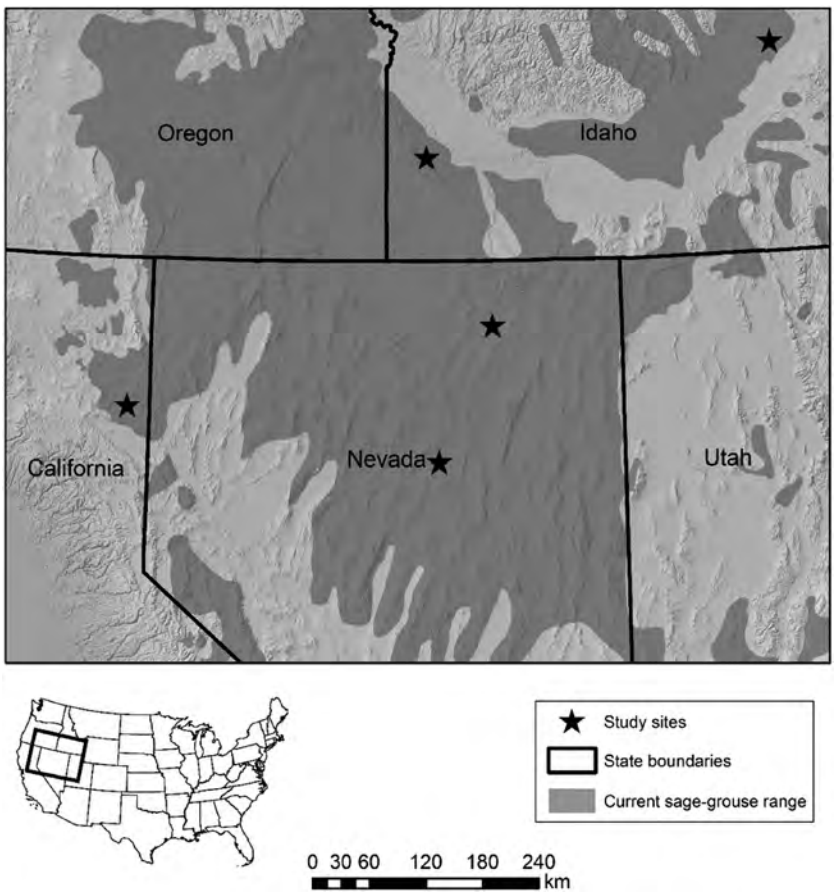



Figure 1. Greater sage-grouse *Centrocercus urophasianus* study areas where aerial integrated infrared imaging system (AIRIS) and ground-based visual (GBV) surveys were assessed for sightability at real and pseudo-leks in California, Nevada and Idaho from 2015 to 2017.



Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Jul 2020
Terms of Use: https://bioone.org/terms-of-use

were similar. Chukar and pheasant were not mixed on the same pseudo-lek (i.e. only one species occurred on a given pseudo-lek).

Placement of individual pheasant and chukar on pseudo-leks (i.e. distance from center point) followed observed patterns of sage-grouse locations on real leks digitized in a geographic information system (GIS) from infrared images recorded in Nevada and Idaho. We then measured distances of each individual sage-grouse to the geometric mean of all sage-grouse present in the image (mean = 16.3 m; standard deviation = 9.4 m) using Euclidian distance tool in ArcMap 10.3. We used these measured distances to estimate Gamma distribution parameters (shape $\alpha = 2.4$; rate $\theta = 0.038$) using the 'MASS' package (Venables and Ripley 2002) in program R (<www.r-project.org>). We chose Gamma distribution because sage-grouse locations were clustered on leks and this distribution was skewed (Kéry 2010). We determined the pseudo-lek size by sampling from a normal distribution based on sage-grouse lek counts from across Nevada reported to the Nevada Dept of Wildlife in 2015. To determine bird placement relative to the pseudo-lek center, we sampled a distance from the Gamma distribution and randomly selected a directional azimuth for each bird. Each psuedo-lek bird was tethered to a stake at the pre-determined location prior to the surveys using paracord attached to its tibiotarsus (see Supplementary material Appendix 1 more information).

## Lek counts

AIRIS counts were recorded at pseudo-leks and nearby real sage-grouse leks sequentially during the morning on survey days. A detailed description of the AIRIS technology and methods used in this study is provided in Supplementary material Appendix 2. We carried out double-blind GBV counts at real leks using two independent observers on the ground simultaneous with AIRIS surveys (Supplementary material Appendix 3).

GBV counts were conducted over two periods: 1) before the AIRIS plane arrived, and 2) during the plane visit. Within each of these primary periods, observers counted and recorded the number of male, female and unknown (i.e. sex could not be determined) grouse three times over a period of 10–15 min. Conducting three successive counts is consistent with most state agency lek count protocols (Connelly et al. 2003). For all double-blind ground counts, we randomly selected either the first or second observer's maximum count of males recorded simultaneous to the AIRIS survey with two exceptions. First, if grouse were visibly disturbed by the plane (e.g. stopped displaying and hid behind or under shrubs), we used the count that occurred prior to the AIRIS survey. Counts obtained before and during the AIRIS survey were highly correlated ($r = 0.97$), indicating the choice was likely to have minimal bias. In addition, we checked the influence of plane activity on our estimates by re-running models using only the GBV count data recoded prior to the AIRIS survey. Second, at Idaho sites in 2016, we used the total number of grouse from our GBV survey, because the AIRIS survey did not distinguish between males and females. We accounted for this difference in count type in the model.

## Sightability modeling using AIRIS and GBV

We used a Bayesian modeling framework to simultaneously estimate AIRIS and GBV sightability from 1) true numbers of birds deployed to pseudo-leks, 2) AIRIS counts of pseudo-leks, 3) AIRIS counts of sage-grouse leks, and 4) GBV counts of sage-grouse leks. This framework allowed for parameter-sharing across multiple models, which provided a unique opportunity to estimate GBV sightability. The first two equations of our model formulated a calibration for AIRIS surveys using pseudo-leks ($P$). A Poisson distribution was specified to model counts as:

$$n_{AP,i} \sim \text{Poisson}\left(\lambda_{P,i}\right) \tag{1}$$

$$\lambda_{P,i} = \omega_{P,i} n_{TP,i} \tag{2}$$

Here, $n_{AP,i}$ is the number of birds on pseudo-lek $i$ counted from the plane, and the rate $\lambda_{P,i}$ is a function of the product of the true number of birds located on each pseudo-lek ($n_{TP,i}$) and a proportional variable ($\omega_{P,i}$). The proportional variable allowed for proportions >1 (overcounting). Thus, $\omega_P$ represented the AIRIS sightability parameter and was modeled as a deterministic function of lek-level covariates ($J$) using a log-link function as:

$$\log\left(\omega_{P,i}\right) = \alpha_P + \sum_{j=1}^{J} \beta_{P,j} X_{P,ij} \tag{3}$$

Therefore, $\omega_P$ represented the proportion of birds on pseudo-lek $i$ recorded by AIRIS cameras (e.g. an estimate <1 suggests AIRIS cameras on average undercounted the true number of birds), and this proportion was determined by covariates and associated model parameters including the intercept ($\alpha_P$) and slope coefficients ($\beta_{P,j}$).

The fourth and fifth equations established the relationship between GBV counts of sage-grouse on real leks and predicted 'true' numbers of sage-grouse. We derived separate posterior distributions of $\omega_P$ based on the conditions observed at real leks ($R$), which we refer to as $\hat{\omega}_{P,i}$ and divided that value into the number of sage-grouse observed from the air for each real lek ($n_{AR,i}$). We added a constant ($C$) of 0.01 to $n_{AR,i}$ to avoid taking the log of 0 when AIRIS counts failed to observe any birds. We assigned a Poisson distribution to the number of sage-grouse observed on the ground $n_{GR,i}$ as:

$$n_{GR,i} \sim \text{Poisson}\left(\lambda_{R,i}\right) \tag{4}$$

$$\lambda_{R,i} = \omega_{R,i}\left(\frac{n_{AR,i} + C}{\hat{\omega}_{P,i}}\right) \tag{5}$$

Thus, $\omega_{R,i}$ represented the proportion of sage-grouse recorded on the ground relative to the predicted 'true' number, providing a GBV sightability parameter. In parallel, we modeled $\omega_{R,i}$ as a deterministic function of lek-level covariates ($J$) using a log link function as:

$$\log\left(\omega_{R,i}\right) = \alpha_R + \sum_{j=1}^{J} \beta_{R,j} X_{R,ij} \tag{6}$$



Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Jul 2020
Terms of Use: https://bioone.org/terms-of-use

We specified vague priors in terms of mean and precision (i.e. inverse-variance) for all model coefficients (intercepts and slopes) including $\alpha_T \sim$ normal(0, 0.0001) and $\beta_T \sim$ normal(0, 0.0001), and subscripts denote coefficients estimated for real or pseudo-leks ($T = \{R, P\}$).

#### *Covariates*

We considered several covariates as potentially influencing the accuracy of AIRIS and GBV counts. However, prior to fitting all covariates, we tested the assumption that captively-raised pheasant and chukar were equally detectable by AIRIS using a model that included only an intercept and coefficient for the two-level species effect (1 = pheasant, 0 = chukar). An estimated coefficient for the species effect with 95% credible interval (CI) overlapping 0 supported similar detectability between the species by AIRIS.

A covariate for count type (i.e. males only or both males and females) was considered for the GBV sightability model. Additionally, we considered temporal effects (minutes before or after sunrise at which count occurred, i.e. 'time since sunrise'), and concealment effects (topographic roughness and shrub canopy cover) for both the GBV sightability and AIRIS sightability models. We calculated time since sunrise for each lek location and date that a count occurred using the spatial package 'sp' (Bivand et al. 2013) in program R. We also calculated average shrub canopy cover from 30-m resolution National Land Cover Database Shrubland Products (NLCD; Xian et al. 2015) and topographic roughness as the variance in elevation from a 30-m digital elevation model (Riley et al. 1999) within 100 m of leks using the zonal statistics tool in ArcMap 10.3.

We first estimated AIRIS and GBV sightability without environmental effects but accounting for count type (see above) and reported estimates of GBV sightability of males attending leks. We then estimated sightability accounting for covariate effects and predicted the average sightability while holding the habitat characteristics at the mean values for real leks. Sightability was not constrained between 0 and 1 because, although rare, overcounting sometimes occurred in AIRIS surveys at pseudo-leks.

Our full AIRIS sightability model included an intercept and four covariates (species, time since sunrise, shrub cover and topographic roughness), and our full GBV sightability model included an intercept and four covariates (count type, time since sunrise, shrub cover and topographic roughness). Covariates were considered supported by data if 95% CI of estimated coefficient (β) did not overlap 0. We also evaluated support based on the posterior probability of nonzeroness derived from a stochastic search variable selection (SSVS) method (George and McCulloch 1996). Specifically, we assigned a Bernoulli prior with probability of inclusion of 0.5 and derived a posterior probability of β being included in the model. This value represents how likely $\beta \neq 0$ given the data. We considered evidence substantial for values >0.6, marginal for 0.5–0.6, and deficient for <0.5.

### Sightability *N*-mixture modeling

In addition to the sightability model using AIRIS data in conjunction with GBV data, we analyzed repeated counts from GBV data only collected at real leks as an alternative approach using a basic binomial *N*-mixture model (Royle 2004). The purpose of this analysis was to compare sightability estimates between the two approaches and provide wildlife managers with alternative methods in accounting for observation error using repeated count designs. As previously described, during sage-grouse lek surveys, GBV observers recorded three repeated ground counts simultaneously with the AIRIS counts. *N*-mixture models were fit to the repeated GBV counts during single morning surveys. Thus, unlike the GBV-AIRIS sightability analysis which used the maximum GBV count, the *N*-mixture model analysis used all three GBV counts recorded during a survey.

For each real lek, we randomly selected one of the two observers and used their repeated GBV counts. We modeled counts at real lek $i$ during count period $j$ as arising from a binomial distribution as $y_{ij} \sim$ binomial($N_i$, $p$), where $N_i$ is abundance at lek $i$, which is a latent state estimated from the repeated counts. The parameter $p$ in the *N*-mixture model can also be thought of as the probability of detecting an individual conditional on availability ($p_d p_d$; i.e. sightability) on a given count. Because these surveys were conducted in a single morning over a relatively short period of time, the component $p_p$ (i.e. probability of presence) was not included because bird movement into and out of leks was not expected. Thus, sightability and abundance were conditional on the set of birds on lek during this time frame (Nichols et al. 2009). We fit simple intercept structures for both $N$ and $p$ using a log and logit link, respectively, and specified vague priors for both intercepts as $\beta_0 \sim$ normal(0, 0.0001). Because state agencies generally report the maximum count when multiple counts occur in a morning, and $p$ by itself is not informative for datasets which only report the maximum from repeated counts, we also calculated a derived maximum sightability, $p_D$, as:

$$\frac{\sum_{i=1}^{I} \max\left(y_{ij}\right) N_i^{-1}}{I}$$

In this equation, every lek has the maximum of its repeated counts divided by its estimated abundance, and the total summation of this value is divided by the total number of leks ($I$) to obtain an average, represented as $p_D$. Only lek counts with >1 displaying male were used in the *N*-mixture analysis (i.e. the maximum of repeated counts had to have 2 or more males recorded).

### Model implementation

All models were fit using the package 'R2jags' (Su and Yajima 2015) in Program R, which interfaced with the MCMC sampler program JAGS (ver. 4.2.0; Plummer 2003). We monitored three posterior chains over 20 000 MCMC iterations, the first 5000 of which were discarded as burn-in. Convergence of the marginal posterior distributions were assessed using the Brooks–Gelman statistic, $\hat{R}$ (Brooks and Gelman 1998). Values of $\hat{R} > 1.1$ suggest lack of convergence. We ran the AIRIS and GBV sightability models simultaneously and saved output from the three MCMC chains for parameter inference. We summarized statistics (i.e. median and 95% CI) from the posterior marginal



Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Jul 2020
Terms of Use: https://bioone.org/terms-of-use

Table 1. Number of pseudo-leks (ring-necked pheasant *Phasianus colchicus* and chukar *Alectoris chukar*) and real leks (greater sage-grouse *Centrocercus urophasianus*) surveyed by site and year to quantify sightability using ground visual surveys and aerial infrared surveys within 6 field sites in the Great Basin during 2015–2017. Pseudo-lek counts were not conducted in 2015.

| | | | Pseudo-lek counts | | Real lek counts | | |
|---|---|---|---|---|---|---|---|
| Site | No. of psuedo-leks | No. of real leks | 2016 | 2017 | 2015 | 2016 | 2017 |
| Northeastern California | 10 | 5 | 0 | 20 | 0 | 0 | 9 |
| Eastern Idaho | 9 | 13 | 9 | 0 | 0 | 13 | 0 |
| Southwestern Idaho | 5 | 8 | 5 | 0 | 0 | 8 | 0 |
| Northeastern Nevada | 24 | 18 | 20 | 15 | 0 | 17 | 10 |
| Northcentral Nevada | 0 | 11 | 0 | 0 | 11 | 0 | 0 |
| Total | 48 | 55 | 34 | 35 | 11 | 38 | 19 |

distributions for parameters monitored in our models. Derived parameters were calculated from the saved MCMC output from both the pseudo-lek and real lek models.

## Results

We conducted surveys at 48 pseudo-leks and 55 real leks (Table 1) and used 69 maximum counts at pseudo-leks and 68 maximum counts at real leks in our analysis (Table 1). Thus, some leks consisted of >1 maximum count based on sampling across years. Pheasant were used during 62 pseudo-lek counts and chukar were used during 7. Most field data were collected in Nevada and Idaho. Sampling effort varied by year and site and we did not conduct pseudo-lek counts in 2015 at any sites (Table 1). On rare occasions sage-grouse were observed to stop displaying or crouch low to the ground during aerial counts.

All parameter estimates from our models converged ($\hat{R} < 1.1$). Based on model parameters, the AIRIS sightability model produced an average sightability ($\omega_P$) of 0.93 (95% CI: 0.87, 0.99), the GBV sightability model produced an average sightability ($\omega_R$) of 0.86 (95% CI: 0.78, 0.95). Thus, the estimated ground count observation error was −14% from the 'true' number of male sage-grouse attending the lek (Fig. 2). Replacing GBV counts with those recorded before the plane arrived also produced an average GBV sightability of 0.86 (95% CI: 0.77, 0.95). Overall, the average counts were similar between paired AIRIS (19.3; SE = 2.1) and GBV (17.9; SE = 2.1). The strong correlation between AIRIS counts and pseudo-lek numbers (i.e. truth; r = 0.94) was similar to the correlation between AIRIS and GBV counts (r = 0.94; Fig. 3a–b). We also found no differences in sightability between pheasant and chukar at pseudo-leks based on counts collected in AIRIS surveys ($\bar{\beta}_{species} = 0.02$, 95% CI: −0.20, 0.23; Supplementary material Appendix 3 Fig. A1). Correlations between the double-blind GBV counts at sage-grouse leks were high (r = 0.99, indicating agreement in counts obtained between observers. However, residuals between the paired counts increased with lek size, suggesting decreasing precision as a function of lek size (Fig. 3c).

Shrub cover reduced sightability for GBV surveys but did not affect AIRIS surveys (Fig. 4) based on non-overlap of 95% CI for β and SSVS analysis (Table 2). We found marginal evidence that sightability increased as time elapsed from sunrise (linear) for GBV surveys (Fig. 4c) but not for AIRIS (Table 2, Fig. 4d). Although weaker, evidence suggests differences in sightability associated with topographic roughness (Table 2). The type of count (males only versus combined males and females) showed some evidence of influencing AIRIS sightability, but 95% CIs overlapped 0. Using a model that included count type and covariates fixed at their median values for sagebrush, roughness, and time since sunrise, we estimated average GBV sightability ($\bar{\omega}_R$) to be 0.85 (95% CI: 0.76, 0.95).

The binomial *N*-mixture model was fit to repeated GBV counts recorded at 31 leks. All parameters converged (all $\hat{R} < 1.1$). The estimated sightability using repeated counts for any given GBV count was 0.82 (95% CI: 0.78, 0.86), whereas maximum sightability derived from the maximum count ($p_D$) among these counts was 0.88 (95% CI: 0.83, 0.93).

## Discussion

Our empirical calibration of AIRIS allowed a novel and robust assessment of effectiveness of GBV counts for sage-grouse population monitoring. Our findings corroborate

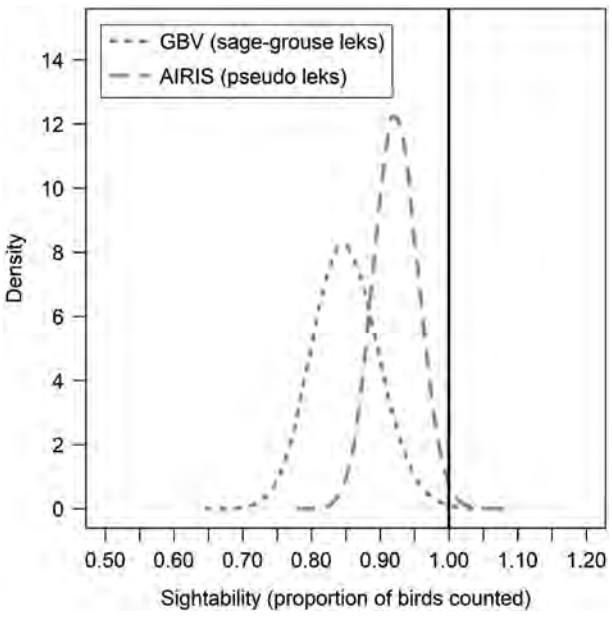



Figure 2. Posterior distributions of the proportion of birds detected at multiple sites in the Great Basin during 2015–2017 using ground-based visual (GBV) surveys and aerial integrated infrared imaging system (AIRIS). Estimates of GBV were derived from real-leks attended by unknown numbers of greater sage-grouse *Centrocercus urophasianus*. Estimates of AIRIS were derived from pseudo-leks with known numbers of ring-necked pheasant *Phasianus colchicus* and chukar *Alectoris chukar*. Perfect detection is denoted by the solid black line.



Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Jul 2020
Terms of Use: https://bioone.org/terms-of-use

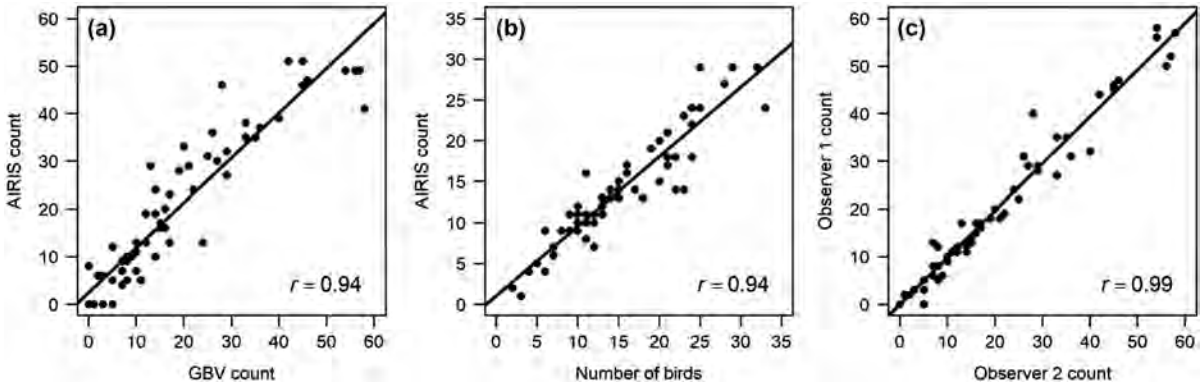



Figure 3. Correlation between counts obtained from (a) aerial infrared imaging system (AIRIS) and ground-based visual (GBV) surveys at real leks with unknown numbers of greater sage-grouse, (b) AIRIS obtained counts of pseudo-leks with known numbers of ring-necked pheasant *Phasianus colchicus* and chukar *Alectoris chukar*, and (c) paired counts of real leks obtained by double-blind observers. Data were collected from multiple sites in the Great Basin from 2015 to 2017.

previous aerial infrared studies of lekking grouse that also reported correlations between infrared cameras and ground counts (Gillette et al. 2013, 2015). However, we extend this study to provide robust estimates based on actual proportion of grouse counted from the aircraft relative to a 'true' number on the ground. Although GBV and AIRIS counts were highly correlated, AIRIS sightability was greater on sage-grouse leks than GBV sightability. Additionally, calibrating AIRIS with known numbers at pseudo-leks and calibrating GBV surveys with AIRIS at sage-grouse leks provided an experimental approach to robustly estimate that GBV surveys observed ~86% of male sage-grouse attending a lek during the survey period. Because our double-blind surveys indicated agreement between observers, especially for smaller leks, failure to detect all males by GBV was not driven intrinsically by individual observer effects.

Aerial infrared technology for wildlife surveys has advanced rapidly and use on sage-grouse lek counts has increased substantially across the western US (J. Romero, Owyhee Air Research, pers. comm.), largely because more leks can be counted per morning especially in remote areas (Gillette et al. 2013, 2015). Because AIRIS and GBV surveys can vary across years at individual leks, population trend estimates may be confounded without appropriately adjusting count data based on methodology.

One option to improve precision and decrease bias of population estimates, is for managers to apply a published estimate of sightability, such as ours, to their maximum lek count data. While this may be a coarse correction for different regions, it can readily be applied to existing lek databases. We therefore provide sightability estimates that may serve as adjustment factors for single maximum lek count data from GBV and AIRIS. These adjustment factors are intended to better approximate true numbers of sage-grouse attending leks and reduce confounding effects of survey type. For example, simply dividing observed counts by the median GBV sightability value reported here, as well as upper and lower 95% credible limits, will provide more accurate estimates of the numbers of males attending a lek during the survey. Additionally, counts obtained with AIRIS can be divided by AIRIS sightability to be comparable with adjusted GBV counts. Adjusted values can then be used to improve accuracy in estimates of population trends and factors influencing population changes by accounting for detection.

A second option to improve population estimates is for managers to develop their own detection probabilities and or corrected population sizes specific to their leks, regions, and survey times. Our use of an *N*-mixture model provided a relatively simple modeling framework to estimate sightability and lek abundance that can be carried out readily by wildlife managers. Most state agency lek databases currently consist only of maximum counts derived from a series of repeated counts conducted in one morning, while the lower counts are discarded. Applying *N*-mixture models to estimate sightability would only require recording and retaining all the repeated count data within each morning in the lek database rather than just the daily or annual maximum count. Single morning successive repeated counts also allow the closure assumption to be met (Royle 2004). The correspondence between our GBV–AIRIS and *N*-mixture results increased our confidence in the reliability of this method for lek counts, and the reduced cost compared to AIRIS surveys makes it an attractive alternative. Future research that critically evaluates the use of *N*-mixture models on repeated counts during single morning lek surveys would be highly beneficial.

We found that the effects of environmental factors on sightability varied among GBV and AIRIS surveys. The most influential factor that decreased sightability for GBV surveys was increased shrub cover at the lek, which was consistent with findings elsewhere (Fremgen et al. 2016). Fremgen et al. (2016) observed a negative effect of shrub height, and both height and cover likely affect visual obstruction. Thus, GBV observers are seemingly limited by visual screening from shrubs when counting sage-grouse from the ground. AIRIS methods overcome this issue to some extent owing to the plane's ability to circle sage-grouse and observe them from multiple angles, as well as infrared camera's ability to detect partially obstructed birds. We found some evidence that time since sunrise influenced sightability of birds using GBV but not AIRIS, which may be explained by increased ambient lighting. However, another recent sightability study (Baumgardt et al. 2017) observed a negative relationship with time since sunrise, which they



Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Jul 2020
Terms of Use: https://bioone.org/terms-of-use

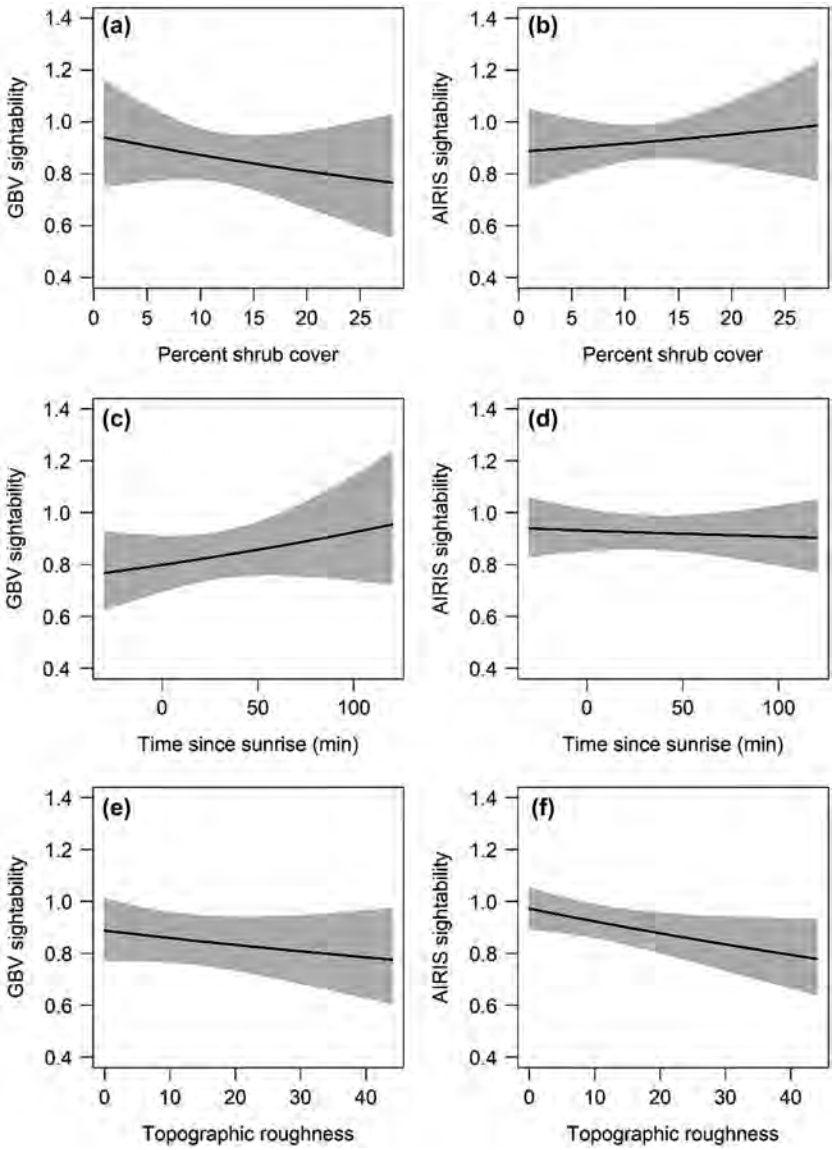



Figure 4. Effects of shrub cover (a and b), time since sunrise (c and d), and topographic roughness (e and f) on sightability estimates for ground-based visual (GBV) surveys (left column) at real leks with unknown numbers of greater sage-grouse *Centrocercus urophasianus* and aerial integrated infrared imaging system (AIRIS) surveys (right column) at pseudo-leks with known numbers of ring-necked pheasant *Phasianus colchicus* or chukar *Alectoris chukar*. GBV (2015–2017) and AIRIS (2016–2017) surveys were conducted at multiple study sites within the Great Basin.

Table 2. Parameter estimates from sightability models fit to pseudo-lek data (AIRIS sightability model) collected from the air (ring-necked pheasant *Phasianus colchicus* and chukar *Alectoris chukar*) and real lek data (GBV sightability model) collected in the air and on the ground (greater sage-grouse *Centrocercus urophasianus*) at study areas in the Great Basin. Coefficients (β) are reported for different covariates with their associated median and 95% credible intervals (CI). Subscripts indicate covariates which included shrub cover ('shrub'), time since sunrise ('tsr'), terrain roughness ('rough'), and intercepts.

| Lek type | Parameter | Median β | 95% CI | P (β = 1)* |
|---|---|---|---|---|
| Pseudo-lek | $\beta_{intercept}$ | −0.060 | −0.253 to 0.135 | na |
| | $\beta_{shrub}$ | 0.004 | −0.010 to 0.017 | 0.435 |
| | $\beta_{tsr}$ | 0.000 | −0.002 to 0.001 | 0.488 |
| | $\beta_{rough}$ | −0.005 | −0.010 to 0.000 | 0.505 |
| Real lek | $\beta_{intercept}$ | −0.145 | −0.466 to 0.171 | na |
| | $\beta_{shrub}$ | −0.008 | −0.025 to −0.010 | 0.640 |
| | $\beta_{tsr}$ | 0.001 | −0.001 to 0.003 | 0.511 |
| | $\beta_{rough}$ | −0.003 | −0.010 to 0.003 | 0.502 |

* Indicator function representing whether β is included in the model using stochastic search variable selection (George and McCulloch 1996). Evidence was considered substantial for values >0.6, marginal for 0.5–0.6, and deficient for <0.5.



Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Jul 2020
Terms of Use: https://bioone.org/terms-of-use

attributed to decreased strutting activity. That study also observed that cloud cover and presence of females influenced sightability (Baumgardt et al. 2017). While we did not record cloud cover, given the absence of time since sunrise effects in AIRIS surveys, we suspect cloud cover is unlikely to influence the ability of the AIRIS to detect male sage-grouse but may be expected to influence sightability in ground counts. Weak evidence suggested that terrain roughness reduced sightability for AIRIS and GBV. This might be explained by fragmentation of field of view for both survey methods. Importantly, our assessment of using variables from relatively high-resolution GIS layers allows managers to use readily-available spatial data to adjust their estimates based on measurements associated with leks (e.g. shrub cover) remotely following lek monitoring, as opposed to conducting field measurements (Fremgen et al. 2016).

The overall lack of covariate effects on AIRIS sightability provide support for the hypothesis that most environmental predictors should not be as concerning in AIRIS surveys as in GBV surveys (Fremgen et al. 2016, Baumgardt et al. 2017). One explanation is that sightability associated with AIRIS is almost entirely comprised of probability of detection ($p_d$) and not probability of being available ($p_a$). This is because the $p_a$ is likely very close to 1.0 given that factors that influence $p_a$ for detection are not influential. In contrast, sightabilty in GBV surveys is likely driven by factors that influence $p_a$, such as visual obstruction by shrubs.

Several features of our study may have influenced our results and are important to consider for application of our methods to other systems. First, our proxy birds varied from sage-grouse in characteristics such as size and plumage. Mean sage-grouse mass across sexes at breeding (2323 g; Beck and Braun 1978) are substantially larger then female pheasant (954 g; Giudice and Ratti 2001) or chukar (680 g; Nagel 1945), suggesting the larger sage-grouse should be at least as detectable by infrared cameras as our proxy birds. Additionally, we did not observe a difference between pheasant and chukar which may imply that size did not have an effect. Furthermore, while the plumage coloration was different among all three species, infrared imagery does not use the visible spectrum so is unaffected by color, and the high-resolution color camera was only used to distinguish sex in the real lek surveys. Second, while sex was not distinguished in some of the surveys, and we found slight evidence of sightability differences among sexes, we accounted for the different survey types in the model and only report sightability estimates for males because male sage-grouse are the primary interest for wildlife agencies and land managers (WAFWA 2015). In using AIRIS for lek surveys, we stress the importance of separating males and females in the counts and having trained technicians capable of accurately identifying the sex of sage-grouse. Third, while our study assessed sightability (i.e. $p_a p_d$), it did not account for other components important for true population abundance estimates previously described by Nichols et al. (2009). One such component was the probability of sage-grouse being present on lek during the time of sampling ($p_p$) which can vary substantially throughout the season and among years (Wann et al. 2019). Additionally, not all lek locations are known (Sedinger 2007), which can lead to underestimation of population abundance, and sage-grouse leks that are easily accessible (e.g. near roads) are more likely to be surveyed which can introduce sampling bias (Applegate 2000, Anderson 2001, Walsh et al. 2004). Our study was not designed to address these issues, but they should be considered when assessing populations. We note, however, the potential application of AIRIS in locating unknown leks and surveying inaccessible leks, and we urge assessments of such uses.

Although AIRIS is a promising tool for lek surveys, this method has advantages and disadvantages compared to GBV surveys. First, AIRIS can be costly, currently averaging approximately $800 per hour (Gillette et al. 2015), whereas GBV methods to survey the same number of leks has approximately one third the cost. However, under time constraints, substantially more leks can be counted in a single morning using AIRIS than conventional methods of GBV surveys (Gillette et al. 2015). Second, flight time often must be scheduled well in advance because of limited availability of suitable aircraft and pilots, potentially constraining the use of AIRIS, whereas GBV surveys can be implemented more readily. Lastly, small aircraft surveys can carry increased safety risk for personnel (Sasse 2003), and weather conditions can additionally limit survey windows (Gillette et al. 2015). An economic assessment contrasting these survey techniques was beyond the scope of our study but see Gillette et al. (2015) for thorough cost-comparison between AIRIS and GBV.

In conclusion, our study provides information that can be used to improve inference to population sizes and trends and can help advance lek survey methods. While decisions of using AIRIS techniques over those of conventional GBV might be based on multiple factors including differences in costs, lek access, etc., likely a combination of both techniques will allow for most effective surveying for population assessments. We found GBV methods captured approximately 86% of males attending leks, while AIRIS increased the proportion of sage-grouse detected to about 93%, on average. Thus, for management application, our estimates may serve as general baseline adjustments on single lek counts for AIRIS and GBV (i.e. maximum counts) methods aimed at standardizing databases and accounting for detection uncertainty. Moreover, we provide adjustments in sightability for specific sites as a function of environmental covariates derived from widely available GIS layers. Lastly, *N*-mixture models using repeated within-morning ground counts from a single observer are useful to estimate sightability and lek abundance, which should be useful in accounting for spatial and temporal trends in observation error. These methods provide multiple options for managers to improve previously collected data and refine their monitoring programs to make better use of lek data for population studies.

*Acknowledgements* – We thank the numerous biologists and technicians that conducted lek counts and assisted in creating pseudo-leks. We are grateful to B. Brussee and K. Mauch (USGS) for assistance with pseudo-lek design, and we extend gratitude to J. Romero, C. Romero and Owyhee Air Research for conducting AIRIS surveys. Mason Valley Pheasant Club provided captively-raised pheasant. Any use of trade, firm or product names is for



Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Jul 2020
Terms of Use: https://bioone.org/terms-of-use

descriptive purposes only and does not imply endorsement by the U.S. Government.

*Funding* – Infrared and ground based lek counts were supported by funding from the Nevada Department of Wildlife, Bureau of Land Management, Idaho Natural Resource and Conservation Service Conservation Innovation Grant (no. 68-0211-15-099), Intermountain West Joint Venture Capacity Grant, and FSA-NRCS Conservation Effects Assessment Project interagency agreement (no. 68-7482-16-503). We appreciate the cooperation and support Idaho Department of Fish and Game, Idaho Master Naturalist Program, and Great Basin Bird Observatory.

*Permits* – Use of animals in this study was approved under Idaho State University Institutional Animal Care and Use Committee Protocol 770.

## References

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. – Wildl. Soc. Bull. 29: 1294–1297.

Applegate, R. D. 2000. Use and misuse of prairie chicken lek surveys. – Wildl. Soc. Bull. 28: 457–459.

Baumgardt, J. A. et al. 2017. Visibility bias for sage-grouse lek counts. – Wildl. Soc. Bull. 41: 461–470.

Beck, T. D. I. and Braun, C. E. 1978. Weights of Colorado sage grouse. – Condor 80: 241–243.

Beck, T. D. I. and Braun, C. E. 1980. The strutting ground count: variation, traditionalism, management needs. – Proc. W. Assoc. Fish Wildl. Agen. 60: 558–556.

Bivand, R. S. et al. 2013. Applied spatial data analysis with R, 2nd edn. – Springer.

Blomberg, E. J. et al. 2013. Annual male lek attendance influences count-based population indices of greater sage-grouse. – J. Wildl. Manage. 77: 1583–1592.

Brooks, S. P. and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. – J. Comput. Graph. Stat. 7: 434–455.

Coates, P. S. et al. 2016. Wildfire, climate and invasive grass interactions negatively impact an indicator species by reshaping sagebrush ecosystems. – Proc. Natl Acad. Sci. USA 113: 12745–12750.

Connelly, J. W. and Schroeder, M. A. 2007. Historical and current approaches to monitoring greater sage-grouse. – In: Reese, K. P. and Bowyer, R. T. (eds), Monitoring populations of sage-grouse. College of Natural Resources Experiment Station Bulletin 88. Univ. of Idaho, Moscow, USA, pp. 3–9.

Connelly, J. W. et al. 2003. Monitoring of greater sage-grouse habitats and populations. Station Bulletin 80. – College of Natural Resources Experiment Station, Univ. of Idaho, Moscow, Idaho, USA.

Fremgen, A. L. et al. 2016. Male greater sage-grouse detectability on leks. – J. Wildl. Manage. 80: 266–274.

Fremgen, A. L. et al. 2019. Weather conditions and date influence male sage grouse attendance rates at leks. – Ibis 161: 35–49.

Garton, E. O. et al. 2015. Greater sage-grouse population dynamics and probability of persistence. Final Report to Pew Charitable Trusts. – <http://www.pewtrusts.org/~/media/assets/2015/04/garton-et-al-2015-greater-sagegrouse-population-dynamics-and-persistence-31815.pdf>.

George, E. I. and McCulloch, R. E. 1996. Stochastic search variable selection. – In: Markov chain Monte Carlo in practice. Springer US.

Gillette, G. L. et al. 2013. Can reliable sage-grouse lek counts be obtained using aerial infrared technology? – J. Fish Wildl. Manage. 4: 386–394.

Gillette, G. L. et al. 2015. Evaluating the potential of aerial infrared as a lek count method for prairie grouse. – J. Fish Wildl. Manage. 6: 486–497.

Giudice, J. H. and Ratti, J. T. 2001. Ring-necked pheasant (*Phasianus colchicus*), ver. 2.0. – In: Rodewald, P. G. (ed.), The birds of North America. Cornell Lab of Ornithology, Ithica, NY, USA.

Green, A. W. et al. 2017. Investigating impacts of oil and gas development on greater sage-grouse. – J. Wildl. Manage. 81: 46–57.

Havens, K. J. and Sharp, E. J. 1998. Using thermal imagery in the aerial survey of animals. – Wildl. Soc. Bull. 26: 17–23.

Kéry, M. 2010. Introduction to WinBUGS for ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses. – Academic Press.

McCaffery, R. and Lukacs, P. M. 2016. A generalized integrated population model to estimate greater sage-grouse population dynamics. – Ecosphere 7: e01585.

Monroe, A. P. et al. 2016. Effect of lek count protocols on greater sage-grouse population trend estimates. – J. Wildl. Manage. 80: 667–678.

Monroe, A. P. et al. 2019. The importance of simulation assumptions when evaluating detectability in population models. – Ecosphere 10: e02791.

Nagel, W. O. 1945. Adaptability of the chukar partridge to Missouri conditions. – J. Wildl. Manage. 9: 207–216.

Nichols, J. D. 1991. Extensive monitoring programmes viewed as long-term population studies: the case of North American waterfowl. – Ibis 133: 89–98.

Nichols, J. D. et al. 2009. Inferences about landbird abundance from count data: recent advances and future directions. – In: Thomson, D. L. et al. (eds), Modeling demographic processes in marked populations. Springer, pp. 201–235.

Patterson, R. L. 1952. The sage grouse in Wyoming. – Wyoming Game and Fish Commission and Sage Books, Inc., Denver, CO, USA.

Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. – In: Hornik, K. et al. (eds), Proc. 3rd Int. workshop on distributed statistical computing (DSC 2003), March 2003, Vienna, Austria, pp. 1–10. <www.r-project.org/conferences/DSC-2003/Proceedings/Plummer.pdf>

Riley, S. J. et al. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. – Intermount. J. Sci. 5: 23–27.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. – Biometrics 60: 108–115.

Sasse, D. B. 2003. Job-related mortality of wildlife workers in the United States, 1937–2000. – Wildl. Soc. Bull. 31: 1015–1020.

Schroeder, M. A. et al. 2004. Distribution of sage-grouse in North America. – Condor 106: 363–376.

Sedinger, J. S. 2007. Improving understanding and assessment of greater sage-grouse populations. – Univ. Idaho Coll. Nat. Resour. Exp. Stat. Bull. 88: 43–56.

Shyvers, J. E. et al. 2018. Dual-frame lek surveys for estimating greater sage-grouse populations. – J. Wildl. Manage. 82: 1689–1700.

Smith, J. T. et al. 2016. Reducing cultivation risk for at-risk species: predicting outcomes of conservation easements for sage-grouse. – Biol. Conserv. 201: 10–19.

Su, Y. S. and Yajima, M. 2015. R2jags: using R to run 'JAGS'. – R package ver. 0.5-7. <https://CRAN.R-project.org/package=R2jags>.

Venables, W. N. and Ripley, B. P. 2002. Modern applied statistics with S, 4th edn. – Springer.

WAFWA. 2015. Greater sage-grouse population trends: an analysis of lek count databases 1965–2015. – Western Association of



Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Jul 2020
Terms of Use: https://bioone.org/terms-of-use

Fish and Wildlife Agencies, Cheyenne, WY. <www.wafwa.org/Documents%20and%20Settings/37/Site%20Documents/News/Lek%20Trend%20Analysis%20final%208-14-15.pdf>.
Walsh, D. P. et al. 2004. Evaluation of the lek-count index for greater sage-grouse. – Wildl. Soc. Bull. 32: 56–68.
Wann, G. T. et al. 2019. Assessing lek attendance of male greater sage-grouse using fine-resolution GPS data: implications for population monitoring of lek mating grouse. – Popul. Ecol. 61: 183–197.
Williams, B. K. et al. 2002. Analysis and management of animal populations, 1st edn. – Academic Press.
Xian, G. et al. 2015. Characterization of shrubland ecosystem components as continuous fields in the northwest United States. – Remote Sens. Environ. 168: 286–300.

Supplementary material (available online as Appendix wlb-00552 at <www.wildlifebiology.org/appendix/wlb-00552>). Appendix 1–3.



Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Jul 2020
Terms of Use: https://bioone.org/terms-of-use

Utah State University
DigitalCommons@USU

All Graduate Theses and Dissertations | Graduate Studies, School of

6-1-2013

# Common Raven Density and Greater Sage-Grouse Nesting Success in Southern Wyoming: Potential Conservation and Management Implications

Jonathan B. Dinkins
*Utah State University*

Recommended Citation
Dinkins, Jonathan B., "Common Raven Density and Greater Sage-Grouse Nesting Success in Southern Wyoming: Potential Conservation and Management Implications" (2013). *All Graduate Theses and Dissertations.* Paper 1700.
http://digitalcommons.usu.edu/etd/1700

This Dissertation is brought to you for free and open access by the Graduate Studies, School of at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact becky.thoms@usu.edu.

UtahStateUniversity
MERRILL-CAZIER LIBRARY

# COMMON RAVEN DENSITY AND GREATER SAGE-GROUSE NESTING SUCCESS IN SOUTHERN WYOMING: POTENTIAL CONSERVATION AND MANAGEMENT IMPLICATIONS

by

Jonathan B. Dinkins

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Wildlife Biology

Approved:

| | |
|---|---|
| Michael R. Conover<br>Co-Major Professor | Shandra Nicole Frey<br>Co-Major Professor |
| David N. Koons<br>Committee Member | Terry A. Messmer<br>Committee Member |
| Wayne A. Wurtsbaugh<br>Committee Member | Mark R. McLellan<br>Dean of Graduate Studies |

UTAH STATE UNIVERSITY
Logan, Utah

2013

# ABSTRACT

Common Raven Density and Greater Sage-Grouse Nesting Success in Southwest Wyoming: Potential Conservation and Management Implications

by

Jonathan B. Dinkins, Doctor of Philosophy

Utah State University, 2013

Major Professors: Dr. Michael R. Conover and Dr. Shandra Nicole Frey
Department: Wildland Resources

My research was focused on greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") nest-site selection, nest success, and hen survival in relation to avian predators. The trade-off between using habitat and avoiding predators is a common decision for prey species including sage-grouse. In Chapter 2, I compared avian predator densities at sage-grouse nest and brood locations to random locations. Sage-grouse were located where densities of small, medium, and large avian predators were 65–68% less than random locations.

The effects of anthropogenic and landscape features on habitat use of sage-grouse hens have not been evaluated relative to avian predator densities. In Chapter 3, I compared anthropogenic and landscape features and avian predator densities among sage-grouse locations (nest, early-brood, late-brood) and random locations. I found sage-grouse hens chose locations with lower avian predator densities compared to random locations, and selected locations farther away from anthropogenic and landscape features.

Depredation of sage-grouse nests can be an influential factor limiting their productivity. Predator removal has been simultaneously proposed and criticized as a potential mitigation measure for low reproductive rates of sage-grouse. In Chapter 4, I hypothesized that sage-grouse nest success would be greater in areas where Wildlife Services lowered common raven (*Corvus corax*: hereafter "raven") density. I found that Wildlife Services decreased raven density by 61% during 2008–2011 but I did not detect a direct improvement to sage-grouse nest success. However, sage-grouse nest success was 22% when ravens were detected within 550 m of a sage-grouse nest and 41% when no raven was detected within 550 m. In Chapter 5, I assessed interactive effects of corvid densities relative to anthropogenic and landscape features on sage-grouse nest success. I found that sage-grouse nest success was positively correlated with rugged habitat.

Survival of breeding-age birds is the most important demographic parameter driving sage-grouse abundance. In Chapter 6, I evaluated the effect of raptor densities, proximity to anthropogenic and landscape features, and hen behavior on survival of sage-grouse hens. I found that sage-grouse hen survival was negatively correlated with golden eagle (*Aquila chrysaetos*) density, proximity to anthropogenic and landscape features, and hen parental investment (nesting and brood-rearing).

(311 pages)

# PUBLIC ABSTRACT

Common Raven Density and Greater Sage-Grouse Nesting Success in Southwest Wyoming: Potential Conservation and Management Implications

by

Jonathan B. Dinkins, Doctor of Philosophy

Utah State University, 2013

Declines in the distribution and abundance of greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") in western North America over the past century have been severe. The goal of my research was to increase the understanding of factors influencing where sage-grouse hens placed their nests, how common ravens (*Corvus corax*: hereafter "raven") impacted sage-grouse nest success, and whether high raptor densities negatively impacted hen survival of sage-grouse. I compared raven and raptor densities at sage-grouse nest and brood locations to available habitat. I also assessed how sage-grouse positioned their nests and broods relative to proximity to man-made structures, forested and riparian habitat, and rough topography. While evaluating the effect of ravens on nest success of sage-grouse, I hypothesized that nest success of sage-grouse would be greater in areas where Wildlife Services lowered the density of ravens. Finally, I evaluated the effect of raptor densities, proximity to man-made structures and forested and riparian habitat, rough topography, and hen behavior on survival of sage-grouse hens.

Several studies on birds have shown that avoidance of predators and dangerous

habitat can have dramatic effects on habitat use by prey species. Sage-grouse hens chose locations with lower raven and raptor densities, selected locations farther away from man-made structures and forested habitat, and used locations that were flatter. Depredation of sage-grouse nests can be an influential factor limiting their populations. I found that Wildlife Services decreased raven density, but I did not detect a direct improvement to sage-grouse nest success. However, sage-grouse nest success was 22% when ravens were seen near a sage-grouse nest and 41% when no raven was seen near a sage-grouse nest. Survival of adult female sage-grouse has been demonstrated to be the most important aspect of a sage-grouse's life-cycle with respect to population growth. I found that sage-grouse hen survival was negatively related with golden eagle (*Aquila chrysaetos*) density when topography was flatter, proximity to man-made structures and forested habitat, and a hen's nesting and brood-rearing status (i.e., whether the hen was incubating eggs for caring for chicks).

# ACKNOWLEDGMENTS

Research funding was provided by the Anadarko Petroleum Corporation, Jack H. Berryman Institute, Lincoln County Predator Management Board, Predatory Animal District of Sweetwater County, School of Energy Resources at the University of Wyoming, South Central Wyoming Local Sage-Grouse Work Group, Southwest Wyoming Local Sage-Grouse Working Group, Uinta County Predator Management Board, Utah Agricultural Experiment Station, Wyoming Animal Damage Management Board, Wyoming Game and Fish Department, and Wyoming Land Conservation Initiative. I especially want to thank Dr. Michael Conover and Dr. Shandra Nicole Frey, my co-advisors, for providing encouragement, direction, feedback, and the opportunity to learn throughout my graduate work. I thank my committee members, Dr. David Koons, Dr. Terry Messmer, and Dr. Wayne Wurtsbaugh, for their insight and support. I particularly want to thank Dr. Jeff Beck, honorary committee member, and Chris Kirol from the University of Wyoming for deciding to collaborate with me on several research projects. I greatly appreciate the logistical support provided by Frank Blomquist, Tom Christiansen, Tom Clayson, Justin Caudill, Matt Holloran, Neil Hymas, Ron Lockwood, Erik Norelius, Dan Oles, Lara Oles, Jeff Short, Norris Tratnik, Andy Warren, Jim Wasseen, Mark Zornes, and many others. This project could not have been completed without many field technicians including George Bowman, Jessica Boyd, Valerie Burd, Suzie Etschmaier, Mike Evans, Cooper Farr, Benjamin Funk, Emily Haug, Hillary Jones, Jessica Julien, Kraig Kelson, Rebecca Laymon, Scott Mabray, Paul Miles, Claire Polfus, Chris Potter, Zach Primeau, Rachel Pyles, Jennylyn Redner, Steve Rowbottom, Nathan

Schmitz, Kurt Smith, Nicholas Schwertner, Robert Watson, Drew White, and Micah Yarbrough. Craig Acres, Jeff Hansen, Vern Howey, Rod Merrell, and Luke Spanbauer of Wildlife Services deserve special thanks for implementing raven control, providing data, and giving feedback on the project. I thank Ted Jensen for flying for radio-collared birds in the winter. Thank you to fellow graduate students Dylan Brown, Dr. Jennifer Borgo, Dr. Michael Guttery, Michael Haney, Rebecca Ruzicka, and Tony Roberts, and volunteers Jordan Linell and Darren Johnson. I also give special thanks to the cooperation of the many landowners throughout southwest and south-central Wyoming for allowing access to private lands including John Espy, Ed Feeley (Uinta Development Company), Niels Hansen, Joe Hickey, Mike Hickey, Charley Jaure, Truman Julian, Carl Larsen, Pat O'Toole, Kathryn Sanger, Bill Taliaferro, and Ray Weber. I especially want to thank my family (Courtney, AnnaBeth, and Bridger) for encouraging me through this journey. Without their understanding, love, support, and hugs, I would not have completed this degree. My wife, Courtney, took care of our kids and me in every way imaginable; I would not have anything without her. My daughter and son were always happy to greet me with hugs after long weeks in the field. My wife's parents, Debbie and Mike Pariera, encouraged me through my graduate education. I finally want to thank my parents, Jerry and Terry Dinkins, for their help throughout my life.

Jonathan B. Dinkins

CONTENTS

Page

ABSTRACT ..... ii

PUBLIC ABSTRACT ..... iv

ACKNOWLEDGMENTS ..... vi

LIST OF TABLES ..... xii

LIST OF FIGURES ..... xix

CHAPTER

1. INTRODUCTION AND LITERATURE REVIEW ..... 1

    RESEARCH OBJECTIVES ..... 6
    LITERATURE CITED ..... 9

2. GREATER SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*) SELECT NEST-SITES AND BROOD-SITES SELECTION AWAY FROM AVIAN PREDATORS ..... 17

    ABSTRACT ..... 17
    INTRODUCTION ..... 18
    METHODS ..... 22

        Study Areas ..... 22
        Sage-grouse Capture and Monitoring ..... 23
        Avian Predator Monitoring ..... 24
        Data Analyses ..... 26

    RESULTS ..... 31
    DISCUSSION ..... 32
    LITERATURE CITED ..... 38

3. GREATER SAGE-GROUSE NEST-SITE AND BROOD-SITE SELECTION IN RELATION TO AVIAN PREDATORS AND ANTHROPOGENIC AND LANDSCAPE FEATURES ..... 56

ABSTRACT....56
INTRODUCTION....58
METHODS....61

Study Areas....61
Sage-grouse Capture and Monitoring....63
Avian Predator Monitoring....64
Anthropogenic and Landscape Feature Variables....67
Data Analyses....69

RESULTS....73
DISCUSSION....76
LITERATURE CITED....80

4. EFFECTS OF COMMON RAVEN REMOVAL ON GREATER SAGE-GROUSE NESTING SUCCESS IN SOUTHERN WYOMING....100

ABSTRACT....100
INTRODUCTION....101
STUDY AREA....105
METHODS....107

Sage-grouse Capture and Monitoring....107
Raven Abundance Monitoring....108
Raven Removal....110
Vegetation Variables....112
Data Analyses....113

Raven density analysis....115
Sage-grouse nest success analysis....117
Spatial autocorrelation....119

RESULTS....120

Raven Density....120
Sage-grouse Nest Success....122

DISCUSSION....124
MANAGEMENT IMPLICATIONS....132
LITERATURE CITED....133

5. GREATER SAGE-GROUSE NEST SUCCESS IN RELATION TO

COVIDS, PROXIMITY TO ANTHROPOGENIC AND LANDSCAPE FEATURES, AND MICROHABITAT IN SOUTHERN WYOMING .....165

ABSTRACT.....165
INTRODUCTION .....166
STUDY AREA .....170
METHODS .....172

Sage-grouse Capture and Monitoring .....172
Corvid Variables .....173
Anthropogenic and Landscape Feature Variables .....176
Microhabitat Variables.....179
Data Analyses .....180

RESULTS .....184
DISCUSSION.....185
MANAGEMENT IMPLICATIONS .....191
LITERATURE CITED .....193

6. GREATER SAGE-GROUSE HEN SURVIVAL: EFFECTS OF RAPTORS, ANTHROPOGENIC AND LANDSCAPE FEATURES, AND HEN BEHAVIOR.....211

ABSTRACT.....211
INTRODUCTION .....212
STUDY AREA .....216
METHODS .....217

Sage-grouse Capture and Monitoring .....217
Sage-grouse Behavior Variables.....219
Raptor Variables .....220
Anthropogenic and Landscape Feature Variables .....222
Data Analyses .....225

RESULTS .....232
DISCUSSION.....236
MANAGEMENT IMPLICATIONS .....243
LITERATURE CITED .....244

7. CONCLUSIONS.....266

LITERATURE CITED .....275

APPENDIX.....281

CURRICULUM VITAE.....285

# LIST OF TABLES

Table Page

2-1 Summary of minimum, maximum, and mean distance (m) to nearest neighbor by location type (brood, nest, or random) reported by year. Data were collected in southwestern and south-central Wyoming, USA during 2008–2010.....47

2-2 Truncated distance (m), number of separate detections of avian predators, and number of avian predators seen from 963 point-count locations. Data were collected in southwestern and south-central, Wyoming, USA during 2008–2010. Program DISTANCE was used to estimate effective detection radii (EDR; m) and standard error (SE).....48

2-3 Model categories and variables considered in generalized linear mixed modeling with spatial eigenvector mapping to account for spatial autocorrelation. Models were developed to compare avian predator densities at locations used by sage-grouse (nest and brood locations) versus random. Data were collected at 963 point-count locations from eight 16-km and four 24-km study sites, 2008–2010, southwestern and south-central, Wyoming, USA.....49

2-4 Generalized linear mixed models comparing avian predator densities between locations used by sage-grouse (nest and brood sites) and random locations. Avian predator models with associated variables were compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). All compared models include parameters generated with spatial eigenvector mapping (SEVM) to correct for spatial autocorrelation. Data were collected at 963 point-count locations from eight 16-km and four 24-km study sites, 2008–2010, southwestern and south-central, Wyoming, USA.....51

2-5 Parameter estimates with *P* values and 95% confidence intervals (CI) from top $AIC_c$ selected generalized linear mixed model (GLMM) with spatial eigenvector mapping (SEVM). The top model compared log transformed avian predator densities between locations used by sage-grouse and random locations based on three size classes (small = magpie + kestrel, medium = raven + *Buteo* hawk + harrier, and large = Golden Eagle). SEVM was used to correct for spatial autocorrelation. Data were collected at 963 point-count locations from eight 16-km and four 24-km study sites, 2008–2010, southwestern and south-central, Wyoming, USA.....52

3-1 Multinomial logistic regression models comparing proximity to anthropogenic and landscape features among locations used by sage-grouse (nest, early-brood, and late-brood locations) and random locations. Anthropogenic and landscape features covariate sets were compared separately with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). The anthropogenic feature covariate set included distance decay functions to the nearest oil and gas structure (0.25-km decay function; $OGS_{0.25}$); power line (1.0-km decay function; $POW_{1.0}$); rural house (1.0-km decay function; $HOM_{1.0}$); major road (1.0-km decay function; $MRD_{1.0}$); gravel road (1.0-km decay function; $GRD_{1.0}$); closest oil and gas structure, communication tower, or house (0.25-km decay function; $WCH_{0.25}$); and closest oil and gas structure, communication tower, house, or power line (0.50-km decay function; $ANTH_{0.50}$). The landscape feature covariate set included distance decay functions to riparian (1.0-km decay function; $RIP_{1.0}$) and forested (0.25-km decay function; $TREE_{0.25}$) habitat and topographic ruggedness calculated at 0.54-km radius ($TRI_{0.54}$). Data were collected from 1,452 point count locations—340 sage-grouse nests, 331 sage-grouse early-brood locations, 121 sage-grouse late-brood locations, and 660 random locations—from eight study sites (16-km diameter) and four study sites (24-km diameter) in southern Wyoming, USA, 2008–2011.....89

3-2 Multinomial logistic regression models comparing avian predator densities and proximity to anthropogenic and landscape features among locations used by sage-grouse (nest, early-brood, and late-brood locations) and random locations. Combinations of singular and additive models created from the top $AIC_c$ selected avian predator model and anthropogenic and landscape feature models were compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). The avian predator model (avian) included log transformed small, medium, and large avian predator densities. The anthropogenic feature model (anthropogenic) included distance decay functions to nearest oil and gas structure (0.25-km decay function; $OGS_{0.25}$), power line (1.0-km decay function; $POW_{1.0}$), rural house (1.0-km decay function; $HOM_{1.0}$), and major road (1.0-km decay function; $MRD_{1.0}$). The landscape feature model (landscape) included a distance decay function to the nearest riparian habitat (1.0-km decay function; $RIP_{1.0}$) and topographic ruggedness calculated at 0.54-km radius ($TRI_{0.54}$). Data were collected from 1,452 point count locations—340 sage-grouse nests, 331 sage-grouse early-brood locations, 121 sage-grouse late-brood locations, and 660 random locations—from eight study sites (16-km diameter) and four study sites (24-km diameter) in southern Wyoming, USA, 2008–2011 .....92

3-3 Parameter estimates with 95% confidence intervals (CI) from top $AIC_c$ selected multinomial logistic regression. The top model compared log transformed avian predator densities (small, medium, and large avian predators); distance decay functions to nearest oil and gas structure (0.25-km decay function; $OGS_{0.25}$), power line (1.0-km decay function; $POW_{1.0}$), rural house (1.0-km decay function; $HOM_{1.0}$), major road (1.0-km decay function; $MRD_{1.0}$), and riparian habitat (1.0-km decay function; $RIP_{1.0}$); and topographic ruggedness calculated at 0.54-km radius ($TRI_{0.54}$) among locations used by sage-grouse (nest, early-brood, and late-brood locations) and random (reference level) locations. Data were collected from 1,452 point count locations—340 sage-grouse nests, 331 sage-grouse early-brood locations, 121 sage-grouse late-brood locations, and 660 random locations—from eight study sites (16-km diameter) and four study sites (24-km diameter) in southern Wyoming, USA, 2008–2011.....94

3-4 Parameter estimates with 95% confidence intervals (CI) from top $AIC_c$ selected multinomial logistic regression. The top model compared log transformed avian predator densities (small, medium, and large avian predators); distance decay functions to nearest oil and gas structure (0.25-km decay function; $OGS_{0.25}$), power line (1.0-km decay function; $POW_{1.0}$), rural house (1.0-km decay function; $HOM_{1.0}$), major road (1.0-km decay function; $MRD_{1.0}$), and riparian habitat (1.0-km decay function; $RIP_{1.0}$); and topographic ruggedness calculated at 0.54-km radius ($TRI_{0.54}$) among sage-grouse locations (nest, early-brood, and late-brood locations) by alternating the reference level. Data were collected from 1,452 point count locations—340 sage-grouse nests, 331 sage-grouse early-brood locations, 121 sage-grouse late-brood locations, and 660 random locations—from eight study sites (16-km diameter) and four study sites (24-km diameter) in southern Wyoming, USA, 2008–2011.....97

4-1 Summary of minimum, maximum, and mean distance (m) to nearest neighbor by location type (nest or random) reported by year. Data were collected in southwestern and south-central Wyoming, USA during 2008–2011.....143

4-2 Raven removal was conducted by USDA/APHIS Wildlife Services in southwest and south-central Wyoming during 2007–2011. Total number of removal events at raven foraging and roost sites around removal study sites. Number of removal events at landfills near removal study sites reported in parenthesis. Removal events quantified as the maximum number of events within 3 and 6 months prior to the last point count (sage-grouse nest or random) within a given year.....144

4-3 Means and standard errors (SE) of variables used to model USDA/APHIS/Wildlife Services (WS) raven removal. Data were collected from 407 and 593 point count locations in removal and non-removal study sites, respectively, in southwestern and south-central Wyoming, USA during 2008–2011 .....145

4-4 Means and standard errors (SE) of variables used to model sage-grouse nest daily survival rate (DSR). Data were collected from 121 and 220 sage-grouse nests at removal and non-removal study sites, respectively, in southwestern and south-central Wyoming, USA during 2008–2011 .....147

4-5 Multinomial-Poisson mixture models assessing the effect of year, year trend, and point count type (sage-grouse nest or random) on raven densities using 'distsamp' in R. Models were analyzed separately for removal and non-removal study sites and then compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). Standard distance sampling data were collected at 250 m discrete distance intervals during May to early-Aug. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA ($n$ = 121 and 220 nests and $n$ = 287and 373 random point count locations for removal and non-removal study sites, respectively) during 2008–2011 .....149

4-6 Parameter estimates of raven density with $P$-values and 95% confidence intervals (CI) from top $AIC_c$ selected multinomial-Poisson mixture models using 'distsamp' in R. Raven densities were modeled with random locations as the reference. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA ($n$ = 121 and 220 nests and $n$ = 287 and 373 random point count locations for removal and non-removal study sites, respectively) during May to early-Aug, 2008–2011.....151

4-7 Multinomial-Poisson mixture models assessing the effect of removal event variables on raven densities using 'distsamp' in R. Models were analyzed separately for removal and non-removal study sites and then compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). Only the top 10 models for removal and non-removal study sites were reported. Removal event variables used in modeling include removal distance, total removal events, removal events at landfills, and removal events other than at landfills. Removal events were analyzed at 7 km, 15 km, and 25 km. The temporal scale (3 or 6 months prior to nest fate or last point count at a random location) of each

model is denoted in parenthesis. Standard distance sampling data were collected at 250 m discrete distance intervals during May to early-Aug. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA ($n$ = 407 and $n$ = 593 for removal and non-removal study sites, respectively) during 2008–2011 .....153

4-8 Generalized linear models assessing daily survival rate (DSR) of sage-grouse nests using Program MARK. Variables used in modeling include sage-grouse age (AGE), year, year trend, study site type (removal or non-removal), raven occupancy (raven occupancy) and density (raven density) at the sage-grouse nest level, and raven density (landscape raven density) and site-specific change in density of ravens at the study site-level. Models were compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). Data were collected from 121 and 220 sage-grouse nests at removal and non-removal study sites, respectively. Sage-grouse were located in eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA during 2008–2011.....155

4-9 Generalized linear models assessing sage-grouse nest daily survival rate (DSR) using Program MARK. Variables used in modeling include sage-grouse nest level (raven occupancy) and site-specific change in raven density (site-level raven), max nest shrub height, average nest shrub canopy cover, Robel visual obstruction, total shrub cover, average total shrub height, grass cover, forb cover, bare ground cover, litter cover, and average perennial grass height. Models were compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). A fully saturated spatiotemporal model was included to assess goodness-of-fit; the fully saturated model included all microhabitat variables, year and study site type (removal and non-removal). Data were collected from 121 and 220 sage-grouse nests at removal and non-removal study sites, respectively. Sage-grouse were located in eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA during 2008–2011 .....157

5-1 Means and standard errors (SE) of variables used to model sage-grouse nest daily survival rate (DSR) for successful and unsuccessful nests. Data were collected from 341 sage-grouse nests at eight 16-km and four 24-km diameter study sites in southwestern and south-central Wyoming, USA during 2008–2011 .....203

5-2 Generalized linear models assessing sage-grouse nest daily survival rate using Program MARK. Variables used in modeling included sage-grouse

nest-level occupancy and site-specific change in corvid densities (study site-level), anthropogenic and landscape features, and microhabitat. Models were compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). A fully saturated spatiotemporal model was included to assess goodness-of-fit; the saturated model included year; study site type; distance to town, landfill, energy well, communication tower, house, power line, all road, and tree stand; topographic ruggedness at 1 km radius ($TRI_{1.0}$) variable; distance to riparian habitat; and all microhabitat variables.....207

5-3 Parameter estimates with 95% confidence intervals (CI) from the top $AIC_c$ selected generalized linear model (see Table 5-2) assessing sage-grouse nest daily survival rate (DSR) using Program MARK. Sage-grouse nest-level raven (raven occupancy) was recorded as raven occupancy during last nest check with sage-grouse on her nest, and topographic ruggedness index at 1 km radius ($TRI_{1.0}$) was quantified as the difference in elevation among adjacent pixels of a digital elevation map.....209

6-1 Descriptions, means, and standard errors (SE) of variables used to model sage-grouse survival with the Anderson-Gill formulation of the Cox proportional hazard model; means and SE were stratified by sage-grouse that survived the duration of the study and those that did not. Variables include raptor densities, anthropogenic features, and landscape features from 3,523 summer (1 May through 31 August) survival intervals. Sage-grouse behavior variables (average weekly movement and average flock size) were from non-reproductive 2,304 sage-grouse locations. Data were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011.....254

6-2 Model comparison of Cox proportional hazard models from the parental investment and anti-predator strategy analyses. Models assessed the effects of 4 covariate sets including site-specific change in raptor densities, anthropogenic features, landscape features, and sage-grouse behavior on sage-grouse hen survival. Models were compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). Data were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA. A total of 427 sage-grouse hens were monitored during 2008–2011.....258

6-3 Parameter estimates of sage-grouse survival (as a hazard ratio—depicting risk of mortality) from top $AIC_c$ selected Cox proportional hazard model for parental investment analysis with *P*-values and 95% confidence

intervals. Data were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011. A total of 427 sage-grouse hens were monitored during 2008–2011.....260

6-4 Parameter estimates of sage-grouse survival (as a hazard ratio—depicting risk of mortality) from top 2 $AIC_c$ selected Cox proportional hazard models for anti-predation strategy analysis with *P*-values and 95% confidence intervals. Data were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011. A total of 427 sage-grouse hens were monitored during 2008–2011.....261

# LIST OF FIGURES

Figure — Page

2-1 Location map of southern Wyoming depicting eight 16-km diameter and four 24-km diameter study sites, 2008–2010, southwestern and south-central, Wyoming, USA. Magnified sections correspond on left to southwest and on right to south-central Wyoming .....53

2-2 Spline correlograms of Pearson residuals from the best $\Delta AIC_c$ ranked generalized linear mixed model with 95% point-wise bootstrapped confidence intervals (A) without spatial eigenvector mapping (SEVM) and (B) with SEVM. Spatial autocorrelation between model residuals was assessed with Moran's similarity index from 0 to 30 (km) .....54

2-3 Comparison of raven, magpie, Golden Eagle, *Buteo* hawk, harrier, and kestrel densities (per $km^2$) among sage-grouse nests, sage-grouse brood locations, and random locations. Data from 3,006 point-count surveys during 2008-2010 at 963 total point-count locations—218 sage-grouse nest locations, 249 sage-grouse brood locations (with 83 separate broods), and 496 random locations—in southwestern and south-central, Wyoming, USA. Densities were generated using radial point-count surveys and DISTANCE at sage-grouse nests, sage-grouse brood locations, and random locations. Error bars are 95% confidence intervals .....55

4-1 Location map of southern Wyoming depicting eight 16-km diameter and four 24-km diameter study sites, southwestern and south-central, Wyoming, USA, 2008–2011. Magnified sections correspond on left to southwest and on right to south-central Wyoming. Map includes locations of 2008–2011 sage-grouse nests, random locations, landfills, towns, and major roads.....159

4-2 Raven density (no./$km^2$) estimates by year, 2008–2011, from the top $AIC_c$ selected multinomial-Poisson mixture models for removal and non-removal study sites. Estimates of raven density were modeled from 287 and 373 random locations in removal and non-removal study sites, respectively. Error bars indicate 95% confidence intervals. Data were collected from four 16-km and one 24-km removal study sites and four 16-km and three 24-km non-removal study sites in southwestern and south-central, Wyoming, USA.....160

4-3 Predictions of raven density (no./$km^2$) from the top $AIC_c$ selected

multinomial-Poisson mixture model of USDA/APHIS/Wildlife Services (WS) removal events at removal study sites with 95% confidence intervals. Predicted effects of the number of landfill (A; within 25 km) and non-landfill (B; within 15 km) based removal events conducted by WS and the effect of distance to nearest removal event (C). All variables calculated within six months of the fate of a sage-grouse nest or last recorded point count at a random location. Data were collected from four 16-km and one 24-km study sites in southwestern and south-central, Wyoming, USA ($n$ = 121 sage-grouse nests and $n$ = 287 random locations), 2008–2011 ..... 161

4-4 Predictions of raven density (no./km$^2$) from the top AIC$_c$ selected multinomial-Poisson mixture model of USDA/APHIS/Wildlife Services (WS) removal events at non-removal study sites with 95% confidence intervals. Predicted effects of the number of removal events conducted by WS between 15 and 25 km and within six months of the fate of a sage-grouse nest or last recorded point count at a random location. Data were collected from four 16-km and three 24-km study sites in southwestern and south-central, Wyoming, USA ($n$ = 220 sage-grouse nests and $n$ = 373 random locations), 2008–2011 ..... 162

4-5 Apparent nest success (%) of 341 sage-grouse nests found in removal and non-removal study sites. Apparent nest success was calculated as the number of hatched nests divided by the total number of nests found. Removal study sites had 23, 28, 28, and 42 nests in 2008–2011, respectively. Non-removal study sites had 41, 57, 55, and 67 nests found during 2008–2011, respectively. Data were collected from four 16-km and one 24-km removal study sites and four 16-km and three 24-km non-removal study sites in southwestern and south-central, Wyoming, USA ..... 163

4-6 Predictions of daily survival rate (DSR) of sage-grouse nests from the top AIC$_c$ selected generalized linear model using Program MARK at removal and non-removal study sites with 95% confidence intervals. Predicted effects of site-specific change in raven density (no./km$^2$) at a study site relative to 2008 (A) and average perennial grass height within 5 m (B) on sage-grouse nest DSR. Raven variables calculated within EDR (550 m) of 'distsamp'. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA ($n$ = 341 sage-grouse nests), 2008–2011 ..... 164

5-1 Predictions of daily survival rate (DSR) of sage-grouse nests from the top AIC$_c$ selected generalized linear model using Program MARK with 95% confidence intervals. Predicted effects of topographic ruggedness

calculated at 1 km radius ($TRI_{1.0}$) on DSR of sage-grouse nests. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA (*n* = 341 sage-grouse nests), 2008–2011 .....210

6-1 Predicted effect with 95% confidence intervals of distance to forested habitat (deciduous and conifer) on sage-grouse hen survival from the top $AIC_c$ selected Cox proportional hazard model from the anti-predation strategy analysis. Predicted effects displayed as the risk of mortality with the y-axis units plotted as exp(coefficient values). All other parameters were held at the mean value. Partial residuals were overlaid on predicted effect plots as solid points. Data from 427 sage-grouse hens were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011 .....263

6-2 Interactive effect of site-specific change in golden eagle density and topographic ruggedness index at 0.27-km radius ($TRI_{0.27}$) on sage-grouse hen survival (as a hazard ratio—depicting risk of mortality) from the parental investment analysis. Predicted effects from the top $AIC_c$ selected Cox proportional hazard model displayed as the risk of mortality with the y-axis units plotted as exp(coefficient values). All other parameters were held at their mean value. Solid points represent observed data overlaid on the predicted surface. Data from 427 sage-grouse hens were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011 .....264

6-3 Predicted effect of average flock size of sage-grouse hens with 95% confidence intervals from the top $AIC_c$ selected Cox proportional hazard model (from the anti-predation strategy analysis) of sage-grouse hen survival. The model included a quadratic of average flock size and an interaction between flock size and sage-grouse age (adult or yearling). Predicted effects of the average flock size of sage-grouse during the summer for adult (A) and yearling (B) hens. Predicted effects displayed as risk of mortality with the y-axis units plotted as exp(coefficient values). Partial residuals were overlaid on predicted effect plots. Data from 427 sage-grouse hens were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011 .....265

# CHAPTER 1

# INTRODUCTION AND LITERATURE REVIEW

Greater sage-grouse (*Centrocercus urophasianus*: hereafter "sage-grouse") distribution and abundance in western North America has declined over the last century (Connelly et al. 2004, Schroeder et al. 2004, Connelly et al. 2011). In 2000, sage-grouse inhabited approximately 56% of their range compared to pre-European settlement (Schroeder et al. 2004), and abundance has declined an average of 2% annually from 1965–2003 (Connelly et al. 2004). This decline led the U.S. Fish and Wildlife Service (2010) to conclude that sage-grouse are warranted for protection under the Endangered Species Act of 1973, but the listing was precluded because other species were at greater threat of extinction. Many factors have been attributed to this decline including reduction of quality sagebrush habitat (human development, drought, and wildfire) and factors affecting survival (i.e., predation, West Nile virus, and hunting; Braun 1998, Connelly et al. 2004, Schroeder et al. 2004, Connelly et al. 2011).

Sage-grouse are highly associated with sagebrush (*Artemisia* spp.) ecosystems, because they rely on sagebrush for food during most of the year, nesting, shelter, and escape cover (Connelly et al. 2004, Schroeder et al. 2004, Connelly et al. 2011). Loss, degradation, and fragmentation of sagebrush habitats have been detrimental to sage-grouse populations. Several studies have suggested that quantity and condition of breeding habitat is the most important factor that dictates the productivity of sage-grouse, because given adequate habitat, sage-grouse would be buffered from other threats

(Connelly et al. 1994, Braun 1998, Schroeder and Baydack 2001, Connelly et al. 2011). However, there are increasing levels of human development in sage-grouse habitat (Connelly et al. 2004, Leu et al. 2008, Doherty et al. 2010, Kirol 2012). One of the consequences of habitat modification and fragmentation associated with human development in native grouse habitats may be increased predation rates (Schroeder and Baydack 2001).

A diverse array of generalist predators have increased in distribution and abundance in sagebrush steppe habitats throughout the western United States by capitalizing on fragmented habitats and human provided resources. For example, densities of common ravens (*Corvus corax*; hereafter "ravens") have increased in Wyoming and throughout the historic range of sage-grouse during the last century, (Andrén 1992, Engel and Young 1992, Boarman et al. 1995, Sauer et al. 2011). Densities of generalist predators are not limited by the density of a particular species of prey (Schroeder and Baydack 2001, Evans 2004, Manzer and Hannon 2005, Coates 2007), and breeding success and survival of ground-nesting birds has been shown to be suppressed by generalist predators, such as ravens (Evans 2004, Manzer and Hannon 2005, Baxter et al. 2007, Bui et al. 2010, Coates and Delehanty 2010).

Trade-offs between using habitat and avoiding predators are common decisions for prey species. Prey species including sage-grouse may minimize risk of predation by avoiding predators, which can be achieved by using habitat with lower abundance of predators and selecting habitat with lower risk of predation (Lima 1998, Verdolin 2006, Cresswell 2008; see also Chapter 2). Thus, sage-grouse may not select optimal nesting or

brood-rearing habitat when the risk of predation is high.

Sage-grouse select nest and brood sites at various scales. At the landscape scale, sage-grouse may avoid areas where there are high densities of avian predators—specifically, American kestrels (*Falco sparverius*; hereafter "kestrels"), *Buteo* hawks, black-billed magpies (*Pica hudsonia*; hereafter "magpies"), golden eagles (*Aquila chrysaetos*), northern harriers (*Circus cyaneus*; hereafter "harriers"), and ravens (Manzer and Hannon 2005, Mezquida et al. 2006, Dinkins et al. 2012). At the microhabitat scale (habitat directly surrounding a sage-grouse location—typically measured <25 m from a sage-grouse nest or brood), sage-grouse predominately choose nest sites in vegetation cover (Connelly et al. 2004). Several studies have reported that sage-grouse select nest sites based on a preference for different microhabitat characteristics, such as sagebrush density (Wallestad and Pyrah 1974, Connelly et al. 2003), sagebrush cover (Doherty et al. 2010, Kirol et al. 2012), shrub height (Gregg et al. 1994), grass height (Gregg et al. 1994, Holloran et al. 2005, Kirol et al. 2012), and grass cover (Kaczor 2008, Kirol et al. 2012). Variability in reported microhabitat characteristic preferences of sage-grouse, with reference to nest and brood site selection, may indicate local differences in available microhabitat. Differences in available microhabitat among studies suggest that cover, in general, is important regardless of the type of vegetation cover that is available (e.g. sagebrush density, shrub height, or grass height). Alternatively, sage-grouse living in areas with different predator compositions may prefer different types of vegetation cover (Connelly et al. 2004, Coates and Delehanty 2010). Thus, the microhabitat characteristics upon which sage-grouse base their selection of nest-sites and the success of those nests

may be a result of available vegetation and predator composition. For example, Coates and Delehanty (2010) found that microhabitat at sage-grouse nest-sites had a variable impact on nest depredation depending on whether a raven or a badger (*Taxidea taxus*) depredated the nest (greater cover protected from ravens, but exposed sage-grouse to greater badger depredation and vice versa).

Although reduction of quality sagebrush habitat is the driving factor that reduced populations of sage-grouse, nest success and hen survival are widely thought to be potential limiting factors for bird populations including sage-grouse (Connelly et al. 2004). Johnson and Braun (1999) and Taylor et al. (2012) found that adult hen survival was the most influential demographic parameter on sage-grouse population growth. Chick survival then nest success were the next most important factors affecting population growth for sage-grouse following adult hen survival. These conclusions may be related to the fact that sage-grouse are relatively long-lived ground-nesting birds with low productivity (Connelly et al. 2000b, Holloran et al. 2005, Connelly et al. 2011). Thus, many aspects of recruiting new individuals into a population are connected to sage-grouse hens (i.e., nest success and chick survival).

Local predator densities can affect habitat selection, nest success, survival, and parental behavior of ground-nesting birds such as prairie grouse species (Schroeder and Baydack 2001, Manzer and Hannon 2005, Coates and Delehanty 2010), farmland birds (Evans 2004), ducks (Sargeant et al. 1995), shorebirds (Smith et al. 2007), and passerines (Norrdahl and Korpimäki 1998, Roos and Pärt 2004, Thomson et al. 2006, Chalfoun and Martin 2009).

Unlike other population limiting factors (e.g., habitat condition, weather, and drought), reduction of predator numbers may be more feasible for wildlife management agencies to reduce predation rates (Cote and Sutherland 1997). For example, raven depredation of sage-grouse nests has been implicated as a potential factor limiting sage-grouse productivity in fragmented habitats (Batterson and Morse 1948, Willis et al. 1993, Gregg et al. 1994, Schroeder and Baydack 2001, Coates et al. 2008, Bui et al. 2010, Coates and Delehanty 2010). Predator removal has been simultaneously proposed and criticized as a potential mitigation measure for low reproductive rates of sage-grouse, specifically nest success. However, there are no predators that specialize on sage-grouse during any life history stage (egg, chick, or adult), and sage-grouse have relatively high nest and adult survival rates compared to other gallinaceous birds (Connelly et al. 2011). No predator management study has provided evidence that lethal removal of predators would benefit sage-grouse on a large scale (Hagen 2011). Thus, Hagen (2011) suggested that predation was not limiting sage-grouse populations, and predator removal may only serve to provide a short-term release of predation rates in fragmented habitats and areas with human-subsidized predator populations.

Survival of breeding-age birds in relation to predator communities has been a focus of sage-grouse research and conservation. Survival and nest success related to predator communities were not likely to have been a problem during pre-European settlement because sage-grouse co-evolved with the predator communities present in sagebrush ecosystems (Schroeder et al. 1999, Schroeder et al. 2001). However, areas of habitat fragmentation and areas with human-subsidized predator populations have

drastically increased in the recent past (Leu et al. 2008). For example, red fox (*Vulpes vulpes*), common raccoon (*Procyon lotor*), and raven have increased in abundance in sage-grouse habitat, especially near human activities (Connelly et al. 2000b, Baxter et al. 2007, Hagen 2011, Sauer et al. 2011). In addition, raptors and corvids use anthropogenic structures as perches and nesting structure (Lammers and Collopy 2007, Prather and Messmer 2010, Slater and Smith 2010).

Sage-grouse hen survival has been related to habitat variables, such as topographic ruggedness and grass, forb, and sagebrush cover, by several studies and reviews (Connelly et al. 1994, Holloran 1999, Schroeder and Baydack 2001, Zablan et al. 2003, Moynahan et al. 2006, Kirol 2012). However, Dahlgren (2009) reported high sage-grouse hen survival rates (0.78 in a high survival year to 0.42 in a low survival year) with relatively lower quality habitat on Parker Mountain, Utah. Dahlgren (2006) described large contiguous sagebrush habitat and minimal vertical structure from human development at Parker Mountain, which may contribute to higher hen survival rates due to a lack of potential roost and nest sites for avian predators. Sage-grouse hens have been known to have high annual survival (48–78% in Wyoming; Holloran 2005, Connelly et al. 2011) with the breeding season having the lowest seasonal survival rate for sage-grouse hens (Connelly et al. 2000a).

## RESEARCH OBJECTIVES

Although sage-grouse biology has been well studied, there has been little research regarding the effects of avian predator abundance on habitat selection of adult sage-

grouse hens, nest success, and survival. My research provides information relative to the potential influences of avian predators on sage-grouse habitat selection, nest success, and survival of sage-grouse hens in relation to anthropogenic (oil and gas infrastructure, roads, power lines) and landscape (forested and riparian habitat and topographic ruggedness) features, and microhabitat.

In Chapter 2, I compared avian predator densities at sage-grouse nests and brood locations to available habitat. This comparison allowed me to assess the ability of sage-grouse to use locations with fewer avian predators during nesting and early brood rearing. In accordance with the predator-avoidance hypothesis, I hypothesized that at the landscape scale, sage-grouse would avoid nesting or raising broods in areas with high densities of avian predators, specifically kestrels, magpies, golden eagles, hawks (*Buteo* spp.), harriers, and ravens. Further, I hypothesized that adult survival would take precedence over nest or brood survival, and that sage-grouse habitat use would be shaped primarily by avoidance of avian predators that were a threat to adult hen survival, and secondarily by avoidance of avian predators that were a threat only to nests and broods. The effects of anthropogenic and landscape features on habitat selection of sage-grouse hens have not been evaluated in the context of avian predator abundance. In Chapter 3, I compared anthropogenic and landscape features and densities of avian predators among sage-grouse locations (nest, early-brood, late-brood) and available habitat.

Subsidized raven populations of increasing size have been anecdotally documented in southwest and south-central Wyoming associated with human activities such as livestock and natural gas development (R. J. Merrell, United States Department

of Agriculture Animal and Plant Health Inspection Service Wildlife Services [WS], personal communication), and raven abundance has increased in Wyoming during the past decade, 2001–2010 (Sauer et al. 2011). Raven control (lethal removal) efforts of varying intensity have been carried out by WS in Carbon, Lincoln, Sweetwater, and Uinta counties in Wyoming, 2007–2011 for the protection of livestock, which provided a unique opportunity to study the potential effects of raven removal on sage-grouse nest success. In Chapter 4, I hypothesized that sage-grouse nest success would be greater in areas where WS lowered the abundance of common ravens (*Corvus corax*: hereafter "raven"). To test this hypothesis, I assessed the change in density of ravens and sage-grouse nest success in areas associated with WS raven removal efforts and areas farther away during 2008–2011. As secondary objectives, I evaluated differences between yearling and adult sage-grouse nest success, and the effect of ravens on nest success at the sage-grouse nest level in relation to microhabitat. In Chapter 5, I tested the hypothesis that the negative effects of corvids would be amplified in areas closer to potential perches and areas with subsidized food resources (anthropogenic and landscape features).

Although avian predators have been reported to prey on sage-grouse, densities of avian predators have not been correlated with sage-grouse survival rates. For example, golden eagles have been implicated as the major sage-grouse predators (Willis et al. 1993, Connelly et al. 2000, Danvir 2002, Dahlgren 2006, Mezquida et al. 2006), and high golden eagle abundance has been suggested to decrease sage-grouse survival (Danvir 2002). However, no sage-grouse study has directly related site-specific densities of avian predators, including golden eagles, to sage-grouse hen survival. In Chapter 6, I evaluated

the effect of raptor densities, proximity to anthropogenic and landscape features, and hen behavior on survival of sage-grouse hens.

The chapters of my dissertation are written as stand-alone manuscripts with Chapters 2 and 3 in the format of the Auk and Chapters 1 and 4–7 in the format of the Journal of Wildlife Management.

**LITERATURE CITED**

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794–804.

Batterson, W. M., and W. B. Morse. 1948. Oregon sage grouse. Oregon Game Commission Fauna Service, Portland, USA.

Baxter, R. J., K. D. Bunnell, J. T. Flinders, and D. L. Mitchell. 2007. Impacts of predation on greater sage-grouse in Strawberry Valley, Utah. Transactions of the North American Wildlife and Natural Resources Conference 72:258–269.

Boarman, W. I., R. J. Camp, M. Hagan, and W. Deal. 1995. Raven abundance at anthropogenic resources in the western Mojave Desert, California. Report to Edwards Air Force Base, California. National Biological Service, Riverside, USA.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139–156.

Bui, T. D., J. M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to

land use in western Wyoming: implications for greater sage-grouse reproductive success. Condor 112:65−78.

Chalfoun, A. D., and T. E. Martin. 2009. Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. Journal of Animal Ecology 78:497−503.

Coates, P. S. 2007. Greater sage-grouse (*Centrocercus urophasianus*) nest predation and incubation behavior. Dissertation, Idaho State University, Pocatello, USA.

Coates, P. S., J. W. Connelly, and D. J. Delehanty. 2008. Predators of greater sage-grouse nests identified by video monitoring. Journal of Field Ornithology 79:421−428.

Coates, P. S., and D. J. Delehanty. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. Journal of Wildlife Management. 74:240–248.

Connelly, J. W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000. Effects of predation and hunting on adult sage grouse (*Centrocercus urophasianus*) in Idaho. Wildlife Biology 6:227–232.

Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53–67 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, California, USA.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of

Fish and Wildlife Agencies. Unpublished Report, Cheyenne, Wyoming, USA.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station Bulletin 80, University of Idaho, Moscow, USA.

Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage grouse ecology. Idaho Department of Fish and Game Job Completion Report W-160-R-19, Boise, Idaho, USA.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000b. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Cote, I. M., and W. J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. Conservation Biology 11:395–405.

Cresswell, W. 2008. Non-lethal effects of predation in birds. Ibis 150:3−17.

Dahlgren, D. K. 2006. Greater sage-grouse ecology and response to experimental management of mountain big sagebrush on Parker Mountain, Utah. Thesis, Utah State University, Logan, USA.

Dahlgren, D. K. 2009. Greater sage-grouse ecology, chick survival, and population dynamics, Parker Mountain, Utah. Dissertation, Utah State University, Logan, USA.

Danvir, R. E. 2002. Sage grouse ecology and management in northern Utah sagebrush-steppe. Deseret Land and Livestock Wildlife Research Report, Deseret Land and

Livestock Ranch and the Utah Foundation for Quality Resource Management, Woodruff, Utah, USA.

Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

Engel, K. A., and L. S. Young. 1992. Daily and seasonal activity patterns of common ravens in southwestern Idaho. Wilson Bulletin 104:462–471.

Evans, K. L. 2004. A review of the potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.

Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetational cover and predation of sage-grouse nests in Oregon. Journal of Wildlife Management 58: 162–166.

Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effects. Pages 95–100 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Holloran, M. J. 1999. Sage-grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. Thesis, University of Wyoming, Laramie, USA.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson.

2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638–649.

Johnson, K. H., and C. E. Braun. 1999. Viability and conservation of an exploited sage-grouse population. Conservation Biology 13:77–84.

Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection of greater sage-grouse in northwestern South Dakota. Thesis, South Dakota State University, Brookings, USA.

Kirol, C. P. 2012. Quantifying habitat importance for greater sage-grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. Thesis, University of Wyoming, Laramie, USA.

Kirol, C. P., J. L. Beck, J. B. Dinkins, and M. R. Conover. 2012. Greater sage-grouse nesting and brood-rearing microhabitat selection in xeric big sagebrush. Condor 114:75–89.

Lammers, W. M., and M. W. Collopy. 2007. Effectiveness of avian predator perch deterrents on electric transmission lines. Journal of Wildlife Management 71:2752–2758.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the West: a large scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. BioScience 48:25–34.

Manzer, D. L., and S. J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. Journal of Wildlife Management 69:110–123.

Mezquida, E. T., S. J. Slater, and C. W. Benkman. 2006. Sage-grouse and indirect interactions: potential implication of coyote control on sage-grouse populations. Condor 108:747–759.

Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2006. Factors contributing to process variance in annual survival of female greater sage-grouse in Montana. Ecological Applications 16:1529–1538.

Norrdahl, K., and E. Korpimäki. 1998. Fear in farmlands: how much does predator avoidance affect bird community structure? Journal of Avian Biology 29:79–85.

Prather, P. R., and T. A. Messmer. 2010. Raptor and corvid response to power distribution line perch deterrents in Utah. Journal of Wildlife Management 74:796–800.

Roos, S., and T. Pärt. 2004. Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). Journal of Animal Ecology 73:117–127.

Sargeant, A. B., M. A. Sovada, and T. L. Shaffer. 1995. Seasonal predator removal relative to hatch rate of duck nests in Waterfowl Production Areas. Wildlife Society Bulletin 23:507–513.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski Jr., and W. A. Link. 2011. The North American breeding bird survey, results and analysis 1966–2010. Version 12.07.2011. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M.

McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage grouse in North America. Condor 106:363–376.

Schroeder, M. A., and R. K. Baydack. 2001. Predation and the management of prairie grouse. Wildlife Society Bulletin 29:24–32.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Birds of North America. Philadelphia, Pennsylvania, USA.

Slater, S. J., and J. P. Smith. 2010. Effectiveness of raptor perch deterrents on an electrical transmission line in southwestern Wyoming. Journal of Wildlife Management 74:1080–1088.

Smith, P. A., H. G. Gilchrist, and J. N. M. Smith. 2007. Effects of nest habitat, food, and parental behavior on shorebird nest success. Condor 109:15–31

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336−347.

Thomson, R. L., J. T. Forsman, F. Sardà -Palomera, and M. Mönkkönen. 2006. Fear factor: prey habitat selection and its consequences in a predation risk landscape. Ecography 29:507–514.

U. S. Fish and Wildlife Service. 2010. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Federal Register 75:13909–14014.

Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457–464.

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

Willis, M. J., G. P. Kiester, Jr., D. A. Immel, D. M. Jones, R. M. Powell, and K. R. Durbin. 1993. Sage grouse in Oregon. Oregon Department of Fish and Wildlife, Wildlife Research Report No.15. Portland, USA.

Zablan, M. A., C. E. Braun, and G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal of Wildlife Management 67:144–154.

# CHAPTER 2

# GREATER SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*) SELECT NEST-SITES AND BROOD-SITES AWAY FROM AVIAN PREDATORS*

ABSTRACT.–Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") distribution and abundance in western North America has declined over the last century. Depredation of sage-grouse nests and predation of chicks can be two of the most influential factors limiting their productivity. Prey species utilize anti-predation behaviors, such as predator avoidance, to reduce the risk of predation. Birds in general balance the dual necessity of selecting cover to hide from visual and olfactory predators to enhance prospects of survival and reproductive success, which may also be achieved by selecting habitat with relatively fewer predators. I compared avian predator densities at sage-grouse nests and brood locations to random locations within available sage-grouse habitat in Wyoming. This comparison allowed me to assess the ability of sage-grouse to avoid avian predators during nesting and early brood-rearing. During 2008–2010, I conducted 10-min point-count surveys at 218 sage-grouse nests, 249 sage-grouse brood locations from 83 sage-grouse broods, and 496 random locations. I found that random locations had higher densities of avian predators compared to sage-grouse nest and brood locations. Sage-grouse nested in areas where there were lower densities of Common Ravens (*Corvus corax*), Black-billed Magpies (*Pica hudsonia*), Golden Eagles (*Aquila chrysaetos*), and *Buteo* hawks compared to random locations. Additionally, sage-grouse selected brood-rearing locations that had lower densities of the same avian

*Jonathan B. Dinkins, Michael R. Conover, Christopher P. Kirol, and Jeffrey L. Beck

predators as during nesting, plus American Kestrels (*Falco sparverius*) compared to random. By selecting nest and brood-rearing locations with lower avian predator densities, sage-grouse may reduce the risk of nest depredation and predation on eggs, chicks, and hens.

## INTRODUCTION

FOOD AND RISK of predation are two factors widely thought to have important influences on the choice of breeding habitat by birds and other animals, and actual habitat choice has often been described as a trade-off between access to resources and risk of predation (Verdolin 2006). Thus, avian species may not select optimal nesting or brood-rearing habitat for foraging when the risk of predation is high. Prey species utilize anti-predation behaviors, such as predator avoidance (predator-avoidance hypothesis), to reduce the risk of predation (Cresswell 2008, and references therein). Local predator densities can affect the productivity, parental behavior, and nest-site selection of ground-nesting birds such as prairie grouse species (Schroeder and Baydack 2001, Manzer and Hannon 2005, Coates and Delehanty 2010), farmland birds (Evans 2004), ducks (Sargeant et al. 1995), shorebirds (Smith et al. 2007), and passerines (Norrdahl and Korpimäki 1998, Roos and Pärt 2004, Thomson et al. 2006, Chalfoun and Martin 2009).

Declines in Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") abundance in western North America over the last century have been severe (Gregg et al. 1994, Johnsgard 2002, Connelly et al. 2004), and recently led the U.S. Fish and Wildlife Service (2010) to conclude that sage-grouse are warranted for protection

under the Endangered Species Act of 1973. Many factors have contributed to this decline including habitat loss, habitat fragmentation, habitat degradation, and predation (Braun 1998, Schroeder et al. 2004). Despite the U.S. Fish and Wildlife Service's assessment, listing was precluded in favor of other species under more severe threat of extinction.

Direct effects of nest predation on nesting productivity of birds is widely recognized, and even in high quality sage-grouse habitat, most sage-grouse nests are lost to predators (Gregg et al. 1994, Connelly et al. 2004, Coates et al. 2008). For example, Common Raven (*Corvus corax*; hereafter "raven") depredation of sage-grouse nests has been documented as a common occurrence in northeastern Nevada on the basis of infrared video cameras set up at nest sites (Coates et al. 2008). High mortality rates on chicks have also been attributed to predators, especially during early brood-rearing (Aldridge 2005, Gregg and Crawford 2009, Guttery 2011).

In addition to direct predator effects, perceived predation risk may have dramatic effects on nest success and chick survival (Cresswell 2008, Martin and Briskie 2009), and prey's perception of predation risk may have negative effects that are strong enough to effect population growth rates (Creel and Christianson 2008, Cresswell 2008, Zanette et al. 2011). For example, Zanette et al. (2011) manipulated perceived predation risk while excluding predators from Song Sparrow (*Melospiza melodia*) nests. In the absence of direct predation, Zanette et al. (2011) found a 40% reduction in offspring production as a result of reduction in the number of eggs laid, proportion of eggs hatched, and proportion of nestlings fledged.

In response to predation risk to adults and their nests, sage-grouse and other birds hide nests from predators by placing them primarily in areas with greater visual obstruction (Connelly et al. 1994, Braun 1998, Connelly et al. 2004, Kirol et al. 2012); hens and broods hide from avian predators through a combination of habitat selection and cryptic behavior (Gregg and Crawford 2009, Guttery 2011). Several studies have reported that sage-grouse select nest-sites based on greater sagebrush density (Wallestad and Pyrah 1974, Connelly et al. 2003), sagebrush cover (Doherty et al. 2010, Kirol et al. 2012), shrub height (Gregg et al. 1994), grass height (Gregg et al. 1994, Holloran et al. 2005), and grass cover (Kaczor 2008, Kirol et al. 2012). Kirol et al. (2012) and Aldridge and Brigham (2002) found that sage-grouse brood hens selected locations with greater percentages of sagebrush and grass cover compared to random locations. Variability in reported nest and brood site habitat use among studies may indicate local differences in habitat and/or predator community composition. However, consistent placement of nests and broods in sites with greater visual cover, regardless of differences in the structure of local habitats, suggests that vertical (e.g., grass and shrub height) and horizontal (e.g., grass and shrub canopy cover) cover influence nest-site and brood-site selection.

Current evidence (Conover et al. 2010) suggests that sage-grouse use nest locations that hide their nests from visual but not olfactory predators. Conover et al. (2010) found that sage-grouse placed nests in areas that had greater vertical and horizontal concealment, taller shrubs, but also fewer updrafts, lower turbulence, and slower wind speeds than random locations. Updrafts, high turbulence, and high wind

speeds are weather conditions that make it difficult for mammalian predators to use olfaction to locate nests (Conover 2007). These results are consistent with results of other sage-grouse research that showed sage-grouse preferred to nest in areas with greater visual cover. Further, locations that have good visual cover often have fewer updrafts, less atmospheric turbulence, and lower wind speeds. Thus, sage-grouse, and birds in general, often balance the dual necessity of selecting cover to hide from visual and olfactory predators to improve chances of surviving to breed successfully. Selection of nest-sites that conceal sage-grouse from visual predators but not olfactory predators suggests that the former are a greater threat to sage-grouse nests. On the other hand, it may be that sage-grouse cannot use olfactory cues to influence nest choice decisions, and visual predators may be a greater threat because their numbers have increased in association with anthropogenic development.

Sage-grouse select nest-sites based on habitat characteristics at local (habitat directly around a nest) and landscape scales (Doherty et al. 2010). In accordance with the predator-avoidance hypothesis, I hypothesized that at the landscape-scale, sage-grouse would avoid nesting or raising broods in areas of high densities of avian predators, specifically, American Kestrels (*Falco sparverius*; hereafter "kestrel"), Black-billed Magpies (*Pica hudsonia*; hereafter "magpies"), Golden Eagles (*Aquila chrysaetos*), hawks (*Buteo* spp.), Northern Harriers (*Circus cyaneus*; hereafter "harrier"), and ravens. Further, I hypothesized that adult survival would take precedence to nest or brood survival, and that sage-grouse habitat use would be shaped primarily by avoidance of avian predators that were a threat to adult hen survival, and secondarily to avian predators

that were a threat only to nests and broods. I tested these hypotheses by comparing avian predator densities at sage-grouse (1) nest and (2) brood locations, and (3) random locations within nesting and brood-rearing habitat.

## METHODS

*Study Areas*.—My study was conducted in southwest and south-central Wyoming at 12 study sites that were either 16 km ($n$ = 8) or 24 km ($n$ = 4) in diameter (Fig. 2-1). Sage-grouse are lekking species, and Holloran and Anderson (2005) found that 384 of 415 (92.5%) sage-grouse nests were within 8.5 km of leks in central and southwest Wyoming. Thus, the study sites in southwest Wyoming were 16-km diameter and approximately centered around leks where hens were captured. I used larger 24-km study sites in south-central Wyoming because sage-grouse were captured at several leks spread over a larger area. Five study sites were located in Lincoln County (16-km diameter each), two in Sweetwater County (one 16-km and one 24-km diameter), two in Uinta County (both 16-km diameter), and three in Carbon County (24-km diameter each). Study sites were chosen to provide a representation of overall sage-grouse nesting habitat in southern Wyoming with a variety of land uses and topographic features. Elevation ranged from 1,950 m to 2,530 m among study sites. Most of my sites were owned and administered by the Bureau of Land Management (BLM) with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in my study sites. All study sites had anthropogenic development consisting mostly of unimproved 4-wheel drive roads. Conventional natural gas, coalbed methane natural gas, and/or

conventional oil extraction activities were present in six (50%) of my study sites; well density within study sites averaged 0.12 ± 0.22 (SD) wells $km^{-2}$ (range = 0.0–0.64 wells $km^{-2}$).

Sagebrush (*Artemisia* spp.) dominated the landscape at all study sites; Wyoming Big Sagebrush (*A. tridentata wyomingensis*) and Mountain Big Sagebrush (*A. t. vaseyana*) were the most common. Black Sagebrush (*A. nova*) and Dwarf Sagebrush (*A. arbuscula*) were found on exposed ridges. Other common shrub species in my study sites included: Antelope Bitterbrush (*Purshia tridentata*), Common Snowberry (*Symphoricarpos albus*), Chokecherry (*Prunus virginiana*), Alderleaf Mountain Mahogany (*Cercocarpus montanus*), Rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), Greasewood (Sarcobatus vermiculatus), Saskatoon Serviceberry (*Amelanchier alnifolia*), and Spiny Hopsage (*Grayia spinosa*). Isolated stands of juniper (*Juniperus* spp.) and Quaking Aspen (*Populus tremuloides*) were found at the higher elevations on north-facing hillsides.

*Sage-grouse Capture and Monitoring*.—I monitored sage-grouse hens during nesting and early brood-rearing from 2008 through 2010. Hens were captured, radio-collared, and released in April of each year. Capture occurred at night using ATVs, spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992). Sage-grouse hens were fitted with 17.5-g or 22-g (<1.5% body mass) necklace radio collars (Holohil Systems Ltd, RI-2D, Ontario, Canada or Advanced Telemetry Systems Inc, A4060, Isanti, Minnesota).

I located hens on a weekly basis with Communications Specialists

(Communications Specialists, R-1000, Orange, California) receivers and 3-way Yagi antennas (Communications Specialists, Orange, California). Potential nests were identified by binoculars at a distance of ~15 m by circling a radio-marked hen until she was sighted under a shrub. Nests were verified by triangulating the hen under the same shrub from >50 m away or thoroughly searching the area of the potential nest when the hen was absent. I continued monitoring nests weekly until it either hatched or failed. I assessed nest fate as successful or unsuccessful after a hen had left its nest. A successful nest was defined as having evidence that at least one egg hatched as determined by shell membrane condition (Wallestad and Pyrah 1974). I classified unsuccessful nests as abandoned (eggs not depredated or hatched) or depredated (at least one egg with evidence of depredation and no eggs hatched).

I located the broods of radio-marked hens weekly with binoculars from a distance of ~15 m. Brood hens were identified by either visually detecting chicks or observing hen behavior that indicated the presence of a brood (e.g., hesitation to flush, feigning injury, or clucking). I classified a sage-grouse hen as a brood hen if there was at least 1 chick with her. Monitoring of broods continued for as long as possible, which was usually until the chicks were at least 3-weeks old, the hen lost her brood, the hen died, or the hen could no longer be located.

*Avian Predator Monitoring*.—Between May and August of each year (sage-grouse nesting and brood-rearing season), I conducted point-count surveys at sage-grouse nests, sage-grouse brood locations, and random locations (hereafter; nest, brood, and random locations) within each study site to compare avian predator densities. Random

locations were selected in habitat considered to be available to sage-grouse for nesting within each study site. To restrict random locations to available nesting habitat, I used ArcMap version 9.2 (ESRI Inc., Redlands, California) to generate random locations only in sagebrush-dominated habitat, which was classified by the Northwest GAP landcover data from 2008. Random locations were at least 1,000 m apart, but in practice, random points in all years averaged over 2,000 m apart (Table 2-1). I generated 12 random locations in each 16-km diameter study site and 18 random locations in each 24-km diameter study site per year (total $n = 504$). A new set of random locations was generated each year to avoid spatial autocorrelation; thus, random locations between years were independent.

I used standard distance sampling techniques (Buckland et al. 1993, Ralph et al. 1995, Thomas et al. 2010) to count and record distance to all corvids and raptors observed during point-counts. I recorded distance from the observer when standing at the center point to where predators were first located (Ralph et al. 1995, Thomas et al. 2010); this minimized possible bias associated with avian predators being attracted to or flushed away from an observer. In the uncommon event that an avian predator was displaced from the center of a point-count location as an observer approached (6% of detected birds), I recorded distance from that avian predator to the center of the point-count location while the observer approached as suggested by Ralph et al. (1995). A 1,500–m rangefinder (American Technologies Network Corp., RE-1500 m, San Francisco, California) was used in conjunction with a GPS unit to estimate distances directly or to validate visually estimated distances.

I conducted 10-min point-count surveys during daylight hours on a weekly basis at each study site. I visited each point-count location 1 to 8 times with most locations visited ≥ 3 times. I did not survey during inclement weather (i.e., in rain or with wind speeds ≥25 km/h; Ralph et al. 1995). Avian predators that could not be identified to species were not included in analyses—2% of detections within truncated distances. Nest and brood point-counts were performed after nests and broods were initially located; thus, nest point-counts were conducted in May and June and brood point-counts were conducted from mid-May to early-August. I performed random point-counts throughout the nesting and early brood-rearing season (May to early-August).

I intermixed the sampling of nest, brood, and random point-counts within each study site, and each week I changed the time of day and the observer that conducted individual point-counts within a study site. The observers conducting point-counts within a particular study site changed each year, but all observers were trained and tested in corvid and raptor identification before conducting point-counts.

To avoid disturbing an incubating hen, nest point-counts were conducted 100 m to 200 m away from a sage-grouse nest but within a line-of-sight of that nest. I also performed brood point-counts 100 m to 200 m away from a brood hen—estimated by triangulation—immediately before verifying that a radio-marked brood hen was still with chicks. This was intended to record avian predator densities before the observer disturbed any avian predators and to avoid flushing a brood hen when a predator was nearby. If the hen did not have chicks, the brood point-count was discarded.

*Data Analyses*.—I used conventional distance sampling in DISTANCE 6.0

release 2 (Thomas et al. 2010) to estimate Ferruginous Hawk (*Buteo regalis*), Golden Eagle, harrier, kestrel, magpie, raven, Red-tailed Hawk (*Buteo jamaicensis*), and Swainson's Hawk (*Buteo swainsoni*) densities for nest, brood, and random locations across all years and all study sites. Ferruginous Hawks ($n$ = 34), Red-tailed Hawks ($n$ = 218), and Swainson's Hawks ($n$ = 46) were combined into a single group (*Buteo* hawks) for analyses because all *Buteo* hawks likely had a similar effect on sage-grouse nest-site selection and most observed *Buteo* hawks were Red-tailed Hawks. For DISTANCE analyses, Golden Eagle, harrier, magpie, and raven detection distances were right truncated 5%; *Buteo* hawk detection distances were right truncated 7.5%; and kestrel detection distances were not right truncated (Table 2-2). I chose truncation distances by determining the smallest truncation that allowed for adequate fit of DISTANCE models.

I fit half-normal and hazard-rate key detection functions with cosine, simple polynomial, and hermite polynomial adjustments. I compared the fit of all possible detection functions with detection varying among point-count types to detection held constant among point-count types. I selected the appropriate key detection function and detection function adjustment for each avian predator species separately using Akaike's information criterion corrected for small sample sizes ($AIC_c$; Burnham and Anderson 2002). For all avian predator species, DISTANCE models with detection held constant were at least 4 $AIC_c$ lower than models with detection varying by point-count type. This was not surprising because all point-counts were in sagebrush-dominated habitat.

I used DISTANCE to estimate observer effective detection radius (EDR), which was defined as the distance that the number of detected birds beyond EDR was equal to

the undetected birds within EDR (Buckland et al. 2001). For example, an EDR of 500 m for hawks would indicate that the number of detected hawks beyond 500 m was equal to the number of undetected hawks less than 500 m from an observer. I also fit DISTANCE models with detection allowed to vary among observers to assess differences in detection among observers, but the latter models did not fit the data well. For this reason, and because EDR did not differ among observers (95% confidence intervals [CI] around EDRs of all observers overlapped for all avian predator species), I did not incorporate observer differences in detection into my DISTANCE analyses.

I adjusted density estimates for survey effort (difference in the number of visits per point-count location) and scaled my density estimates by the maximum number of visits per point-count location. Survey effort was accounted for in DISTANCE by dividing the total number of detected avian predators at each point-count location by that point-count's proportion of actual visits to the maximum number of visits (e.g., the total number of Golden Eagles detected at point-count x = 3, visits to point-count x = 5, total visits possible = 8; thus, for DISTANCE analyses point-count x was given a golden eagle count of 3 / 0.625 = 4.8, which was then scaled appropriately in DISTANCE by dividing by 8; Thomas et al. 2010).

I used 95% CIs to compare raven, magpie, Golden Eagle, *Buteo* hawk, harrier, and kestrel densities separately at nest, brood, and random locations. Confidence intervals were generated empirically using density estimates and standard errors from DISTANCE with avian predator counts pooled over all study sites and years.

In addition to DISTANCE analyses, I modeled differences in avian predator

densities between locations used by sage-grouse (nest and brood locations) and random locations with an information theoretic approach (Anderson 2008). Modeling was done with binomial generalized linear mixed models (GLMM) with restricted maximum likelihood (REML) estimation of degrees of freedom; locations used by sage-grouse were coded 1 and random locations 0. I fit GLMMs with function lmer in package lme4 (R 2.10.1; The R Foundation for Statistical Computing 2009). I calculated avian predator densities from the raw count data within the DISTANCE estimated EDR for each avian predator species. I thus compared avian predator densities using species-specific EDRs because I did not find differences in detection among brood, nest, and random point-count types. The raw densities were standardized by the number of visits to each point-count location. I log transformed raw avian predator densities to reduce the affects of influential observations. I used log transformed raw avian predator species densities to create additive variables (Table 2-3). This allowed me to compare 6 models between locations used by sage-grouse and random locations in which avian predator species were treated either (1) individually, (2) as a single group that ignored size and behavior, (3) as small or large predators, (4) as small, medium, or large predators, (5) by distinguishing between low-flying predators (L), omnivores (O), or soaring (S) species, or (6) by separating species as a threat primarily to adult hen (A), incubating hen (N), or brood-rearing hen (B) (Table 2-3). I compared models with associated variables with $AIC_c$ and Akaike weights ($w_i$). Multicollinearity was not a problem because no avian predator species were correlated ($r \leq 0.17$) and variance inflation factors (VIF) for avian predator species were VIF $\leq 1.18$. Mixed models were used to incorporate study site as a

random factor, which accounted for study site differences including fragmentation, anthropogenic structures, landscape features, and vegetation.

DISTANCE estimates are known to be robust to spatial autocorrelation (Thomas et al. 2010). Nonetheless, spatial autocorrelation violates the independence assumption for GLMM, and therefore I used spline correlograms of Pearson residuals with 95% point-wise bootstrap CIs to assess spatial autocorrelation. GLMM residuals were spatially autocorrelated ≤ 2,500 m (Fig. 2-2). I used spatial eigenvector mapping (SEVM) as specified by Dormann et al. (2007) to account for spatial autocorrelation in model residuals (Fig. 2-2). I created an inverse weighted distance matrix to generate eigenvectors, where point-count locations > 8 km apart were not considered to be correlated. This distance related directly to the radius of my 16-km diameter study sites; however, 8 km was also larger than the home range size of breeding Golden Eagles (1.9–92.0 $km^2$; DeLong 2004) and breeding ravens (0.3–45.8 $km^2$; Boarman and Heinrich 1999), which had the largest home ranges of the avian predators in this study. Furthermore, I treated all point-count locations, regardless of type or year, within 8 km as correlated with the degree of correlation related to the distance among point-count locations. I found the smallest number of eigenvectors required to remove spatial autocorrelation (Moran's similarity index: $P \geq 0.1$) for each GLMM by using function ME in package spdep (R 2.10.1; The R Foundation for Statistical Computing 2009); I then refit each GLMM with eigenvectors included as fixed effects to account for residual spatial autocorrelation.

# RESULTS

I conducted 3,006 point-count surveys over the three years at 963 point-count locations. This comprised 218 sage-grouse nest locations, 249 sage-grouse brood locations (with 83 separate broods), and 496 random locations (Table 2-1). On the whole, sage-grouse selected nest and brood locations with lower densities of avian predators than random locations (Fig. 2-3). I visited each brood between 1 to 9 weeks posthatch (mean = 3.04 ± 2.13 SD). In all years, distance to nearest neighboring location was shortest for broods. Distance between nearest nest and random locations were 2 to 3 times greater than brood locations and similar to each other (Table 2-1). Golden Eagles and ravens were the most commonly detected avian predators, *Buteo* hawks and magpies had an intermediate number of detections, and harriers and kestrels had the lowest number of detections (Table 2-2). EDR estimates ranged from 294 m for magpies to 1,006 m for Golden Eagles, and differed by avian predator species (Table 2-2). This verified the necessity of selecting detection functions for each avian predator species separately. All avian predator species or species groups had more than the 60–80 detections that Buckland et al. (1993) suggested was necessary for reliable density estimates (Table 2-2).

Comparison of 95% CIs showed that *Buteo* hawk, Golden Eagle, magpie, and raven estimated densities were significantly lower at sage-grouse nest and brood locations than random locations (Fig. 2-3). Kestrel densities were significantly lower at sage-grouse brood locations but similar at sage-grouse nest locations compared to random locations (Fig. 2-3). Harrier densities were similar at sage-grouse nest, brood, and

random locations (Fig. 2-3); however, random and brood location CIs were only slightly overlapping.

The spline correlogram of Pearson residuals from the top $AIC_c$ ranked GLMM showed that SEVM with 34 eigenvectors accounted for spatial autocorrelation (Fig. 2-2). The top $AIC_c$ ranked GLMM model with SEVM was that which recognized and distinguished among small, medium, and large species (Table 2-4); coefficients for all three size classes were negative and did not overlap zero (Table 2-5). Negative coefficients indicated lower small, medium, and large avian predator densities at locations used by sage-grouse compared to random locations. Sage-grouse nest and brood locations had lower densities of all three size classes of avian predators (Table 2-5).

## DISCUSSION

I found that sage-grouse selected habitat with lower densities of avian predators at nests and brood locations as predicted by the predator-avoidance hypothesis. By selecting habitat with lower densities of avian predators, sage-grouse lower their exposure to avian predation, and risk of reproductive failure. My three-size class model had $w_i = 0.91$ (Table 2-4), suggesting that sage-grouse avoided avian predators at nest and brood locations on the basis of the size of avian predators rather than individual species identity, equivalence of all species, foraging behavior of predators, or presumed threat to sage-grouse reproductive stage.

Although I estimated avian predator densities across all years, I did not expect the pattern of sage-grouse avoidance of avian predators to differ among years. The inclusion

of SEVM in my GLMM analyses dealt with spatial autocorrelation and bias associated with nest-site fidelity between years, weekly movements of broods, and similarities in habitat within and among study sites. DISTANCE estimates are known to be robust to lack of independence of observation locations because distance sampling is setup to be a snap-shot in time (Thomas et al. 2010). My sampling was designed to attempt to count the greatest proportion of avian predators within a study site each week as suggested by Thomas et al. (2010) and Ralph et al. (1995). Conducting all point-counts within a study site in one day reduced the possibility of double-counting individual avian predators during that week's visit. Counting the same individual during different weeks, regardless of the particular point-count location, was properly scaled by accounting for survey effort. Replication of point-counts by sampling multiple weeks was done to increase the proportion of avian predators detected as suggested by Thomas et al. (2010).

I found raven abundances at sage-grouse nest and brood locations were lower than at random locations in available sagebrush habitat. In western Wyoming, Bui et al. (2010) claimed that raven density around sage-grouse nesting and brood-rearing areas ($1.0 \pm 0.2$ [SE] ravens/$km^2$) was marginally higher than raven densities in available sagebrush habitat ($0.7 \pm 0.2$ [SE] ravens/$km^2$); however, these results were not significantly different. The discrepancy between my results and Bui et al. (2010) may be a function of greater anthropogenic development and human activity in their study areas or raven behavioral adaptations related to available resources. Regardless, I agree with Bui et al. (2010) that as avian predators, especially ravens, increase in abundance in sage-grouse habitat, quality nesting and brood-rearing habitat will become more limited. This is

consistent with predation risk trade-offs and non-lethal predator effects, such as avoidance of risky habitats or habitats occupied by predators (Evans 2004, Verdolin 2006, Cresswell 2008).

To my knowledge, my study is the first to document raven densities potentially impacting sage-grouse nest-site selection. However, my finding is not surprising because raven densities impact the nest success of prairie grouse species (Gregg et al. 1994, Manzer and Hannon 2005, Coates and Delehanty 2010). In southern Alberta, sharp-tailed grouse (*Tympanuchus phasianellus*) had 8-times greater nest success in landscapes with less than three corvids/km$^2$ as opposed to landscapes with greater than or equal to three corvids/km$^2$ (Manzer and Hannon 2005). Sage-grouse nest success in northeastern Nevada was related to the number of ravens per 10-km transect with the odds of a nest failure increasing 7.4% with every additional raven (Coates and Delehanty 2010). Around Jackson and Pinedale, Wyoming, Bui et al. (2010) found that higher occupancy rates of ravens was correlated with failed sage-grouse nests.

Magpies depredate sage-grouse nests (Holloran and Anderson 2003), and they are capable of consuming animals as large as sage-grouse chicks (Trost 1999). Magpies are known to be associated with riparian areas but also forage in sagebrush habitats (Trost 1999). Thus, sage-grouse avoidance of magpies during nesting may be related to sage-grouse avoidance of riparian areas within or adjacent to sagebrush habitat; however, sage-grouse are known to utilize riparian areas for foraging chicks (Connelly et al. 2004, Crawford et al. 2004). My results indicate sage-grouse select habitat for brood rearing with lower abundances of magpies, even while balancing the need to utilize habitats, such

as riparian habitats, that provide forage to meet the energetic requirements of chicks. Sage-grouse hens typically move broods to riparian areas after early-brood rearing (Crawford et al. 2004, Gregg and Crawford 2009), which may correspond with chicks being more mobile and less susceptible to predation by magpies.

Golden Eagles are the primary predator of adult sage-grouse (Schroeder et al. 1999, Schroeder and Baydack 2001, Mezquida et al. 2006). In southwestern Wyoming, MacLaren et al. (1988) found that birds contributed to approximately 9% of the diet of nesting Golden Eagles, and sage-grouse was their primary avian prey. In Utah, 55% of radio-marked sage-grouse were killed by raptors, which Danvir (2002) attributed mainly to Golden Eagles. Hence, I was not surprised that sage-grouse pay particular attention to them in locating where to nest and raise their brood. Ferruginous Hawks, Red-tailed Hawks, and Swainson's Hawks take some adult sage-grouse but probably not substantial numbers of them (MacLaren 1988); harriers have been witnessed hunting sage-grouse adults and chicks (Schroeder et al. 1999, Schroeder and Baydack 2001, Fletcher et al. 2003). My GLMM analysis indicated that sage-grouse were avoiding all *Buteo* hawks, harriers, and ravens as a group based on their body size rather than differentiating among them.

My GLMM results showed that sage-grouse were able to avoid small, medium, and large avian predators. This suggests that sage-grouse are not subject to predator facilitation by avian predators. Predator facilitation predicts that anti-predation behaviors that protect prey species from one type of predator may expose them to predation from other types of predators (Kotler et al. 1992, Korpimäki et al. 1996). For example, the risk

of predation by Eurasian Eagle Owls (*Bubo bubo*) resulted in gerbils (*Gerbillus allenbyi* and *G. pyramidum*) selecting habitat that increased their exposure to predation by Greater Sand Vipers (*Cerastes cerastes*; Kotler et al. 1992). By hiding from and avoiding avian predators, sage-grouse may reduce their risk of predation from avian predators of multiple sizes, while potentially exposing themselves to olfactory (mammalian) predation. However, the possible effects of predator facilitation between visual predators and olfactory predators are beyond the scope of this study and warrant further research.

Sage-grouse preferentially select for greater visual concealment cover for nesting to hide themselves and their nests from visual predators (Conover et al. 2010), and the probability of raven depredation of a sage-grouse nest has been found to be greater at nests with relatively less canopy cover (Coates and Delehanty 2010). This selection for hiding from and avoiding visual predators through indirect (i.e., habitat features and anthropogenic structures) and possibly direct means entails selection at multiple scales. At the local-scale, sage-grouse appear to be selecting for sites where they are visually concealed from avian predators (Connelly et al. 2004, Doherty et al. 2010, Kirol et al. 2012). At landscape-scales, sage-grouse may be selecting for areas where avian predators are less abundant. Sage-grouse selection of habitat at multiple scales achieves the same thing—reduced risk from avian predators.

Predator avoidance behavior is a common consequence of predation risk (Cresswell 2008). Sage-grouse avoidance of predators has been addressed in the context of using cover to hide from predators; however, nesting and brood-rearing sage-grouse

may also directly avoid avian predators. Previous research has not looked at the possibility of sage-grouse directly avoiding predators, but studies on other avian species have demonstrated direct avoidance of avian predators. For example, large numbers of Western Sandpipers (*Calidris mauri*) avoided migration stopover areas with Peregrine Falcons (*Falco peregrinus*) present (Ydenberg et al. 2002), sandpipers also shortened duration at migratory stopover locations possibly to avoid migrating Peregrine Falcons (Ydenberg et al. 2004), Tengmalm's Owls (*Aegolius funereus*) nested away from Ural Owl (*Strix uralensis*) nests (Hakkarainen and Korpimäki 1996), Black Kite (*Milvus migrans*) nests were located away from nesting Eurasian Eagle Owls (Sergio et al. 2003), Skylarks (*Alauda arvensi*) and Yellowhammers (*Emberiza citrinella*) avoided nesting close to European Kestrel (*Falco tinnunculus*) nests (Norrdahl and Korpimäki 1998), Red-backed Shrikes (*Lanius collurio*) avoided nesting near magpie and Hooded Crow (*Corvus corone cornix*) breeding territories (Roos and Pärt 2004), and nesting Pied Flycatchers (*Ficedula hypoleuca*) avoided Eurasian Sparrowhawk (*Accipiter nisus*) nests (Thomson et al. 2006).

Increases in avian predator densities are likely to result in higher depredation rates on sage-grouse nests and reduced chick survival (Evans 2004, Cresswell 2008). Sage-grouse hens likely avoid avian predators for their own survival in addition to reducing depredation rates on their nests and chicks. Thus, the presence of greater abundances of avian predators, specifically corvids and raptors, may induce changes in sage-grouse behavior associated to habitat usage. Sage-grouse have been found to reduce time off of their nests when they inhabit areas near high abundances of ravens (Coates and

Delehanty 2008); thus, in addition to using indirect mechanisms, sage-grouse may be using avian predator abundance directly to evaluate predation risk while nesting. Habitat that has high quality cover and forage may become functionally unavailable to sage-grouse when avian predator densities are at high levels. In Cresswell's (2008) review of non-lethal effects of predator-avoidance, he illustrated that several studies on birds indicate that presence of a predator had dramatic impacts on prey species use of habitat. These effects were found to be as great or greater than the effects of direct predation. Regardless of the mechanisms behind sage-grouse hen selection of habitat with fewer avian predators, My results illustrate that sage-grouse were capable of avoiding areas with relatively higher densities of small, medium, and large avian predators or more specifically ravens, magpies, Golden Eagles, *Buteo* hawks, and kestrels compared to available sagebrush habitat.

## LITERATURE CITED

ANDERSON, D. R. 2008. Model based inferences in the life sciences. Springer Science, New York.

ALDRIDGE, C. L. 2005. Identifying habitats for persistence of Greater Sage-Grouse (*Centrocercus urophasianus*) in Alberta, Canada. Ph.D. dissertation, University of Alberta, Edmonton.

ALDRIDGE, C. L., AND R. M. BRIGHAM. 2002. Sage-grouse nesting and brood habitat use in southern Canada. Journal of Wildlife Management 66:433–444.

BOARMAN, W. I., AND B. HEINRICH. 1999. Common Raven (*Corvus corax*). *In* The Birds

of North America, no. 476 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

BRAUN, C. E. 1998. Sage grouse declines in western North America: What are the problems? Proceedings of the Western Association of Fish and Wildlife Agencies 78:139−156.

BUCKLAND, S. T., ANDERSON, D. R., BURNHAM, K. P., AND LAAKE, J. L. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, New York.

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, AND L. THOMAS. 2001. Introduction to Distance Sampling. Oxford University Press, New York.

BUI, T. D., J. M. MARZLUFF, AND B. BEDROSIAN. 2010. Common Raven activity in relation to land use in western Wyoming: Implications for Greater Sage-Grouse reproductive success. Condor 112:65−78.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: A practical information–theoretic approach, 2nd ed. Springer-Verlag, New York.

CHALFOUN, A. D., AND T. E. MARTIN. 2009. Habitat structure mediates predation risk for sedentary prey: Experimental tests of alternative hypotheses. Journal of Animal Ecology 78:497−503.

COATES, P. S., J. W. CONNELLY, AND D. J. DELEHANTY. 2008. Predators of Greater Sage-

Grouse nests identified by video monitoring. Journal of Field Ornithology 79:421−428.

COATES, P. S., AND D. J. DELEHANTY. 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. Condor 110:627−638.

COATES, P. S., AND D. J. DELEHANTY. 2010. Nest predation of Greater Sage-Grouse in relation to microhabitat factors and predators. Journal of Wildlife Management. 74:240–248.

CONNELLY, J. W., S. T. KNICK, M. A. SCHROEDER, AND S. J. STIVER. 2004. Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Unpublished Report, Cheyenne, Wyoming.

CONNELLY, J. W., K. P. REESE, AND M. A. SCHROEDER. 2003. Monitoring of Greater Sage-Grouse habitats and populations. College of Natural Resources Experiment Station Bulletin 80. University of Idaho, Moscow.

CONNELLY, J. W., K. P. REESE, W. L. WAKKINEN, M. D. ROBERTSON, AND R. A. FISCHER. 1994. Sage grouse ecology. Idaho Department of Fish and Game Job Completion Report W-160-R-19, Boise.

CONOVER, M. R. 2007. Predator−Prey Dynamics: The Use of Olfaction. Taylor and Francis, Boca Raton, Florida.

CONOVER, M. R., J. S. BORGO, R. E. DRITZ, J. B. DINKINS, AND D. K. DAHLGREN. 2010. Greater Sage-Grouse select nest sites to avoid visual predators but not olfactory predators. Condor 112:331−336.

CRAWFORD, J. A., R. A. OLSON, N. E. WEST, J. C MOSLEY, M. A. SCHROEDER, T. D.

WHITSON, R. F. MILLER, M. A. GREGG, AND C. S. BOYD. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2−19.

CREEL, S., AND D. CHRISTIANSON. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23:194−201.

CRESSWELL, W. 2008. Non-lethal effects of predation in birds. Ibis 150:3−17.

DANVIR, R. E. 2002. Sage grouse ecology and management in northern Utah sagebrush-steppe. Deseret Land and Livestock Wildlife Research Report, Deseret Land and Livestock Ranch and the Utah Foundation for Quality Resource Management, Woodruff.

DELONG, J. P. 2004. Effects of management practices on grassland birds: Golden Eagle. Northern Prairie Wildlife Research Center, Jamestown. [Online.] Available at http://www.npwrc.usgs.gov/resource/literatr/grasbird/goea/goea.htm

DOHERTY, K. E., D. E. NAUGLE, AND B. L. WALKER. 2010. Greater Sage-Grouse nesting habitat: The importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

DORMANN, C, F., J. M. MCPHERSON, M. B. ARAÚJO, R. BIVAND, J. BOLLIGER, G. CARL, R. G. DAVIES, A. HIRZEL, W. JETZ, W. D. KISSLING, I. KÜHN, R. OHLEMÜLLER, P. R. PERES-NETO, B. REINEKING, B. SCHRÖDER, F. M. SCHURR, AND R. WILSON. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. Ecography 30:609 –628.

EVANS, K. L. 2004. The potential for interactions between predation and habitat change

to cause population declines of farmland birds. Ibis 146:1–13.

FLETCHER, Q. E., C. W. DOCKRILL, D. J. SAHER, AND C. L. ALDRIDGE. 2003. Northern Harrier (*Circus cyaneaus*) attacks on Greater Sage-Grouse (*Centrocercus urophasianus*) in southern Alberta. Canadian Field-Naturalist 117:479–480.

GIESEN, K. M., T. J. SCHOENBERG, AND C. E. BRAUN. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

GREGG, M. A., AND J. A. CRAWFORD. 2009. Survival of Greater Sage-Grouse chicks and broods in the northern Great Basin. Journal of Wildlife Management 73:904–913.

GREGG, M. A., J. A. CRAWFORD, M. S. DRUT, AND A. K. DELONG. 1994. Vegetational cover and predation of sage-grouse nests in Oregon. Journal of Wildlife Management 58: 162–166.

GUTTERY, M. R. 2011. Ecology and management of a high elevation southern range Greater Sage-Grouse population: Vegetation manipulation, early chick survival, and hunter motivations. Ph.D. dissertation, Utah State University, Logan.

HAKKARAINEN, H., AND E. KORPIMÄKI. 1996. Competitive and predatory interactions among raptors: An observational and experimental study. Ecology 77:1134–1142.

HOLLORAN, M. J., AND S. H. ANDERSON. 2003. Direct identification of northern sage-grouse (*Centrocercus urophasianus*) nest predators using remote sensing cameras. Canadian Field-Naturalist 117:308–310.

HOLLORAN, M. J., AND S. H. ANDERSON. 2005. Spatial distribution of Greater Sage-Grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.

HOLLORAN, M. J., B. J. HEATH, A. G. LYON, S. J. SLATER, J. L. KUIPERS, AND S. H.

ANDERSON. 2005. Greater Sage-Grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638–649.

JOHNSGARD, P. A. 2002. Grassland Grouse and Their Conservation. Smithsonian Institution Press, Washington, D. C.

KACZOR, N. W. 2008. Nesting and brood-rearing success and resource selection of Greater Sage-Grouse in northwestern South Dakota. M.S. thesis, South Dakota State University, Brookings.

KIROL, C. P., J. L. BECK, J. B. DINKINS, AND M. R. CONOVER. 2012. Greater Sage-Grouse nesting and brood-rearing microhabitat selection in xeric big sagebrush. Condor 114:75–89.

KORPIMÄKI, E., V. KOIVUNEN, AND H. HAKKARAINEN. 1996. Microhabitat use and behavior of voles under weasel and raptor predation risk: Predator facilitation? Behavioral Ecology 7:30–34.

KOTLER, B. P., L. BLAUSTEIN, AND J. S. BROWN. 1992. Predator facilitation: The combined effects of snakes and owls on the foraging behavior of gerbils. Annales Zoologici Fennici. 29:199–206.

MACLAREN, P. A., S. H. ANDERSON, AND D. E. RUNDE. 1988. Food habits and nest characteristics of breeding raptors in southwestern Wyoming. Great Basin Naturalist 48:548–553.

MANZER, D. L., AND S. J. HANNON. 2005. Relating grouse nest success and corvid density to habitat: A multi-scale approach. Journal of Wildlife Management 69:110–123.

MARTIN, T. E., AND J. V. BRISKIE. 2009. Predation on dependent offspring: A review of

the consequences for mean expression and phenotypic plasticity in avian life history traits. The Year in Evolutionary Biology 1168:201–217.

MEZQUIDA, E. T., S. J. SLATER, AND C. W. BENKMAN. 2006. Sage-grouse and indirect interactions: Potential implication of coyote control on sage-grouse populations. Condor 108:747–759.

NORRDAHL, K., AND E. KORPIMÄKI. 1998. Fear in farmlands: How much does predator avoidance affect bird community structure? Journal of Avian Biology 29:79–85.

RALPH, C. J., S. DROEGE, AND J. R. SAUER. 1995. Managing and monitoring birds using point counts: standards and applications. USDA Forest Service Gen. Tech. Rep. PSW-GTR-149, Berkeley.

ROOS, S., AND T. PÄRT. 2004. Nest predators affect spatial dynamics of breeding Red-backed Shrikes (*Lanius collurio*). Journal of Animal Ecology 73:117–127.

SARGEANT, A. B., M. A. SOVADA, AND T. L. SHAFFER. 1995. Seasonal predator removal relative to hatch rate of duck nests in Waterfowl Production Areas. Wildlife Society Bulletin 23:507–513.

SCHROEDER, M. A., C. L. ALDRIDGE, A. D. APA, J. R. BOHNE, C. E. BRAUN, S. D. BUNNELL, J. W. CONNELLY, P. A. DEIBERT, S. C. GARDNER, M. A. HILLIARD, G. D. KOBRIGER, S. M. MCADAM, C. W. MCCARTHY, J. J. MCCARTHY, D. L. MITCHELL, E. V. RICKERSON, AND S. J. STIVER. 2004. Distribution of sage grouse in North America. Condor 106:363–376.

SCHROEDER, M. A., AND R. K. BAYDACK. 2001. Predation and the management of prairie grouse. Wildlife Society Bulletin 29:24–32.

SCHROEDER, M. A., J. R. YOUNG, AND C. E. BRAUN. 1999. Sage grouse (*Centrocercus urophasianus*). *In* Birds of North America, no. 425 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

SERGIO, F., L. MARCHESI, AND P. PEDRINI. 2003. Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. Journal of Animal Ecology 72: 232–245.

SMITH, P. A., H. G. GILCHRIST, AND J. N. M. SMITH. 2007. Effects of nest habitat, food, and parental behavior on shorebird nest success. Condor 109:15–31.

THOMAS, L., S. T. BUCKLAND, E. A. REXSTAD, J. L. LAAKE, S. STRINDBERG, S. L. HEDLEY, J. R. B. BISHOP, R. A. MARQUES, AND K. P. BURNHAM. 2010. Distance software: Design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

THOMSON, R. L., J. T. FORSMAN, F. SARDÀ -PALOMERA, AND M. MÖNKKÖNEN. 2006. Fear factor: Prey habitat selection and its consequences in a predation risk landscape. Ecography 29: 507–514.

TROST, C. H. 1999. Black-billed Magpie (*Pica hudsonia*). *In* The Birds of North America, no. 398 (A. Poole, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

U. S. FISH AND WILDLIFE SERVICE. 2010. Endangered and Threatened Wildlife and Plants; 12-month findings for petitions to list the Greater Sage-Grouse (*Centrocercus urophasianus*) as threatened or endangered. Federal Register

75:13909–14014.

VERDOLIN, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457–464.

WAKKINEN, W. L., K. P. REESE, J. W. CONNELLY, AND R. A. FISCHER. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

WALLESTAD, R. O., AND D. B. PYRAH. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

YDENBERG, R. C., R. W. BUTLER, D. B. LANK, C. G. GUGLIELMO, M. LEMON, AND N. WOLF. 2002. Trade-offs, condition dependence and stopover site selection by migrating sandpipers. Journal of Avian Biology 33:47–55.

YDENBERG, R. C., R. W. BUTLER, D. B. LANK, B. D. SMITH, AND J. IRELAND. 2004. Western Sandpipers have altered migration tactics as Peregrine Falcon populations have recovered. Proceedings of the Royal Society of London Series B 271:1263–1269.

ZANETTE, L. Y., A. F. WHITE, M. C. ALLEN, M. CLINCHY. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. Science 334:1398–1401.

TABLE 2-1. Summary of minimum, maximum, and mean distance (m) to nearest neighbor by location type (brood, nest, or random) reported by year. Data were collected in southwestern and south-central Wyoming, USA during 2008–2010.

| Year | Location Type | *n* | Min | Mean | Max | SD |
|---|---|---|---|---|---|---|
| 2008 | Brood | 92 | 15.3 | 790.7 | 4272.1 | 917.6 |
| | Nest | 54 | 240.6 | 2302.0 | 11811.8 | 2356.3 |
| | Random | 160 | 1000.0 | 2011.9 | 7215.6 | 1305.1 |
| 2009 | Brood | 103 | 2.8 | 831.5 | 5718.8 | 1120.3 |
| | Nest | 78 | 102.5 | 2099.0 | 8911.5 | 2091.8 |
| | Random | 174 | 1000.0 | 2122.1 | 7073.1 | 1093.9 |
| 2010 | Brood | 54 | 61.8 | 1128.4 | 9675.9 | 1707.8 |
| | Nest | 86 | 106.5 | 2042.6 | 10011.4 | 2279.2 |
| | Random | 162 | 1030.8 | 2493.0 | 6135.5 | 1016.0 |

TABLE 2-2. Truncated distance (m), number of separate detections of avian predators, and number of avian predators seen from 963 point-count locations. Data were collected in southwestern and south-central, Wyoming, USA during 2008–2010. Program DISTANCE was used to estimate effective detection radii (EDR; m) and standard error (SE).

| Avian predator species | Truncated distance | Number of detections | Avian predators counted | EDR | SE |
|---|---|---|---|---|---|
| Common Raven | 1800 | 546 | 853 | 606.8 | 22.3 |
| Black-billed Magpie | 850 | 138 | 157 | 294.2 | 19.1 |
| Golden Eagle | 2500 | 376 | 434 | 1006.3 | 42.7 |
| *Buteo* hawk | 1650 | 242 | 298 | 439.1 | 26.0 |
| Northern Harrier | 1100 | 100 | 107 | 318.4 | 26.3 |
| American Kestrel | 1500 | 118 | 129 | 397.1 | 36.1 |

TABLE 2-3. Model categories and variables considered in generalized linear mixed modeling with spatial eigenvector mapping to account for spatial autocorrelation. Models were developed to compare avian predator densities at locations used by sage-grouse (nest and brood locations) versus random. Data were collected at 963 point-count locations from eight 16-km and four 24-km study sites, 2008–2010, southwestern and south-central, Wyoming, USA.

| Model categories | Variables |
|---|---|
| Individual species[a] | GOEA = Golden Eagle |
| | BUT = *Buteo* hawks |
| | CORA = Common Raven |
| | NOHA = Northern Harrier |
| | BBMA = Black-billed Magpie |
| | AMKE = American Kestrel |
| Single group | GOEA+BUT+CORA+NOHA+BBMA+AMKE |
| Small and large | Small = BBMA+AMKE |
| | Large = GOEA+BUT+CORA+NOHA |
| Small, medium and large | Small = BBMA+AMKE |
| | Medium = BUT+CORA+NOHA |
| | Large = GOEA |
| Behavior | Soaring = GOEA+BUT |
| | Low flight = NOHA+AMKE |

| | |
|---|---|
| | Omnivore = CORA+BBMA |
| Stage | Adults = GOEA+BUT+NOHA |
| | Brooding hen = AMKE |
| | Nesting hen = CORA+BBMA |

[a] Variables in this model were used to compile the variables in all other model categorizations

TABLE 2-4. Generalized linear mixed models comparing avian predator densities between locations used by sage-grouse (nest and brood sites) and random locations. Avian predator models with associated variables were compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). All compared models include parameters generated with spatial eigenvector mapping (SEVM) to correct for spatial autocorrelation. Data were collected at 963 point-count locations from eight 16-km and four 24-km study sites, 2008–2010, southwestern and south-central, Wyoming, USA.

| Models | $k$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| Small, medium and large[a] | 39 | 675.01 | 0.00 | 0.91 |
| Small and large[a] | 36 | 679.71 | 4.69 | 0.09 |
| GOEA+CORA+BBMA | 37 | 690.39 | 15.38 | 0.00 |
| GOEA+BUT+CORA+NOHA+BBMA+AMKE[a] | 39 | 691.65 | 16.64 | 0.00 |
| GOEA+BUT+CORA+NOHA+BBMA | 38 | 692.25 | 17.24 | 0.00 |
| ALL[a] | 34 | 695.57 | 20.56 | 0.00 |
| Medium and large | 36 | 698.17 | 23.15 | 0.00 |
| Small | 35 | 698.67 | 23.66 | 0.00 |
| GOEA+BUT+CORA+BBMA+AMKE | 38 | 699.46 | 24.45 | 0.00 |
| Adult +Brood hen+Nesting hen[a] | 36 | 704.95 | 29.94 | 0.00 |
| Intercept-only model = 1,259.13 | | | | |

[a] Denotes models with all species of avian predators incorporated into the model.

TABLE 2-5. Parameter estimates with *P* values and 95% confidence intervals (CI) from top $AIC_c$ selected generalized linear mixed model (GLMM) with spatial eigenvector mapping (SEVM). The top model compared log transformed avian predator densities between locations used by sage-grouse and random locations based on three size classes (small = magpie + kestrel, medium = raven + *Buteo* hawk + harrier, and large = Golden Eagle). SEVM was used to correct for spatial autocorrelation. Data were collected at 963 point-count locations from eight 16-km and four 24-km study sites, 2008–2010, southwestern and south-central, Wyoming, USA.

| | | | | | 95% CI | |
|---|---|---|---|---|---|---|
| Variable [a] | Estimate | SE | *Z* | *P* | Lower | Upper |
| Small | -0.19 | 0.05 | -3.653 | <0.0001 | -0.30 | 0.09 |
| Medium | -0.23 | 0.04 | -5.906 | <0.0001 | -0.31 | 0.15 |
| Large | -0.31 | 0.08 | -3.975 | <0.0001 | -0.47 | 0.16 |

[a] Model included 34 SEVM variables

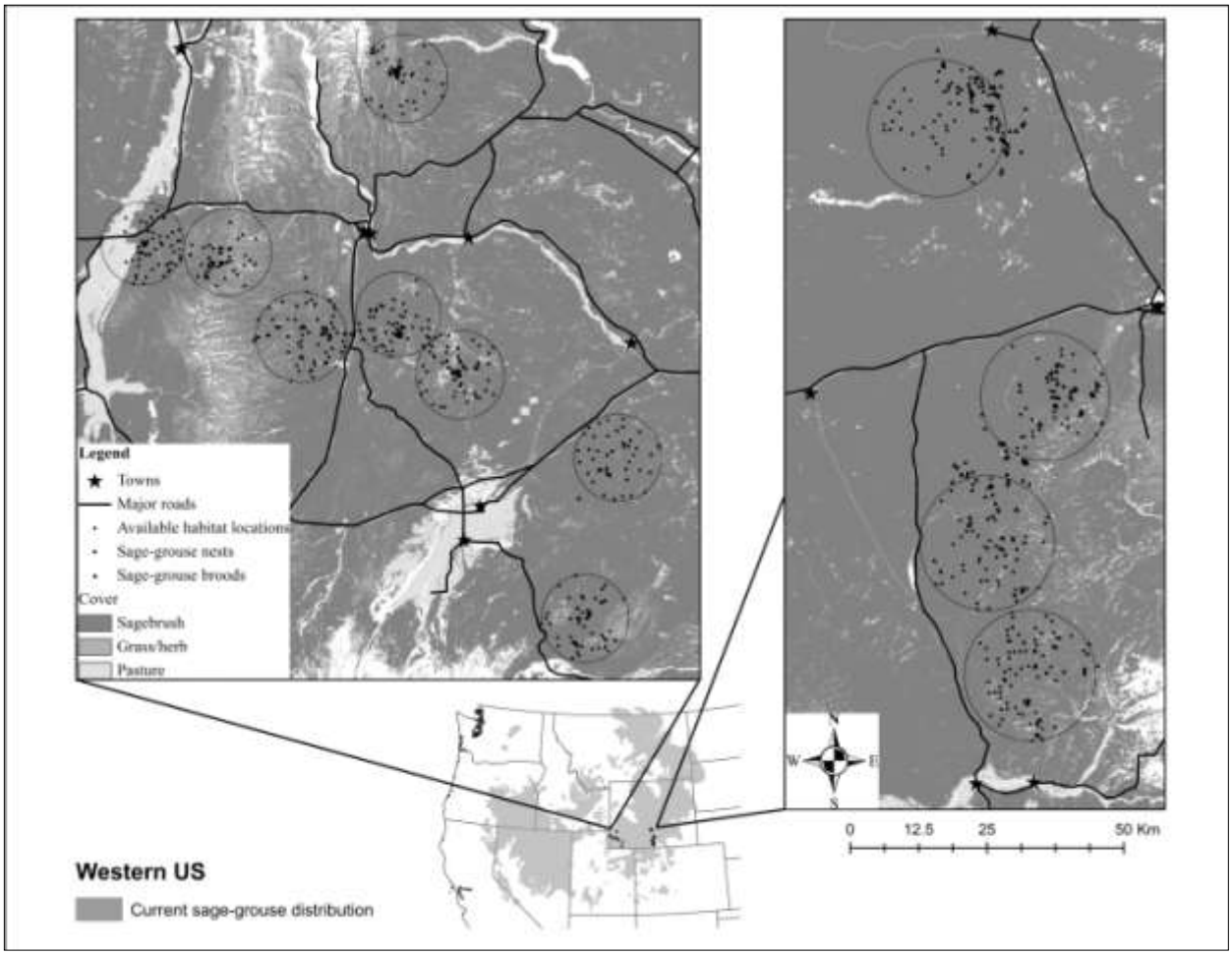



FIG. 2-1. Location map of southern Wyoming depicting eight 16-km diameter and four 24-km diameter study sites, 2008–2010, southwestern and south-central, Wyoming, USA. Magnified sections correspond on left to southwest and on right to south-central Wyoming.

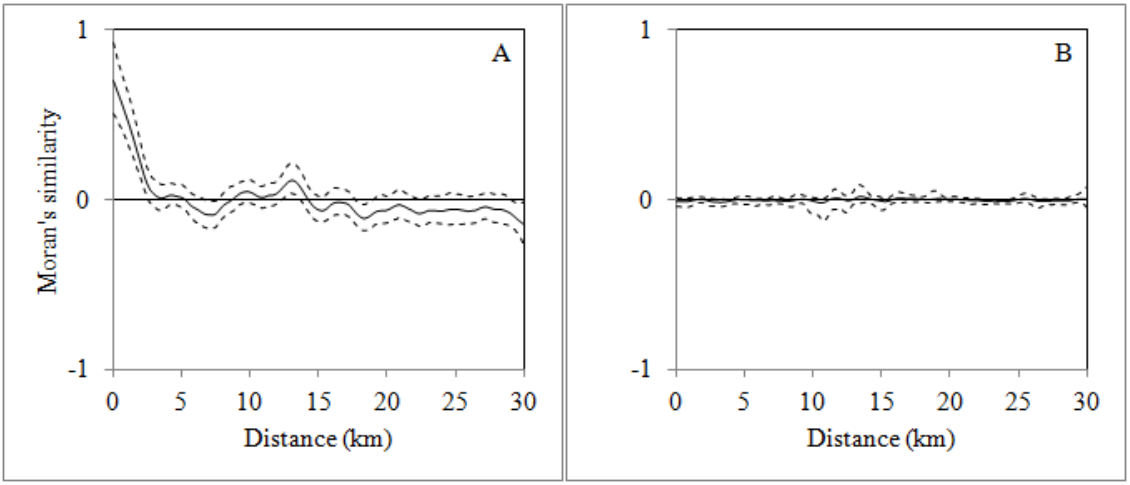



FIG. 2-2. Spline correlograms of Pearson residuals from the best $\Delta AIC_c$ ranked generalized linear mixed model with 95% point-wise bootstrapped confidence intervals (A) without spatial eigenvector mapping (SEVM) and (B) with SEVM. Spatial autocorrelation between model residuals was assessed with Moran's similarity index from 0 to 30 (km).

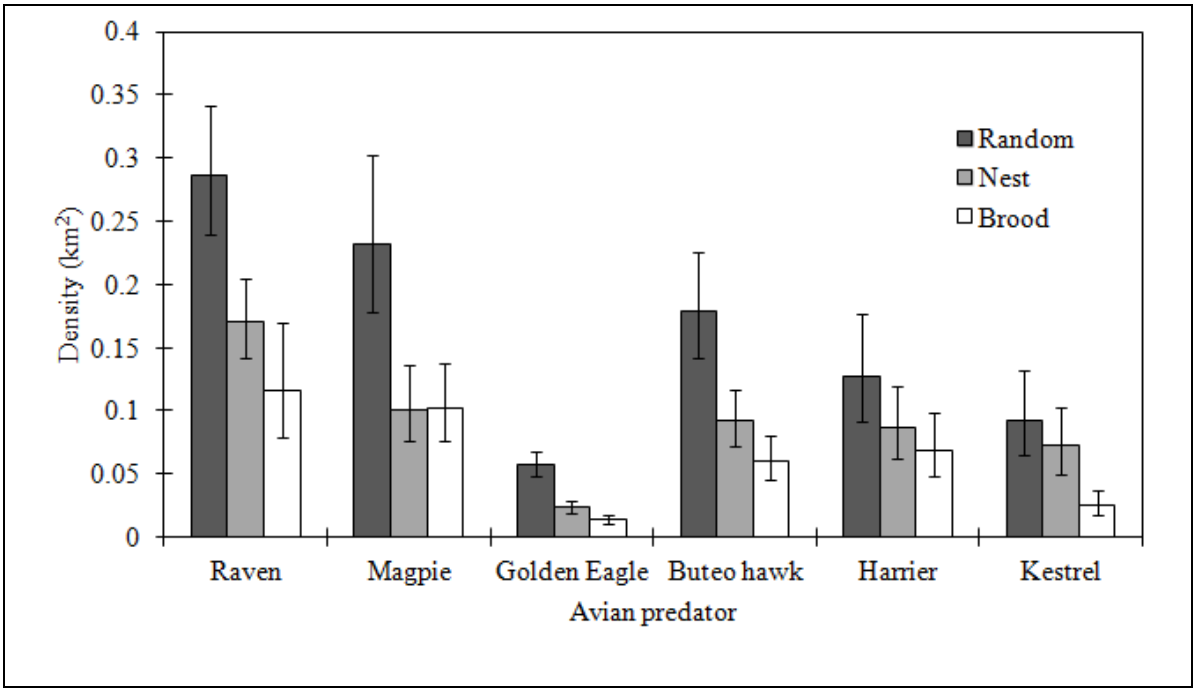



FIG. 2-3. Comparison of raven, magpie, Golden Eagle, *Buteo* hawk, harrier, and kestrel densities (per $km^2$) among sage-grouse nests, sage-grouse brood locations, and random locations. Data from 3,006 point-count surveys during 2008-2010 at 963 total point-count locations—218 sage-grouse nest locations, 249 sage-grouse brood locations (with 83 separate broods), and 496 random locations—in southwestern and south-central, Wyoming, USA. Densities were generated using radial point-count surveys and DISTANCE at sage-grouse nests, sage-grouse brood locations, and random locations. Error bars are 95% confidence intervals.

# CHAPTER 3

# GREATER SAGE-GROUSE NEST-SITE AND BROOD-SITE SELECTION IN RELATION TO AVIAN PREDATORS AND ANTHROPOGENIC AND LANDSCAPE FEATURES

ABSTRACT.—Trade-offs between using habitat and avoiding predators are common decisions for prey species such as ground-nesting birds. Prey species including Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") minimize risk of predation by avoiding predators through direct (avoid predators that are seen) and indirect (avoid riskier habitat) mechanisms. Effects of anthropogenic and landscape features on habitat selection of sage-grouse hens have not been evaluated in the context of local predator communities. From 2008–2011, I conducted 10-min point count surveys at 792 sage-grouse locations (340 nests, 331 early-brood [chicks <4 weeks of age], and 121 late-brood [chicks 4–8 weeks of age]) and 660 random locations. Brood locations were compiled from 124 separate sage-grouse broods. Using multinomial logistic regression, I compared anthropogenic and landscape features and densities of small (American Kestrel [*Falco sparverius*] and Black-billed Magpie [*Pica hudsonia*]), medium (*Buteo* spp., Common Raven [*Corvus corax*], and Northern Harrier [*Circus cyaneus*]), and large (Golden Eagle [*Aquila chrysaetos*]) avian predators among nest, early-brood, late-brood, and random locations within available sage-grouse habitat. Anthropogenic features included proximity to oil and gas structures, communication towers, power lines, roads, and rural houses; and landscape features included proximity to forested and riparian

habitats and topographic ruggedness. These comparisons allowed me to assess the relative importance of direct and indirect mechanisms of avian predator avoidance and habitat partitioning of sage-grouse hens at different reproductive stages. I found sage-grouse hens used both direct and indirect mechanisms to lower their exposure to predation and nest depredation, but avian predator densities independently described habitat selection of sage-grouse better than anthropogenic and landscape features combined. For direct avoidance, sage-grouse chose locations with lower densities of small, medium, and large avian predators compared to random locations. For indirect avoidance, sage-grouse selected locations farther away from oil and gas structures and major roads at all reproductive stages, power lines at brood locations, and riparian habitat at nest locations compared to random locations. Sage-grouse used locations closer to riparian habitat during late brood-rearing, which indicates use of areas with relatively more food to meet energy requirements of growing chicks. My analysis also suggested sage-grouse chose flatter locations at nest locations compared to random locations. My results suggest that the magnitude of direct avoidance of avian predators and the selection of proximity to anthropogenic and landscape features by sage-grouse hens were dependent on a sage-grouse's reproductive stage. Avoidance of avian predators and anthropogenic and landscape features allowed female sage-grouse to lower their risk of predation and nest depredation, while using habitat to meet energetic requirements of hens and chicks.

## INTRODUCTION

PREDATOR-AVOIDANCE BEHAVIORS can have dramatic effects on the selection of habitat by birds and other terrestrial animals and can be achieved indirectly by reducing use of risky habitats (habitats correlated with higher risk of predation) or directly by avoiding predators that are seen (Lima 1998, Verdolin 2006, Cresswell 2008; see Chapter 2). Both indirect and direct mechanisms of predator avoidance are connected to an animal's perceived risk of predation (Cresswell 2008, Martin and Briskie 2009). Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse"), a species of conservation concern (Braun 1998, Schroeder et al. 2004, Connelly et al. 2011), have recently been shown to select habitat with lower densities of avian predators (see Chapter 2). In Chapter 2, findings are presented showing that sage-grouse avoided avian predators at nest and brood locations based on the size of avian predator species rather than individual species identity. However, there were no comparisons of potential mechanisms of avoidance, such as indirect versus direct avoidance.

Anthropogenic features can be used as perches or nest structure by avian predators or can be areas that provide food subsides. American Kestrels (*Falco sparverius*; hereafter "kestrel"), Common Ravens (*Corvus corax*; hereafter "raven"), Golden Eagles (*Aquila chrysaetos*), Ferruginous Hawks (*Buteo regalis*), Red-tailed Hawks (*Buteo jamaicensis*), and Swainson's Hawks (*Buteo swainsoni*) have been found to use power lines for nesting and perching and areas around power lines for foraging (Lammers and Collopy 2007, Prather and Messmer 2010, Slater and Smith 2010). Roads

provide food resources in the form of animals killed by vehicles that attract predators. Mammalian (Bradley and Fagre 1988, Frey and Conover 2006) and avian (Boarman 1993, Boarman et al. 1995) predators also use areas near roads, because predators have increased search ability and foraging efficiency in these areas. Several studies have demonstrated sage-grouse avoid habitat with man-made features, such as oil and gas infrastructure (Aldridge 2005, Holloran 2005, Walker et al. 2007, Doherty 2008, Carpenter et al. 2010, Holloran et al. 2010), power-lines (Hanser et al. 2011), and roads (Holloran 2005, Aldridge and Boyce 2007). Thus, birds including sage-grouse may avoid man-made features to avoid the avian predators they attract.

In addition to avoidance of tall man-made structures (structures >2 m tall) and roads, prey species including sage-grouse may avoid avian predators by avoiding landscape features that represent riskier habitat such as riparian areas, conifer forests, and rough terrain. In northeastern Wyoming, Doherty et al. (2010) found that sage-grouse selected nesting habitat with lower terrain roughness and percent cover of conifer, grassland, and riparian habitat; they also found that sage-grouse selected areas with greater density of sagebrush (*Artemisia* spp.) at the patch-scale (100 m to 350 m) compared to random locations within sagebrush. Greater density of sagebrush at relatively larger scales may reduce the foraging efficiency (i.e., predator's search ability) of visual predators by increasing the number of locations available for a sage-grouse to be located, which has the potential to increase sage-grouse demographic parameters such as survival and nest success. For example, Brewer's Sparrows' (*Spizella breweri*) nesting in areas with greater shrub cover and greater density of vacant potential nest-sites had better

nest success (Chalfoun and Martin 2009).

Previous research has not compared the relative importance of indirect versus direct predator avoidance in prey species' use of habitat. Sage-grouse may avoid avian predators indirectly by avoiding anthropogenic or landscape features that might attract avian predators or directly by observing them; however, it is more likely that sage-grouse use both indirect and direct means. Thus, I used sage-grouse as a model prey species to test the importance of both indirect and direct predator avoidance. From 2008–2011, I recorded avian predator densities and calculated distances from anthropogenic and landscape features to determine the importance of direct predator avoidance relative to indirect avoidance by sage-grouse hens. I hypothesized that sage-grouse primarily avoid nesting and raising their chicks in areas with high densities of avian predators and secondarily avoid anthropogenic and landscape features that posed greater risk of predation.

As a secondary objective, I evaluated habitat partitioning of sage-grouse females during different reproductive stages (nesting, early-brood-rearing [hereafter early-brood], and late-brood-rearing [hereafter late-brood]) in relation to avian predator densities and distance to anthropogenic and landscape features. Habitat partitioning is the differential use of habitat among groups of animals, and it commonly occurs between different reproductive stages (Bañuelos et al. 2008; e.g., the food resource and shelter requirements of hens on nests are different than brood-rearing hens). Predator avoidance may also be connected to prey species' decision making process regarding partitioning of habitat. Thus, I hypothesized that sage-grouse hens (1) primarily avoided avian predators that

were a threat to adult hen survival during all reproductive stages, and secondarily avoided avian predators that were only a threat to nests and chicks; and (2) selected riparian habitat to meet the energetic requirement of adults and chicks after chicks were less vulnerable to predation.

## METHODS

*Study Areas*.—My study was conducted in southwest and south-central Wyoming. I had 12 study sites, each 16 or 24 km in diameter (eight study sites of 16-km diameter and four study sites of 24-km diameter). Holloran and Anderson (2005) found that 92.5% of 415 observed nests were within 8.5 km of leks where they were captured in central and southwest Wyoming. Thus, the study sites in southwest Wyoming were 16-km diameter and approximately centered around leks where hens were captured. Study sites in south-central Wyoming were 24-km, because sage-grouse were captured at several nearby leks over a larger area. Five study sites were located in Lincoln County (16-km diameter each), two in Sweetwater County (one 16-km diameter and one 24-km diameter), two in Uinta County (both 16-km diameter), and three in Carbon County (24-km diameter each). Study sites were chosen to provide a representation of overall sage-grouse nesting habitat in southern Wyoming with a variety of land uses and topographic features. Elevation ranged from 1,950 m to 2,600 m among all study sites. Most of my study sites were federally owned and administered by the Bureau of Land Management with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in my study sites. All study sites had anthropogenic development, which consisted

mostly of unimproved 4-wheel drive roads. Conventional natural gas, coalbed methane natural gas, and/or conventional oil extraction activities were present in six (50%) of my study sites; mean well density among all study sites was 0.12 ± 0.22 SD wells $km^{-2}$ (min–max = 0.0–0.64 wells $km^{-2}$).

The landscape at all study sites was dominated by sagebrush; Wyoming Big Sagebrush (*A. tridentata wyomingensis*) and Mountain Big Sagebrush (*A. t. vaseyana*) were the most common. Black Sagebrush (*A. nova*) and Dwarf Sagebrush (*A. arbuscula*) were found on exposed ridges. Other common shrub species in the study sites included Alderleaf Mountain Mahogany (*Cercocarpus montanus*), Antelope Bitterbrush (*Purshia tridentata*), Chokecherry (*Prunus virginiana*), Common Snowberry (*Symphoricarpos albus*), Greasewood (*Sarcobatus vermiculatus*), Rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), Saskatoon Serviceberry (*Amelanchier alnifolia*), and Spiny Hopsage (*Grayia spinosa*). Isolated stands of juniper (*Juniperus* spp.) and Quaking Aspen (*Populus tremuloides*) were found at the higher elevations on north-facing hillsides. Common forb species included Arrowleaf Balsamroot (*Balsamorhiza sagittata*), Buckwheat (*Eriogonum* spp.), Common Yarrow (*Achillea millefolium*), Dandelion (*Taraxacum* spp.), Desert Parsley (*Cymopterus* spp.), Phlox (*Phlox* spp.), Lupine (*Lupinus* spp.), Sego Lily (*Calochortus nuttallii*), and Wild Onion (*Allium* spp.). Common grass species included: Bluegrasses (*Poa* spp.), Bluebunch Wheatgrass (*Pseudoroegneria* spicata), Green Needlegrass (*Nassella viridula*), Needle and Thread (*Hesperostipa comata*), Prairie Junegrass (*Koeleria macrantha*), and Western Wheatgrass (*Pascopyrum smithii*). Cheatgrass (*Bromus tectorum*) was present, but not widespread in

any of the study sites.

*Sage-grouse Capture and Monitoring*.—I monitored sage-grouse hens during nesting and brood-rearing from 2008-2011. Hens were captured, radio-collared, and released in April of each year. I captured hens at night using ATVs, spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992). Sage-grouse hens were fitted with 17.5-g or 22-g (<1.5% body mass) necklace radio collars (RI-2D, Holohil Systems Ltd, Ontario, Canada; or A4060, Advanced Telemetry Systems Inc, Isanti, Minnesota).

I located hens on a weekly basis with Communications Specialists (R-1000, Communications Specialists, Orange, California) receivers and 3-way Yagi antennas (Communications Specialists, Orange, California). Potential nests were identified with binoculars from ~15 m by circling a radio-marked hen until she was visually spotted under a shrub. Nests were verified by triangulating the hen under the same shrub from ≥50 m away or thoroughly searching the area of the potential nest when the hen was absent. I continued monitoring nests weekly until the nest hatched or failed. I assessed nest fate as successful or unsuccessful after a hen had left her nest. A successful nest was defined as having evidence that at least one egg hatched as determined by shell membrane condition (Wallestad and Pyrah 1974). I classified unsuccessful nests as abandoned (eggs not depredated or hatched) or depredated (at least one egg with evidence of depredation and no eggs hatched).

I located the broods of radio-marked hens weekly with binoculars from ~15 m. Brood hens were identified by either visually detecting chicks or observing hen behavior that indicated the presence of a brood (e.g., hesitation to flush, feigning injury, or

clucking). I classified a sage-grouse hen as a brood hen if there was evidence of at least one chick with that hen. Monitoring of broods continued for as long as possible, which was usually until the chicks were at least 3 weeks old, the hen lost her brood, the hen died, or the hen could no longer be located (most broods were monitored 3–8 weeks post-hatch).

*Avian Predator Monitoring*.—Between May and August of each year (sage-grouse nesting and brood-rearing season), I conducted point count surveys at sage-grouse nests, sage-grouse brood locations, and random locations (hereafter; nest, brood, and random locations respectively) within each study site to compare avian predator densities. Random locations were selected in habitat considered to be available to sage-grouse for nesting within each study site. To restrict random locations to available nesting habitat, I used ArcMap version 9.2 and 10.0 (ESRI Inc., Redlands, California) to generate random locations only in sagebrush-dominated habitat, which was classified by the Northwest ReGAP landcover data from 2008 (Lennartz 2007). Random locations were designated to be ≥1,000 m apart, but after random selection average nearest neighbor distances among random point count locations was >2,000 m. I generated 12 random locations in each 16-km diameter study site and 18 random locations in each 24-km diameter study site per year. A new set of random locations was generated each year to avoid spatial autocorrelation; thus, random locations among years were independent.

To quantify avian predators, I used standard distance sampling techniques (Ralph et al. 1995, Buckland et al. 2001, Thomas et al. 2010), which entailed counting all avian predators observed during point counts and recording their distance from the observer

(when standing at the center of the point count location). I recorded distance as the distance from the observer to where an avian predator was first located (Ralph et al. 1995, Thomas et al. 2010); this minimized possible bias associated with avian predators being attracted to or flushed away from an observer. When an avian predator was displaced from the center of a point count location as an observer approached (6% of all detected birds), I recorded distance from that avian predator to the center of the point count location while the observer approached as suggested by Ralph et al. (1995). This was done when the approach of an observer resulted in an avian predator moving away from the center of the point count location. A 1500–m rangefinder (RE-1500 m, American Technologies Network Corp., San Francisco, California) in conjunction with a global positioning system (GPS) was used to estimate distances directly or to validate visually estimated distances.

To avoid disturbing an incubating hen, nest point counts were conducted 100–200 m away from a sage-grouse nest but within a line-of-sight of that sage-grouse nest. I also performed brood point counts 100–200 m away from a brood hen—estimated by triangulation—immediately before verifying that a radio-marked brood hen was still with chicks. This was intended to record avian predator densities before the observer disturbed any avian predators and to avoid flushing a brood hen when a predator was nearby. If the hen did not have chicks, the brood point count was discarded.

Observers were trained and tested in corvid and raptor identification before conducting point counts. Point counts were 10 min in length, and I conducted them during daylight hours on a weekly basis at each study site. I visited each point count

location 1 to 8 times with most locations visited ≥3 occasions. I did not survey for avian predators in inclement weather (i.e., when raining or wind speeds greater than 25 km/h; Ralph et al. 1995). Unidentified birds were not included in analyses; these contributed 2% of detections within truncated observation distances. Nest and brood point counts were performed after nests or broods were initially located; thus, nest point counts were conducted in May and June and brood point counts were conducted from mid-May to early-August. I performed random point counts throughout the nesting and early brood-rearing season (May to early-August).

I intermixed the sampling of nest, brood, and random point counts within each study site. To minimize observer bias, I changed the time of day and the observer that conducted individual point counts within a study site each week (i.e., each individual point count location regardless of type—nest, brood, or random—would be conducted at a different time of day each week and by a different observer as best as possible). The observers conducting point counts within a particular study site changed each year. Thus, I minimized observer bias by changing the observer who collected data at each individual point count location.

All avian predator variables were calculated from the raw count data within effective detection radii (EDR) estimated with DISTANCE, version 6.0 release 2 (Thomas et al. 2010) as specified in Chapter 2. Thus, *Buteo* hawk, Golden Eagle, Northern Harrier (*Circus cyaneus*; hereafter "harrier"), kestrel, Black-billed Magpie (*Pica hudsonia*; hereafter "magpie"), and raven densities were individually calculated within 450 m, 1000 m, 350 m, 400 m, 300 m, and 600 m, respectively, of each point

count location (see Chapter 2 for further details). The raw densities were standardized by the number of visits to each point count location. I used raw avian predator densities calculated by species to create small (magpie and kestrel), medium (*Buteo* hawk, harrier, and raven), and large (Golden Eagle) avian predator variables, which was shown in Chapter 2 to best describe sage-grouse avoidance of avian predators. I log transformed raw avian predator densities to reduce the effect of influential observations.

*Anthropogenic and Landscape Feature Variables*.—I used ArcMap 10.0 to calculate point count proximity (Euclidean distance) to anthropogenic features that could be used as perch or nest sites by avian predators or could provide food subsidies. Anthropogenic structures that were >2 m in height were considered available for perching or nesting by avian predators. I quantified the distance from point count locations to the nearest oil and gas structure (energy well, compressor station, transfer station, refinery, or other energy extraction related buildings), major road, gravel road, communication tower, house, and power line for each point count location. Ongoing energy development was occurring in half of my study sites, which required me to assess the dates that energy-related structures and roads were added or removed from the landscape.

In distance calculations, I only included oil and gas structures and roads that existed when each point count was conducted. I obtained information on oil and gas structures, including date construction started on the structure and date when wells were plugged and abandoned (date structure was removed), from the Wyoming Oil and Gas Conservation Commission (WOGCC; 2012). I verified the spatial location and existence

of older structures with color aerial satellite imagery from summer 2006 and August 2009 obtained from the National Agriculture Imagery Program (NAIP; U.S. Department of Agriculture [USDA] 2010). Aerial imagery from NAIP is produced by the USDA on a 3-year rotation; thus, I used WOGCC data and on the ground GPS units to map energy development that occurred after August 2009.

I used 2009 NAIP imagery to digitize the location of major roads, all roads, communication towers, and houses within a 5-km buffer around study sites; roads constructed between August 2009 and September 2011 were mapped on the ground with GPS units. Major roads included paved, improved gravel roads, and railroads; whereas, all roads included major roads and all unimproved 4-wheel drive roads. All transmission and distribution power lines within a 5-km buffer around study sites were mapped on the ground with GPS units; telephone lines not associated with a power line were included in power line mapping.

Neither sage-grouse nor avian predators were likely to discriminate between many of different types of anthropogenic structures. Thus, I created 2 anthropogenic structure variables that represented the nearest (1) distance to either an oil and gas structure, communication tower, or house (WCH); and (2) distance to either an oil and gas structure, communication tower, house, or power line (ANTH). This was in addition to distances from point count locations to individual types of anthropogenic structures.

Similar to anthropogenic features, some types of landscape features could be used as perches or nest structure by avian predators, or could be areas with higher productivity that attract predators. Thus, I used ArcMap 10.0 to calculate the distance from every

point count location to forested (deciduous or conifer stands) and riparian habitats. Tree stands and riparian habitat were identified with Northwest ReGAP landcover data from 2011 (Lennartz 2007), and verified with NAIP imagery from 2009. Topography with greater surface roughness has the potential to create topographic structures (e.g., hilltops, knolls, and cliff edges) that provide vantage points similar to perches. For every point count location, I used ArcMap 10.0 to extract topographic ruggedness index (TRI) values generated by Hanser et al. (2011) for the Wyoming Basins Ecoregion; TRI variables were developed using a moving window analysis at 0.27-km, 0.54-km, 1-km, and 3-km radii (0.23-$km^2$, 0.92-$km^2$, 3.14-$km^2$, and 28.26-$km^2$ scales, respectively). Riley et al. (1999) created TRI to describe the roughness of landscapes, and the index is quantified as the difference in elevation among adjacent pixels of a digital elevation map; the index is then averaged over a user-defined area.

Euclidean distance is not a good measure of habitat selection by wildlife, because the response of a species to anthropogenic or landscape features often decline as distance increases (Carpenter et al. 2010, Fedy and Martin 2011, Hanser et al. 2011). Thus, I calculated distance decay functions to allow for nonlinear avoidance of anthropogenic or landscape features, which were expressed as:

Decay function = exp^(Euclidean distance to feature (km)/-decay distance) 1)

I calculated all decay functions with 3 decay distances (0.25 km, 0.50 km, and 1 km). Decay functions scaled distance variables between 0 and 1 with greater values corresponding to point count locations closer to anthropogenic or landscape features.

*Data Analyses*.—To evaluate habitat selection of nesting and brood-rearing sage-

grouse hens in reference to avoidance of avian predators and anthropogenic and landscape features, I fit multinomial logistic regression models with maximum likelihood using function multinom in package nnet version 7.3-4 in R (R 2.14.2; R Foundation for Statistical Computing 2009). Multinomial logistic regression models have been used to model habitat selection of wildlife species with >2 response categories. I categorized point count locations into 4 response categories (1) random, (2) sage-grouse nest, (3) early-brood (chicks <4 weeks of age), and (4) late-brood (chicks 4–8 weeks of age). Multinomial logistic regression uses 1 category as the reference for comparisons with all other categories. To compare sage-grouse habitat selection to available sagebrush habitat (random locations), I made comparisons of sage-grouse locations to random locations by coding random locations as the reference category. I then alternated nest and early-brood as the reference category to compare between sage-grouse locations. Modeling of sage-grouse habitat selection was conducted with an information theoretic approach (Anderson 2008). I compared models with Akaike's information criterion corrected for small sample sizes ($AIC_c$) and Akaike weights ($w_i$; Burnham and Anderson 2002) with function aictab in package aiccmodavg version 1.25 in R. I employed sequential $AIC_c$ modeling of covariate sets, which was suggested by Arnold (2010) as an appropriate approach for identifying and ranking the most parsimonious models. Non-informative covariates (85% confidence intervals [CIs] of parameter estimates overlapped 0) were eliminated within each covariate set before comparing top $AIC_c$ selected models among covariate sets (Arnold 2010). I classified models within 2 $AIC_c$ of the null model as being non-competitive (Burnham and Anderson 2002); thus, any model within 2 $AIC_c$ of the null

was omitted from further analyses.

Anthropogenic and landscape covariate sets were evaluated sequentially (Step 1) then compared with the best avian predator model from Chapter 2 (Step 2). Details on avian predator modeling procedures can be found in Chapter 2. I did not include WCH or ANTH with any anthropogenic structure variable that was used to create WCH or ANTH. The best variable describing the effect of anthropogenic structures on habitat selection by sage-grouse was determined through $AIC_c$ selection within the anthropogenic feature covariate set. For all distance decay functions, I chose the best decay distance (0.25 km, 0.50 km, and 1 km) for each distance variable by comparing all 3 decay distances with $AIC_c$. I compared models with individual TRI variables measured at 0.27-km, 0.54-km, 1-km, and 3-km radii with $AIC_c$ to choose the best spatial scale for the TRI variable to be used in the landscape feature covariate set; the TRI variable scale with the lowest $AIC_c$ was used in all further modeling. As the final modeling step, I compared all top $AIC_c$ selected models from every covariate set (models within 2 $AIC_c$ of the top model within each covariate set) among each other and as additive models with combinations of the avian predator model and anthropogenic and landscape feature covariate set models. I based my inference on models within 2 $AIC_c$ of the top selected model (Burnham and Anderson 2002). I prevented multicollinearity by only including one variable of any pair of variables that co-varied in any model ($r$ >0.65) as determined with a Pearson's correlation matrix. In this situation I eliminated one co-varying variable from further analysis by retaining the variable that made the most biological sense. Variance inflation factors (VIF) for all predictor variables were ≤5, which indicated that the variances of

coefficient values were not drastically increased by the inclusion of any predictor variable; thus, collinearity was not a major problem.

Although I could not test for spatial autocorrelation in multinomial logistic regressions, avian predator densities derived from distance sampling techniques are robust to lack of independence of observation locations because distance sampling is setup to be a snap-shot in time (Thomas et al. 2010). My avian predator sampling was designed to count the greatest proportion of avian predators within a study site each week while not counting the same avian predator more than once per week as suggested by Ralph et al. (1995) and Thomas et al. (2010). Conducting all point counts within a study site in one day reduced the possibility of double-counting individual avian predators during that week's visit. Counting the same individual avian predator during different weeks, regardless of the particular point count location, was properly scaled by accounting for survey effort. Replication of point counts by sampling multiple weeks was done to increase the proportion of avian predators detected as suggested by Thomas et al. (2010). When evaluating avian predator densities between sage-grouse and random locations, the findings from Chapter 2 accounted for spatial autocorrelation in generalized linear mixed models; however, accounting for spatial autocorrelation did not significantly change coefficient values of their avian predator models. Furthermore, multinomial logistic regression only requires that successive habitat selection choices be independent (Agresti 2007). I made the assumption that successive locations from the same sage-grouse were sufficiently far apart in time to be effectively independent. This was reasonable because sage-grouse locations were ~1 week apart in my study.

# RESULTS

I conducted 4,441 point count surveys at 1,452 locations during 2008–2011 including 340 sage-grouse nest, 331 sage-grouse early-brood, 121 sage-grouse late-brood, and 660 random locations. Brood locations were compiled from 124 separate sage-grouse broods. I counted 196 *Buteo* hawks, 295 Golden Eagles, 77 harriers, 105 kestrels, 143 magpies, and 688 ravens within species-specific EDRs (see Chapter 2), which equated to 248 small, 961 medium, and 295 large avian predators. Brood, nest, and random locations were on average 841 m, 1,997 m, and 2,301 m apart, respectively. There was no evidence of multicollinearity between avian predator variables and anthropogenic or landscape feature variables, because avian predator variables did not co-vary with any other variable ($r^2 < 0.02$) and VIF $\leq 5$.

During Step 1 of sequential modeling, I found sage-grouse selection of nest and brood locations was partially based on anthropogenic and landscape feature variables (Table 3-1). The top $AIC_c$ selected anthropogenic feature model ($w_i = 0.99$) included proximity to oil and gas structures, power lines, rural houses, and major roads; and the top $AIC_c$ selected landscape feature model ($w_i = 0.50$) included proximity to riparian habitat and TRI (Table 3-1). Proximity to oil and gas structures was best described as a distance decay function calculated with the 0.25-km distance decay ($OGS_{0.25}$). Power lines, rural houses, major roads, and riparian habitat were best described as distance decay functions calculated with the 1-km distance decay ($POW_{1.0}$, $HOM_{1.0}$, $MRD_{1.0}$, and $RIP_{1.0}$, respectively). Thus, the effect of proximity to oil and gas structures on sage-

grouse selection of nesting and brood locations became negligible closer to sage-grouse locations compared to proximity to all other predictive anthropogenic and landscape features (i.e., the effect of distance from sage-grouse locations to oil and gas structures [0.25-km distance decay function] decayed faster than the effects of distance to power lines, rural houses, major roads, and riparian habitat [1-km distance decay functions]). I found TRI calculated at the 0.54-km radius ($TRI_{0.54}$) fit the data best.

During Step 2 of sequential modeling, my analyses indicated that sage-grouse hen selection of nest and brood locations was best described by avian predator densities in conjunction with proximity to anthropogenic and landscape features with $w_i = 1.00$ (Table 3-2). Even though the best model incorporated avian predator densities and anthropogenic and landscape feature variables, the avian predator density model ($AIC_c$ = 88.57) independently described sage-grouse selection of nest and brood locations much better than the anthropogenic and landscape feature ($AIC_c$ = 313.52) model (Table 3-2). This indicated that small, medium, and large avian predators had a relatively greater correlation with sage-grouse selection of nest and brood locations compared to anthropogenic and landscape features.

Greater densities of small, medium, and large avian predators were negatively correlated with sage-grouse nest, early-brood, and late-brood locations compared to random locations (Table 3-3). My analysis also indicated that early-brood and late-brood sage-grouse locations had lower avian predator densities compared to nesting sage-grouse (Table 3-4). During each reproductive stage, sage-grouse avoided small and medium avian predators at similar magnitudes, and also exhibited greater avoidance of large avian

predators than small or medium avian predators (Tables 3-3 and 3-4).

Sage-grouse responded to anthropogenic features by avoiding them regardless of the sage-grouse's reproductive stage. I found nesting, early-brood, and late-brood sage-grouse were farther away from oil and gas structures and major roads compared to random locations (Table 3-3). Early-brood and late-brood sage-grouse were farther away from power lines compared to random locations (Table 3-3). In contrast to the avoidance of other anthropogenic structures, my analysis indicated that early-brood and late-brood sage-grouse were closer to houses compared to random locations and nest locations (Tables 3-3 and 3-4).

For landscape feature variables, I found sage-grouse differed in their response to proximity to riparian habitat and TRI depending on their reproductive stage. Compared to random locations, sage-grouse selected nest locations farther away from riparian habitat, early-brood sage-grouse neither selected for nor avoided habitat based on proximity to riparian habitat, and late-brood sage-grouse selected locations closer to riparian habitat (Table 3-3). However, both early-brood and late-brood locations were closer to riparian habitat compared to nest locations, and late-brood locations were closer to riparian habitat than early-brood locations (Table 3-4). Sage-grouse nest-sites were located in areas with flatter topography compared to random locations (Table 3); I did not find this effect at sage-grouse early-brood or late-brood locations. Sage-grouse at early-brood and late-brood locations selected relatively more rugged topography compared to nesting sage-grouse (Table 3-4).

# DISCUSSION

Sage-grouse hens used direct and indirect mechanisms to lower their exposure to predation and nest depredation particularly from avian predators. In general, sage-grouse avoided risky habitat by directly avoiding areas with higher densities of small, medium, and large avian predators and indirectly by avoiding areas close to anthropogenic and landscape features. Similar to previous research, my analyses confirmed that sage-grouse select locations farther away from anthropogenic and landscape features that could be used as perches or provide subsidized food resources for predators, which included oil and gas structures (Aldridge 2005, Holloran 2005, Walker et al. 2007, Doherty 2008, Holloran et al. 2010, Kirol 2012) and major roads (Holloran 2005, Aldridge and Boyce 2007) at all reproductive stages, power lines (Hanser et al. 2011) at brood locations, and riparian habitat (Doherty et al. 2010, Dzialak et al. 2011) at nest locations. Sage-grouse also chose flatter locations at nest-sites similar to findings from Doherty et al. (2010), Dzialak et al. (2011), and Kirol (2012). Habitat partitioning during vulnerable reproductive stages by female sage-grouse relative to predation risk and food availability was a means for sage-grouse hens to lower their risk of predation and nest depredation, while using habitat to meet energetic requirements of hens and chicks (Connelly et al. 2004, Aldridge and Boyce 2007, Dzialak et al. 2011).

High densities of avian predators including *Buteo* hawks (MacLaren et al. 1988, Schroeder et al. 1999, Schroeder and Baydack 2001), Golden Eagles (MacLaren et al. 1988, Danvir 2002), harriers (Schroeder et al. 1999, Thirgood et al. 2000, Fletcher et al.

2003), kestrels (Schroeder et al. 1999), magpies (Holloran and Anderson 2003, Vander Haegen et al. 2002), and ravens (Manzer and Hannon 2005, Bui et al. 2010, Coates and Delehanty 2010) have the potential to negatively affect nest success or adult and chick survival of grouse species, and one of the responses of prey species to the presence of these predators is avoidance (Lima 1998, Evans 2004, Cresswell 2008, Dinkins et al. 2012). Similar to Dinkins et al. (2012), my analysis indicated that sage-grouse avoidance of avian predators occurred during many reproductive stages—nesting, early-brood, and late-brood—but at different magnitudes. My results also suggest sage-grouse hens have the ability to distinguish between threats to their survival, nests, and offspring.

Large avian predators (Golden Eagles) were avoided by sage-grouse hens at greater magnitudes than smaller avian predators within each reproductive stage suggesting sage-grouse hens were predominantly concerned with their own survival (i.e., smaller parameter estimates for large avian predators compared to small and medium avian predators when comparing sage-grouse locations to random locations; Table 3-3). It was not surprising that sage-grouse hens protected themselves from their primary predator (Golden Eagle; Schroeder et al. 1999, Schroeder and Baydack 2001, Mezquida et al. 2006), because sage-grouse are a relatively long-lived bird (Connelly et al. 2011). Johnson and Braun (1999) and Taylor et al. (2012) found adult survival was the most influential demographic parameter on sage-grouse population growth, and they also illustrated that following adult survival, chick survival then nest success were the next most important factors affecting population growth for sage-grouse. My results also

indicate that early-brood and late-brood locations had greater magnitudes of avian predator avoidance than nest locations, which can be explained by the greater mobility of broods compared to nests and the duration of time spent in a particular location. Thus, reducing risk of nest depredation and chick mortality by avoiding small and medium sized avian predators likely increased sage-grouse reproductive output.

In addition to avoidance of avian predators, sage-grouse selected habitat in response to anthropogenic and landscape features. As expected, I found that sage-grouse primarily used direct avoidance of avian predators and secondarily avoided riskier habitat. Direct and indirect avoidance of avian predators were not necessarily linked (correlated) from the perspective of a sage-grouse, because indirect cues (perches and areas with subsidized food for predators) were not correlated with any avian predator species ($r^2 < 0.02$). This indicated that anthropogenic and landscape features may not be the best indicators of potential predation risk, but represent areas of greater perceived risk of predation by sage-grouse. Prey species' ability to predict and avoid risky habitat increases survival and reproductive success, but the ability to directly avoid predators is more beneficial than indirect cues of predation risk (Thomson et al. 2006). Both mechanisms presumably achieve reduced predation rates; however, there may be other population limiting effects as a result of predator avoidance such as reduced foraging ability of prey species in areas of lower habitat quality (Lima 1998, Evans 2004, Cresswell 2008).

Habitat use is a trade-off among protection from exposure to the environment (weather), starvation, and predation (Verdolin 2006), which can be considered habitat

partitioning. Similar to Dzialak et al. (2011), my results confirmed that sage-grouse have opposing responses to proximity to riparian habitat depending on reproductive stage. Sage-grouse were farther away from riparian habitat while nesting, but chose locations closer to riparian areas during late-brood. Nesting occurred away from riparian areas, because starvation was not a factor for nesting sage-grouse hens. However, chicks have increasing energetic demands as they grow, and sage-grouse hens typically move broods to riparian areas after early-brood-rearing (Crawford et al. 2004, Gregg and Crawford 2009). Riparian habitats provide forbs and invertebrates that meet the energetic demands of growing sage-grouse chicks (Connelly et al. 2004, Aldridge and Boyce 2007, Dzialak et al. 2011). Sage-grouse appear to minimize the negative effects of increased predation risk associated with riparian areas by directly avoiding avian predators and indirectly by avoiding riparian habitat during relatively more vulnerable reproductive stages (nest and early-brood). Sage-grouse early-brood and late-brood locations were closer to rural houses compared to random and nest locations, which may be explained by the distribution of rural houses in higher quality sagebrush habitat (more productive); however, this is speculative and deserves more research. Thus, sage-grouse selection of brood locations closer to rural houses was likely a response similar to their response to riparian habitat.

Predation risk trade-offs and non-lethal predator effects, such as avoidance of risky habitats and habitats occupied by greater density of avian predators (Evans 2004, Verdolin 2006, Cresswell 2008), are mechanisms that explain habitat partitioning of female sage-grouse. High densities of avian predators and close proximity to

anthropogenic and landscape features—specifically oil and gas infrastructure, power lines, major roads, riparian habitat, and rugged topography—are likely to result in reduced adult survival and higher depredation rates on sage-grouse nests (Lima 1998, Evans 2004, Cresswell 2008). My results indicated that both direct (avian predators) and indirect (oil and gas structures, power lines, roads, rugged topography, and riparian habitat) mechanisms were used by sage-grouse to presumably avoid predation and nest depredation. Sage-grouse use of habitat was negatively connected to avian predator densities with quality sage-grouse habitat presumably having lower densities of small, medium, and large avian predators. The presence of greater abundances of avian predators may induce changes in sage-grouse behavior associated to habitat usage. Thus, human manipulation of habitat that structurally changes habitat and promotes greater density of avian predators may limit sage-grouse populations, because habitat that has high quality cover and forage may become functionally unavailable to sage-grouse when avian predator densities are at high levels and anthropogenic features are nearby.

## LITERATURE CITED

AGRESTI, A. 2007. An Introduction to Categorical Data Analysis, 2nd ed. John Wiley and Sons, Hoboken, New Jersey.

ALDRIDGE, C. L. 2005. Identifying habitats for persistence of Greater Sage-Grouse (*Centrocercus urophasianus*) in Alberta, Canada. Ph.D. dissertation, University of Alberta, Edmonton, Canada.

ALDRIDGE, C. L., AND M. S. BOYCE. 2007. Linking occurrence and fitness to persistence:

Habitat-based approach for endangered Greater Sage-Grouse. Ecological Applications 17:508–526.

ANDERSON, D. R. 2008. Model Based Inference in the Life Sciences: A Primer on Evidence. Springer Science, New York.

ARNOLD, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175–1178.

BAÑUELOS, M., M. QUEVEDO, AND J. OBESO. 2008. Habitat partitioning in endangered Cantabrian Capercaillie (*Tetrao urogallus cantabricus*). Journal of Ornithology 149:245–252.

BOARMAN, W. I. 1993. When a native predator becomes a pest: A case study. Pages 191–206 *in* Conservation and Resource Management (S. K. Majumdar, E. W. Miller, D. E. Baker, E. K. Brown, J. R. Pratt, and R. F. Schmalz, Eds.). Pennsylvania Academy of Science, Easton, Pennsylvania.

BOARMAN, W. I., R. J. CAMP, M. HAGAN, AND W. DEAL. 1995. Raven abundance at anthropogenic resources in the western Mojave Desert, California. Report to Edwards Air Force Base, California. National Biological Service, Riverside.

BRADLEY, L. C., AND D. B. FAGRE. 1988. Coyote and Bobcat responses to integrated ranch management practices in south Texas. Journal of Range Management 41:322−327.

BRAUN, C. E. 1998. Sage grouse declines in western North America: What are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139–156.

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, AND L. THOMAS. 2001. Introduction to Distance Sampling. Oxford University Press, New York.

BUI, T. D., J. M. MARZLUFF, AND B. BEDROSIAN. 2010. Common Raven activity in relation to land use in western Wyoming: Implications for Greater Sage-Grouse reproductive success. Condor 112:65−78.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model Selection and Multimodel Inference: A Practical Information–Theoretic Approach, 2nd ed. Springer-Verlag, New York.

CARPENTER, J., C. L. ALDRIDGE, AND M. S. BOYCE. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 74:1806−1814.

CHALFOUN, A. D., AND T. E. MARTIN. 2009. Habitat structure mediates predation risk for sedentary prey: Experimental tests of alternative hypotheses. Journal of Animal Ecology 78:497−503.

COATES, P. S., AND D. J. DELEHANTY. 2010. Nest predation of Greater Sage-Grouse in relation to microhabitat factors and predators. Journal of Wildlife Management 74:240–248.

CONNELLY, J. W., C. A. HAGEN, AND M. A. SCHROEDER. 2011. Characteristics and dynamics of Greater Sage-Grouse populations. Pages 53–67 *in* Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and Its Habitats (S. T. Knick and J. W. Connelly, Eds.). Studies in Avian Biology, University of California Press, Berkeley.

CONNELLY, J. W., S. T. KNICK, M. A. SCHROEDER, AND S. J. STIVER. 2004. Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Unpublished Report, Cheyenne, Wyoming.

CRAWFORD, J. A., R. A. OLSON, N. E. WEST, J. C MOSLEY, M. A. SCHROEDER, T. D. WHITSON, R. F. MILLER, M. A. GREGG, AND C. S. BOYD. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2−19.

CRESSWELL, W. 2008. Non-lethal effects of predation in birds. Ibis 150:3−17.

DANVIR, R. E. 2002. Sage grouse ecology and management in northern Utah sagebrush-steppe. Deseret Land and Livestock Wildlife Research Report, Deseret Land and Livestock Ranch and the Utah Foundation for Quality Resource Management, Woodruff, Utah.

DOHERTY, K. E. 2008. Sage-grouse and energy development integrating science with conservation planning to reduce impacts. Ph.D. dissertation, University of Montana, Missoula.

DOHERTY, K. E., D. E. NAUGLE, AND B. L. WALKER. 2010. Greater Sage-Grouse nesting habitat: The importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

DZIALAK, M. R., C. V. OLSON, S. M. HARJU, S. L. WEBB, J. P. MUDD, J. B. WINSTEAD, AND L. D. HAYDEN-WING. 2011. Identifying and prioritizing Greater Sage-Grouse nesting and brood-rearing habitat for conservation in human-modified landscapes.

PloS One 6:1–18.

EVANS, K. L. 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.

FEDY, B., AND K. MARTIN. 2011. The influence of fine-scale habitat features on regional variation in population performance of alpine White-tailed Ptarmigan. Condor 113:306–315.

FLETCHER, Q. E., C. W. DOCKRILL, D. J. SAHER, AND C. L. ALDRIDGE. 2003. Northern Harrier (*Circus cyaneaus*) attacks on Greater Sage-Grouse (*Centrocercus urophasianus*) in southern Alberta. Canadian Field-Naturalist 117:479–480.

FREY, S. N., AND M. R. CONOVER. 2006. Habitat use by meso-predators in a corridor environment. Journal of Wildlife Management 70:1111–1118.

GIESEN, K. M., T. J. SCHOENBERG, AND C. E. BRAUN. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

GREGG, M. A., AND J. A. CRAWFORD. 2009. Survival of greater sage-grouse chicks and broods in the northern Great Basin. Journal of Wildlife Management 73:904–913.

HANSER, S. E., M. LEU, S. T. KNICK, AND C. L. ALDRIDGE. 2011. Sagebrush Ecosystem Conservation and Management: Ecoregional Assessment Tools and Models for the Wyoming Basins. Allen Press, Lawrence, Kansas.

HOLLORAN, M. J. 2005. Greater Sage-Grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Ph.D. dissertation, University of Wyoming, Laramie.

HOLLORAN, M. J., AND S. H. ANDERSON. 2003. Direct identification of northern sage-

grouse (*Centrocercus urophasianus*) nest predators using remote sensing cameras. Canadian Field-Naturalist 117:308–310.

HOLLORAN, M. J., AND S. H. ANDERSON. 2005. Spatial distribution of Greater Sage-Grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.

HOLLORAN, M. J., R. C. KAISER, AND W. A. HUBERT. 2010. Yearling Greater Sage-Grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

JOHNSON, K. H., AND C. E. BRAUN. 1999. Viability and conservation of an exploited sage-grouse population. Conservation Biology 13:77–84.

KIROL, C. P. 2012. Quantifying habitat importance for Greater Sage-Grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. M. S. thesis, University of Wyoming, Laramie.

LAMMERS, W. M., AND M. W. COLLOPY. 2007. Effectiveness of avian predator perch deterrents on electric transmission lines. Journal of Wildlife Management 71:2752–2758.

LENNARTZ, S. 2007. USGS Gap Analysis Program (GAP) species distribution model. Sanborn Map Corporation. Portland, Oregon.

LIMA, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. BioScience 48:25–34.

MACLAREN, P. A., S. H. ANDERSON, AND D. E. RUNDE. 1988. Food habits and nest characteristics of breeding raptors in southwestern Wyoming. Great Basin Naturalist 48:548–553.

MANZER, D. L., AND S. J. HANNON. 2005. Relating grouse nest success and corvid density to habitat: A multi-scale approach. Journal of Wildlife Management 69:110–123.

MARTIN, T. E., AND J. V. BRISKIE. 2009. Predation on dependent off-spring: A review of the consequences for mean expression and phenotypic plasticity in avian life history traits. Annals of the New York Academy of Sciences 1168:201–217.

MEZQUIDA, E. T., S. J. SLATER, AND C. W. BENKMAN. 2006. Sage-grouse and indirect interactions: Potential implication of coyote control on sage-grouse populations. Condor 108:747–759.

PRATHER, P. R., AND T. A. MESSMER. 2010. Raptor and corvid response to power distribution line perch deterrents in Utah. Journal of Wildlife Management 74:796–800.

RALPH, C. J., S. DROEGE, AND J. R. SAUER. 1995. Managing and monitoring birds using point counts: Standards and applications. United States Department of Agriculture, Forest Service General Technical Report PSW-GTR-149, Berkeley, California.

RILEY, S. J., S. D. DEGLORIA, AND R. ELLIOT. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:1–4.

SCHROEDER, M. A., C. L. ALDRIDGE, A. D. APA, J. R. BOHNE, C. E. BRAUN, S. D. BUNNELL, J. W. CONNELLY, P. A. DEIBERT, S. C. GARDNER, M. A. HILLIARD, G. D. KOBRIGER, S. M. MCADAM, C. W. MCCARTHY, J. J. MCCARTHY, D. L. MITCHELL, E. V. RICKERSON, AND S. J. STIVER. 2004. Distribution of sage grouse

in North America. Condor 106:363–376.

SCHROEDER, M. A., AND R. K. BAYDACK. 2001. Predation and the management of prairie grouse. Wildlife Society Bulletin 29:24–32.

SCHROEDER, M. A., J. R. YOUNG, AND C. E. BRAUN. 1999. Sage grouse (*Centrocercus urophasianus*). *In* Birds of North America, no. 425 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

SLATER, S. J., AND J. P. SMITH. 2010. Effectiveness of raptor perch deterrents on an electrical transmission line in southwestern Wyoming. Journal of Wildlife Management 74:1080–1088.

TAYLOR, R. L., B. L. WALKER, D. E. NAUGLE, AND L. S. MILLS. 2012. Managing multiple vital rates to maximize Greater Sage-Grouse population growth. Journal of Wildlife Management 76:336−347.

THIRGOOD, S. J., S. M. REDPATH, P. ROTHERY, AND N. J. AEBISCHER. 2000. Raptor predation and population limitation in Red Grouse. Journal of Animal Ecology 69:504–516.

THOMAS, L., S. T. BUCKLAND, E. A. REXSTAD, J. L. LAAKE, S. STRINDBERG, S. L. HEDLEY, J. R. B. BISHOP, R. A. MARQUES, AND K. P. BURNHAM. 2010. Distance software: Design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

THOMSON, R. L., J. T. FORSMAN, F. SARDÀ -PALOMERA, AND M. MÖNKKÖNEN. 2006. Fear factor: Prey habitat selection and its consequences in a predation risk landscape.

Ecography 29:507–514.

U.S. DEPARTMENT OF AGRICULTURE. 2010. 2009 NAIP survey: Summary report. Farm Service Agency, Aerial Photography Field Office, Salt Lake City, Utah.

VANDER HAEGEN, W. M., M. A. SCHROEDER, AND R. M. DEGRAAF. 2002. Predation on real and artificial nests in shrubsteppe landscapes fragmented by agriculture. Condor 104:496–506.

VERDOLIN, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457–464.

WAKKINEN, W. L., K. P. REESE, J. W. CONNELLY, AND R. A. FISCHER. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

WALKER, B. L., D. E. NAUGLE, AND K. E. DOHERTY. 2007. Greater Sage-Grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

WALLESTAD, R. O., AND D. B. PYRAH. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

WYOMING OIL AND GAS CONSERVATION COMMISSION (WOGCC). 2012. WOGCC homepage. [Online.] Available at http://wogcc.state.wy.us.

TABLE 3-1. Multinomial logistic regression models comparing proximity to anthropogenic and landscape features among locations used by sage-grouse (nest, early-brood, and late-brood locations) and random locations. Anthropogenic and landscape features covariate sets were compared separately with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). The anthropogenic feature covariate set included distance decay functions to the nearest oil and gas structure (0.25-km decay function; $OGS_{0.25}$); power line (1.0-km decay function; $POW_{1.0}$); rural house (1.0-km decay function; $HOM_{1.0}$); major road (1.0-km decay function; $MRD_{1.0}$); gravel road (1.0-km decay function; $GRD_{1.0}$); closest oil and gas structure, communication tower, or house (0.25-km decay function; $WCH_{0.25}$); and closest oil and gas structure, communication tower, house, or power line (0.50-km decay function; $ANTH_{0.50}$). The landscape feature covariate set included distance decay functions to riparian (1.0-km decay function; $RIP_{1.0}$) and forested (0.25-km decay function; $TREE_{0.25}$) habitat and topographic ruggedness calculated at 0.54-km radius ($TRI_{0.54}$). Data were collected from 1,452 point count locations—340 sage-grouse nests, 331 sage-grouse early-brood locations, 121 sage-grouse late-brood locations, and 660 random locations—from eight study sites (16-km diameter) and four study sites (24-km diameter) in southern Wyoming, USA, 2008–2011.

| Models[a] | $k$ | $\Delta AIC_c$ | $w_i$ | Deviance |
|---|---|---|---|---|
| Anthropogenic covariate set | | | | |
| $OGS_{0.25}$, $POW_{1.0}$, $HOM_{1.0}$, $MRD_{1.0}$ [a] | 15 | 0.00 | 0.99 | 3539.60 |

| | | | | |
|---|---|---|---|---|
| $OGS_{0.25}$, $POW_{1.0}$, $HOM_{1.0}$ | 12 | 9.19 | 0.01 | 3554.92 |
| $OGS_{0.25}$, $POW_{1.0}$, $MRD_{1.0}$ | 12 | 17.88 | 0.00 | 3563.60 |
| $OGS_{0.25}$, $POW_{1.0}$ | 9 | 20.77 | 0.00 | 3572.58 |
| $OGS_{0.25}$, $MRD_{1.0}$ | 9 | 26.80 | 0.00 | 3578.60 |
| $HOM_{1.0}$, $MRD_{1.0}$ | 9 | 28.28 | 0.00 | 3580.10 |
| $WCH_{0.25}$, $POW_{1.0}$, $MRD_{1.0}$ | 12 | 28.89 | 0.00 | 3574.62 |
| $WCH_{0.25}$, $POW_{1.0}$ | 9 | 30.63 | 0.00 | 3582.44 |
| $POW_{1.0}$, $MRD_{1.0}$ | 9 | 33.42 | 0.00 | 3585.24 |
| $POW_{1.0}$ | 6 | 35.25 | 0.00 | 3593.12 |
| $ANTH_{0.50}$, $MRD_{1.0}$ | 9 | 36.44 | 0.00 | 3588.26 |
| $OGS_{0.25}$ | 6 | 38.26 | 0.00 | 3596.14 |
| $WCH_{0.25}$, $MRD_{1.0}$ | 9 | 38.41 | 0.00 | 3590.22 |
| $ANTH_{0.50}$ | 6 | 44.67 | 0.00 | 3602.54 |
| $MRD_{1.0}$ | 6 | 44.72 | 0.00 | 3602.60 |
| $HOM_{1.0}$ | 6 | 47.03 | 0.00 | 3604.90 |
| $WCH_{0.25}$ | 6 | 48.28 | 0.00 | 3606.16 |
| $GRD_{1.0}$ | 6 | 49.44 | 0.00 | 3607.32 |
| Intercept only | 3 | 55.20 | 0.00 | 3619.12 |
| Landscape covariate set | | | | |
| $RIP_{1.0}$, $TRI_{0.54}$ [b] | 9 | 0.00 | 0.50 | 3569.22 |
| $TREE_{0.25}$, $RIP_{1.0}$ | 9 | 1.26 | 0.27 | 3570.48 |

| | | | | |
|---|---|---|---|---|
| $TREE_{0.25}$, $RIP_{1.0}$, $TRI_{0.54}$ | 12 | 1.60 | 0.22 | 3564.74 |
| $RIP_{1.0}$ | 6 | 8.52 | 0.01 | 3583.80 |
| $TRI_{0.54}$ | 6 | 25.38 | 0.00 | 3600.66 |
| $TREE_{0.25}$, $TRI_{0.54}$ | 9 | 27.68 | 0.00 | 3596.90 |
| $TREE_{0.25}$ | 6 | 29.81 | 0.00 | 3605.10 |
| Intercept only | 3 | 37.79 | 0.00 | 3619.12 |

[a]$AIC_c$ = 3569.94

[b]$AIC_c$ = 3587.34

TABLE 3-2. Multinomial logistic regression models comparing avian predator densities and proximity to anthropogenic and landscape features among locations used by sage-grouse (nest, early-brood, and late-brood locations) and random locations. Combinations of singular and additive models created from the top $AIC_c$ selected avian predator model and anthropogenic and landscape feature models were compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). The avian predator model (avian) included log transformed small, medium, and large avian predator densities. The anthropogenic feature model (anthropogenic) included distance decay functions to nearest oil and gas structure (0.25-km decay function; $OGS_{0.25}$), power line (1.0-km decay function; $POW_{1.0}$), rural house (1.0-km decay function; $HOM_{1.0}$), and major road (1.0-km decay function; $MRD_{1.0}$). The landscape feature model (landscape) included a distance decay function to the nearest riparian habitat (1.0-km decay function; $RIP_{1.0}$) and topographic ruggedness calculated at 0.54-km radius ($TRI_{0.54}$). Data were collected from 1,452 point count locations—340 sage-grouse nests, 331 sage-grouse early-brood locations, 121 sage-grouse late-brood locations, and 660 random locations—from eight study sites (16-km diameter) and four study sites (24-km diameter) in southern Wyoming, USA, 2008–2011.

| Models | $k$ | $\Delta AIC_c$ | $w_i$ | Deviance |
|---|---|---|---|---|
| Avian, anthropogenic, landscape [a] | 30 | 0.00 | 1.00 | 3171.92 |
| Avian, anthropogenic | 24 | 36.56 | 0.00 | 3220.94 |
| Avian, landscape | 18 | 50.67 | 0.00 | 3247.42 |

| | | | | |
|---|---|---|---|---|
| Avian | 12 | 88.57 | 0.00 | 3297.58 |
| Anthropogenic, landscape | 18 | 313.52 | 0.00 | 3510.26 |
| Anthropogenic | 12 | 351.18 | 0.00 | 3560.18 |
| Landscape | 9 | 354.13 | 0.00 | 3569.22 |
| Intercept only | 3 | 391.92 | 0.00 | 3619.12 |

[a]$AIC_c$ = 3125.62

TABLE 3-3. Parameter estimates with 95% confidence intervals (CI) from top $AIC_c$ selected multinomial logistic regression. The top model compared log transformed avian predator densities (small, medium, and large avian predators); distance decay functions to nearest oil and gas structure (0.25-km decay function; $OGS_{0.25}$), power line (1.0-km decay function; $POW_{1.0}$), rural house (1.0-km decay function; $HOM_{1.0}$), major road (1.0-km decay function; $MRD_{1.0}$), and riparian habitat (1.0-km decay function; $RIP_{1.0}$); and topographic ruggedness calculated at 0.54-km radius ($TRI_{0.54}$) among locations used by sage-grouse (nest, early-brood, and late-brood locations) and random (reference level) locations. Data were collected from 1,452 point count locations—340 sage-grouse nests, 331 sage-grouse early-brood locations, 121 sage-grouse late-brood locations, and 660 random locations—from eight study sites (16-km diameter) and four study sites (24-km diameter) in southern Wyoming, USA, 2008–2011.

| | | | | 95% CI | |
|---|---|---|---|---|---|
| Group | Variable | Estimate | SE | Lower | Upper |
| Nest | | | | | |
| | Intercept | -2.63 | 0.58 | -3.79 | -1.48* |
| | Small avian predator | -0.06 | 0.03 | -0.12 | -0.00* |
| | Medium avian predator | -0.08 | 0.02 | -0.13 | -0.04** |
| | Large avian predator | -0.17 | 0.04 | -0.25 | -0.08* |
| | $OGS_{0.25}$ | -1.63 | 0.80 | -3.21 | -0.05* |
| | $POW_{1.0}$ | -0.54 | 0.47 | -1.47 | 0.39 |

| | | | | | |
|---|---|---|---|---|---|
| | $HOM_{1.0}$ | 1.31 | 0.77 | -0.21 | 2.82 |
| | $MRD_{1.0}$ | -2.64 | 0.87 | -4.35 | -0.94* |
| | $RIP_{1.0}$ | -0.63 | 0.26 | -1.14 | -0.12* |
| | $TRI_{0.54}$ | -0.02 | 0.01 | -0.04 | -0.01* |
| Early brood | | | | | |
| | Intercept | -13.03 | 1.30 | -15.58 | -10.47* |
| | Small avian predator | -0.33 | 0.06 | -0.46 | -0.21* |
| | Medium avian predator | -0.32 | 0.04 | -0.40 | -0.24* |
| | Large avian predator | -0.62 | 0.12 | -0.85 | -0.39* |
| | $OGS_{0.25}$ | -3.11 | 1.12 | -5.32 | -0.89* |
| | $POW_{1.0}$ | -1.65 | 0.59 | -2.83 | -0.49* |
| | $HOM_{1.0}$ | 3.21 | 0.79 | 1.64 | 4.78* |
| | $MRD_{1.0}$ | -2.14 | 0.86 | -3.83 | -0.44* |
| | $RIP_{1.0}$ | -0.01 | 0.27 | -0.55 | 0.59 |
| | $TRI_{0.54}$ | -0.01 | 0.01 | -0.03 | 0.01 |
| Late brood | | | | | |
| | Intercept | -13.49 | 1.66 | -16.76 | -10.21* |
| | Small avian predator | -0.30 | 0.08 | -0.46 | -0.14* |
| | Medium avian predator | -0.32 | 0.06 | -0.43 | -0.21* |
| | Large avian predator | -0.49 | 0.14 | -0.76 | -0.22* |
| | $OGS_{0.25}$ | -10.01 | 4.18 | -18.23 | -1.78* |

| | | | | |
|---|---|---|---|---|
| $POW_{1.0}$ | -1.77 | 0.86 | -3.46 | -0.07* |
| $HOM_{1.0}$ | 4.19 | 0.92 | 2.37 | 6.01* |
| $MRD_{1.0}$ | -3.01 | 1.45 | -5.87 | -0.16* |
| $RIP_{1.0}$ | 1.43 | 0.37 | 0.70 | 2.16* |
| $TRI_{0.54}$ | 0.00 | 0.01 | -0.01 | 0.02 |

*Denotes a 95% confidence interval that does not include zero.

TABLE 3-4. Parameter estimates with 95% confidence intervals (CI) from top $AIC_c$ selected multinomial logistic regression. The top model compared log transformed avian predator densities (small, medium, and large avian predators); distance decay functions to nearest oil and gas structure (0.25-km decay function; $OGS_{0.25}$), power line (1.0-km decay function; $POW_{1.0}$), rural house (1.0-km decay function; $HOM_{1.0}$), major road (1.0-km decay function; $MRD_{1.0}$), and riparian habitat (1.0-km decay function; $RIP_{1.0}$); and topographic ruggedness calculated at 0.54-km radius ($TRI_{0.54}$) among sage-grouse locations (nest, early-brood, and late-brood locations) by alternating the reference level. Data were collected from 1,452 point count locations—340 sage-grouse nests, 331 sage-grouse early-brood locations, 121 sage-grouse late-brood locations, and 660 random locations—from eight study sites (16-km diameter) and four study sites (24-km diameter) in southern Wyoming, USA, 2008–2011.

| | | | | 95% CI | |
|---|---|---|---|---|---|
| Group [a] | Variable | Estimate | SE | Lower | Upper |
| Early-brood vs. Nest | | | | | |
| | Intercept | -11.14 | 1.39 | -13.88 | -8.40* |
| | Small avian predator | -0.26 | 0.07 | -0.39 | -0.13* |
| | Medium avian predator | -0.20 | 0.03 | -0.27 | -0.14* |
| | Large avian predator | -0.45 | 0.12 | -0.69 | -0.22* |
| | $OGS_{0.25}$ | -1.53 | 1.25 | -3.97 | 0.92 |
| | $POW_{1.0}$ | -0.99 | 0.65 | -2.27 | 0.28 |

| | | | | | |
|---|---|---|---|---|---|
| | $HOM_{1.0}$ | 1.86 | 0.84 | 0.20 | 3.52* |
| | $MRD_{1.0}$ | 0.65 | 1.08 | -1.47 | 2.77 |
| | $RIP_{1.0}$ | 0.61 | 0.30 | 0.03 | 1.19* |
| | $TRI_{0.54}$ | 0.02 | 0.01 | 0.00 | 0.03* |
| Late-brood vs. Nest | | | | | |
| | Intercept | -11.40 | 1.76 | -14.88 | -7.93* |
| | Small avian predator | -0.22 | 0.09 | -0.39 | -0.05* |
| | Medium avian predator | -0.20 | 0.05 | -0.29 | -0.10* |
| | Large avian predator | -0.32 | 0.14 | -0.60 | -0.05* |
| | $OGS_{0.25}$ | -8.52 | 4.20 | -16.80 | -0.24* |
| | $POW_{1.0}$ | -1.09 | 0.90 | -2.86 | 0.68 |
| | $HOM_{1.0}$ | 2.85 | 0.96 | 0.95 | 4.75* |
| | $MRD_{1.0}$ | -0.32 | 1.61 | -3.49 | 2.84 |
| | $RIP_{1.0}$ | 2.05 | 0.39 | 1.28 | 2.82* |
| | $TRI_{0.54}$ | 0.03 | 0.01 | 0.01 | 0.04* |
| Late-brood vs. Early-brood | | | | | |
| | Intercept | -0.26 | 2.08 | -4.35 | 3.84 |
| | Small avian predator | 0.04 | 0.10 | -0.16 | 0.24 |
| | Medium avian predator | 0.01 | 0.05 | -0.10 | 0.11 |
| | Large avian predator | 0.13 | 0.18 | -0.22 | 0.47 |
| | $OGS_{0.25}$ | -6.99 | 4.23 | -15.32 | 1.33 |

| | | | | |
|---|---|---|---|---|
| $POW_{1.0}$ | -0.10 | 0.92 | -1.90 | 1.71 |
| $HOM_{1.0}$ | 0.99 | 0.83 | -0.64 | 2.62 |
| $MRD_{1.0}$ | -0.97 | 1.52 | -3.97 | 2.02 |
| $RIP_{1.0}$ | 1.44 | 0.38 | 0.70 | 2.18* |
| $TRI_{0.54}$ | 0.01 | 0.01 | -0.01 | 0.03 |

[a] The second category was denoted as the reference level to display parameter estimates.

*Denotes a 95% confidence interval that does not include zero.

# CHAPTER 4

# EFFECTS OF COMMON RAVEN REMOVAL ON GREATER SAGE-GROUSE NESTING SUCCESS IN SOUTHERN WYOMING

**ABSTRACT** Predator removal has been simultaneously proposed and criticized as a potential mitigation measure for low reproductive rates of greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse"). Depredation of sage-grouse nests can be an influential factor limiting their productivity, and most failed sage-grouse nests are depredated by predators including common ravens (*Corvus corax*: hereafter "raven"). In Wyoming, lethal removal of ravens was conducted by USDA/APHIS/Wildlife Services (WS) for the protection of livestock. I hypothesized that sage-grouse nest success would be greater in areas where WS lowered the abundance of ravens. I assessed the change in density of ravens and nest success of sage-grouse in areas within 15 km of WS raven removal efforts and areas farther away. I also evaluated sage-grouse nest success in relation to: 1) differences between yearling and adult sage-grouse, and 2) the effect of ravens (nest site-level and study site-level) on nest success of sage-grouse in relation to microhabitat. During 2008–2011, I conducted 3,842 10-minute point count surveys at 341 sage-grouse nests and 660 random locations in southern Wyoming. Point counts were conducted to assess raven density. I found that raven densities at removal study sites decreased 61% between 2008 and 2011, whereas raven densities at non-removal study sites increased 42% between 2008 and 2011. A year × study site type (removal or non-removal) model did not fit the data well, which suggested that I did not

detect a direct improvement to nest success of sage-grouse from reduction of ravens by WS; however, generalized linear modeling indicated that higher nest success of sage-grouse was correlated with study sites that had lower values of site-specific change in raven density (raven density relative to a particular study site [study site-level] with lower values of site-specific change in raven density found in removal study sites after removal had occurred). Nest success of sage-grouse was negatively impacted by occupancy of ravens within 550 m of a sage-grouse nest (nest site-level). Nest success of sage-grouse nests that were not occupied by ravens during the last nest check was estimated at 41% (95% confidence interval [CI] = 35% to 46%) using a 28-day incubation period with Program MARK; whereas, the success of nests occupied by ravens was estimated at only 22% (95% CI = 11% to 37%). My mixed results with respect to the potential benefit of raven removal by WS indicated that there was not a strong connection between raven removal and increased sage-grouse nest success; nevertheless, predator removal may have a place in sage-grouse management as an interim mitigation measure when sage-grouse populations are subjected to high densities of ravens. However, long-term solutions to reduce human-subsidized raven populations are necessary to address the growing raven and sage-grouse conflict.

## INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*: hereafter "sage-grouse") distribution and abundance in western North America has declined over the last century (Gregg et al. 1994, Johnsgard 2002, Connelly et al. 2004). This decline has recently led

the U.S. Fish and Wildlife Service (2010) to conclude that sage-grouse are warranted for protection under the Endangered Species Act of 1973, but the listing was precluded in favor of other species under severe threat of extinction. Many factors have been attributed to this decline including habitat loss, habitat fragmentation, habitat degradation, and predation (Braun 1998, Schroeder et al. 2004). Several studies have suggested that quantity and condition of breeding habitat is the most important factor that dictates the productivity of sage-grouse (Connelly et al. 1994, Braun 1998, Schroeder and Baydack 2001, Coates 2007, Hagen 2011). However, even in excellent sage-grouse habitat, most sage-grouse nests are lost to predators such as red fox (*Vulpes vulpes*), badgers (*Taxidea taxus*), coyotes (*Canis latrans*), black-billed magpies (*Pica hudsonia*: hereafter "magpie"), and common ravens (*Corvus corax*: hereafter "ravens"; Willis et al. 1993, Gregg et al. 1994, Heath et al. 1997, Holloran 1999, Connelly et al. 2004). Unlike other population limiting factors (e.g., habitat, weather, and drought), predation can realistically be reduced by wildlife management agencies (Cote and Sutherland 1997). However, there are no predators that specialize on sage-grouse during any life history stage (egg, chick, or adult), and sage-grouse have relatively high nest and adult survival rates (Connelly et al. 2011). Thus, Hagen (2011) suggested that in general predation is not limiting sage-grouse populations, and predator removal may only serve to provide a short-term release of predation rates in fragmented habitats and areas with human-subsidized predator populations.

In contrast, breeding success of other ground-nesting birds has been shown to be suppressed by generalist predators, such as ravens, magpies, red fox, coyotes, and

badgers (Evans 2004). Generalist predators can reach high densities in landscapes with human-associated resources. Their densities are not limited by the density of a particular species of prey (Schroeder and Baydack 2001, Evans 2004, Manzer and Hannon 2005, Coates 2007). These factors enable a generalist predator to potentially suppress prey populations. Sage-grouse populations may also be impacted by increases in generalist predator populations, or decreases in the primary prey of generalist predators that cause these predators to switch prey (Schroeder and Baydack 2001, Connelly et al. 2004).

There are increasing levels of human development in sage-grouse habitat, which has brought a range of new stresses to sage-grouse from habitat fragmentation to predation (Connelly et al. 2004, Doherty et al. 2010, Kirol 2012). Human activities are impacting sage-grouse habitat resulting in increased fragmentation, and one of the consequences of fragmentation may be increased predation rates (Schroeder and Baydack 2001). During the last century, densities of ravens have increased in Wyoming and throughout the historic range of sage-grouse (Larsen and Dietrich 1970, Andrén 1992, Engel and Young 1992, Boarman et al. 1995, Sauer et al. 2011). Ravens utilize human-provided food resources, such as road-kill, dead livestock, and garbage (Knight and Call 1980, Boarman 1993, Boarman et al. 1995), especially during winter. Raven depredation of sage-grouse nests has been implicated as a potential factor limiting sage-grouse productivity in fragmented habitats (Batterson and Morse 1948, Willis et al. 1993, Gregg et al. 1994, Schroeder and Baydack 2001, Coates and Delehanty 2010, Bui et al. 2010). Raven depredation on sage-grouse nests is a common occurrence in northeast Nevada

based on infrared video cameras set up at nest sites (Coates et al. 2008), and sage-grouse nest success in northeast Nevada was related to the number of ravens per 10-km transect with nest failure rates increasing 7.4% with every additional raven/10 km (Coates and Delehanty 2010).

Leu et al. (2008) developed a corvid-presence risk model to predict the presence of ravens in sage-grouse habitat based on average daily raven movements from Boarman and Heinrich (1999). Factors used to model the increased risk of corvid-presence were populated areas, campgrounds, rest stops, agricultural land, and landfills (Leu et al. 2008). In the corvid-presence risk model, 58% of all sage-grouse habitat was classified as high or medium risk of corvid presence, whereas only 7% of sage-grouse habitat was classified as negligible risk of corvid presence (Leu et al. 2008). In addition, lambing and calving areas are known to provide short-term food rich areas that attract ravens from vast distances during the spring (Heinrich 1988, Marzluff and Heinrich 1991). Higher raven densities around livestock areas increase the likelihood that ravens will depredate sage-grouse nests around these areas.

Subsidized raven populations of increasing size have been anecdotally documented in southwest and south-central Wyoming associated with human activities (e.g., livestock and natural gas development; R. J. Merrell, United States Department of Agriculture Animal and Plant Health Inspection Service Wildlife Services [WS], personal communication), and raven abundance has increased in Wyoming during the past decade, 2001–2010 (Sauer et al. 2011). Raven control (lethal removal; hereafter “raven removal”) efforts of varying intensity have been carried out by WS in Carbon, Lincoln, Sweetwater,

and Uinta counties in Wyoming, 2007–2011 for the protection of livestock, which provided a unique opportunity to study the potential effects of raven removal on sage-grouse nest success. I hypothesized that sage-grouse nest success would be greater in areas where WS lowered the abundance of ravens. To test this hypothesis, I assessed the change in density of ravens and sage-grouse nest success in areas associated with WS raven removal efforts and areas farther away during 2008–2011. As secondary objectives, I evaluated differences between yearling and adult sage-grouse nest success, and the effect of ravens on nest success at the sage-grouse nest level in relation to microhabitat.

## STUDY AREA

My study was conducted in southwest and south-central Wyoming. I had 12 study sites, each 16 or 24 km in diameter (eight study sites of 16-km diameter and four study sites of 24-km diameter; Fig. 4-1). To evaluate sage-grouse response to raven removal in a similar area, study sites in southwest Wyoming were 16-km diameter and approximately centered around leks where hens were captured based on results found by Holloran and Anderson (2005). Study sites in south-central Wyoming were 24 km, because sage-grouse were captured at several nearby leks over a larger area. Five out of 12 study sites were within 15 km of WS raven removal activities (Fig. 4-1). Study sites within 15 km of WS raven removal were considered ‘removal study sites’, those at a distance >15 km were considered ‘non-removal study sites’. Five study sites were located in Lincoln County, two in Sweetwater County, two in Uinta County, and three in Carbon County. Study sites were chosen to provide a representation of overall sage-grouse

nesting habitat in southern Wyoming with a variety of land uses, topographic features, and raven management.

Removal and non-removal study sites had similar topographic features, weather, and vegetation. Elevation ranged from 1,950 m to 2,600 m among removal study sites and 1,925 m to 2,550 m among non-removal study sites. Most of the land within all of the study sites was federally owned and administered by the Bureau of Land Management with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in the study sites. All study sites had anthropogenic development, which consisted mostly of unimproved 4-wheel drive roads. Conventional natural gas, coalbed methane natural gas, and/or conventional oil extraction activities were present in two of the removal study sites and four of the non-removal study sites.

The landscape at all study sites was dominated by sagebrush (*Artemisia* spp.); Wyoming big sagebrush (*A. tridentata wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) were the most common. Black sagebrush (*A. nova*) and dwarf sagebrush (*A. arbuscula*) were found on exposed ridges. Other common shrub species in the study sites included alderleaf mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), chokecherry (*Prunus virginiana*), common snowberry (*Symphoricarpos albus*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), Saskatoon serviceberry (*Amelanchier alnifolia*), and spiny hopsage (*Grayia spinosa*). Isolated stands of juniper (*Juniperus* spp.) and quaking aspen (*Populus tremuloides*) were found at the higher elevations on north-facing hillsides. Common forb species included arrowleaf balsamroot (*Balsamorhiza sagittata*),

buckwheat (*Eriogonum* spp.), common yarrow (*Achillea millefolium*), dandelion (*Taraxacum* spp.), desert parsley (*Cymopterus* spp.), phlox (*Phlox* spp.), lupine (*Lupinus* spp.), sego lily (*Calochortus nuttallii*), and wild onion (*Allium* spp.). Common grass species included: bluegrasses (*Poa* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), green needlegrass (*Nassella viridula*), needle and thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), and western wheatgrass (*Pascopyrum smithii*). Cheatgrass (*Bromus tectorum*) was present, but not widespread in any of the study sites.

## METHODS

### Sage-grouse Capture and Monitoring

From 2008 to 2011, I monitored sage-grouse hens during the nesting season (late-April to mid-July). Hens were captured, radio-collared, and released in April of each year. I captured hens at night using ATVs, spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992, Connelly et al. 2003). Sage-grouse hens were fitted with 17.5-g or 22-g (<1.5% body mass) necklace radio collars (Holohil Systems Ltd, RI-2D, Ontario, Canada or Advanced Telemetry Systems Inc, A4060, Isanti, MN, USA). I aged sage-grouse hens as yearlings or adults by examining outer primaries (Patterson 1952).

Between May 1 and July 15, I located hens weekly with VHF receivers (Communications Specialists, R-1000, Orange, CA, USA) and 3-way Yagi antennas (Communications Specialists, Orange, CA, USA). Potential nests were identified with binoculars from ~15 m by circling a radio-marked hen until she was visually spotted under a shrub. I used handheld global positioning system (GPS) units (eTrex, Garmin

Inc., Olathe, Kansas) to record hen locations. Location accuracy on the GPS ranged from 2 – 8 m.

Nests were verified by triangulating the hen under the same shrub from ≥50 m away or thoroughly searching the area of the potential nest when the hen was absent. I continued monitoring nests weekly until the nest hatched or failed. I assessed nest fate as successful or unsuccessful after a hen had left her nest. A successful nest was defined as having evidence that at least 1 egg hatched as determined by shell membrane condition (Wallestad and Pyrah 1974). I classified unsuccessful nests as abandoned (eggs not depredated or hatched) or depredated (at least one egg with evidence of depredation).

**Raven Abundance Monitoring**

Between May 1 and August 1 of each year, I conducted point count surveys at sage-grouse nests and random locations within each study site to compare raven densities. To avoid disturbing an incubating hen, nest point counts were conducted 100–200 m away from a sage-grouse nest but within a line-of-sight of that sage-grouse nest. Random locations were selected in habitat considered to be available to sage-grouse for nesting within each study site. To restrict random locations to available nesting habitat, I used ArcMap 10.0 (ESRI Inc., Redlands, California) to generate random locations only in sagebrush-dominated habitat, which was classified by the Northwest GAP landcover data from 2008. Random locations were designated to be >1000 m apart; however, random selection led to average nearest neighbor distances among random point count locations of >2000 m (Table 4-1). I generated 12 random locations in each 16-km diameter study

site and 18 random locations in each 24-km diameter study site per year. I generated a new set of random locations each year to avoid spatial autocorrelation; thus, random locations among years were independent.

I used standard distance sampling techniques (Ralph et al. 1995, Buckland et al. 2001, Thomas et al. 2010), which entailed counting all ravens observed during point counts and recording each raven's distance from the observer (when standing at the center of the point count location). I recorded distance as the distance from the observer to where a raven was first located (Ralph et al. 1995, Thomas et al. 2010); this minimized possible bias associated with ravens being attracted to or flushed away from an observer. When a raven was displaced from the center of a point count location as an observer approached (6.4% of all detected ravens), I recorded distance from that raven to the center of the point count location while the observer approached as suggested by Ralph et al. (1995). This was done when the approach of an observer resulted in a raven moving away from the center of the point count location. A 1500–m rangefinder (American Technologies Network Corp., RE-1500 m, San Francisco, California) in conjunction with a GPS was used to estimate distances directly or to validate visually estimated distances.

Observers were trained and tested in corvid and raptor identification before conducting point counts. Point counts were 10 min in length, and I conducted them during daylight hours on a weekly basis at each study site. I visited each point count location 1 to 8 times with most locations visited ≥3 occasions. I did not survey for ravens in inclement weather (i.e., when raining or wind speeds greater than 25 km/h; Ralph et al. 1995). Unidentified birds were not included in analyses; these contributed to 2% of

detections within truncated observation distances. Nest point counts were performed after nests were initially located; thus, nest point counts were conducted in May to early-July. I performed random point counts May to 1 August each year.

I intermixed the sampling of nest and random point counts within each study site. To minimize observer bias, I changed the time of day and the observer that conducted individual point counts within a study site each week (i.e., each individual point count location regardless of type—nest or random—was conducted at a different time of day each week and by a different observer as best as possible). The observers conducting point counts within a particular study site changed each year.

**Raven Removal**

WS began lethally removing ravens in Carbon, Lincoln, and Sweetwater counties in March 2007 and Uinta County in February 2008 (R. J. Merrell, personal communication). Removal of ravens was conducted in response to livestock depredation; thus, WS removal activities were implemented at raven foraging areas or roosts near areas used by livestock (0–15 km). WS removal activities were more focused on raven foraging areas (lambing and calving grounds and landfills; Table 4-2) from February 2009 to June 2011.

WS personnel performed concentrated raven removal using DRC-1339 (3-chloro-p-toluidine hydrochloride) by treating 1.3-cm meat cubes or dog food or shooting them with shotguns (R. J. Merrell, personal communication); however, direct removal was uncommon (Carbon, Lincoln, Sweetwater, and Uinta counties four year total $n = 57$

ravens). Typical WS raven removal methods entailed pre-baiting with non-treated bait for a few days to acclimate ravens to foraging on bait (meat cubes or dog food) before applying DRC-1339 to bait (R. J. Merrell, personal communication). The amount of DRC-1339 and bait applied at individual removal locations was proportional to the number of ravens WS personnel witnessed in that area. DRC-1339 concentration was applied as specified by the U.S. Environmental Protection Agency label ($LD_{50}$ = 5.6 mg/kg; Larsen and Dietrich 1970). Each spatiotemporal specific application of DRC-1339 or direct removal was considered a 'removal event'.

To assess the efficacy of WS raven removal, I constructed spatiotemporal variables to describe the number of proportional removal events around nest and random point count locations during 2008–2011. Time was incorporated by including all removal events that occurred within 3 or 6 months prior to a sage-grouse nest's fate or prior to the last date a random point count was conducted. The distance to the nearest removal event within 3 or 6 months was calculated for each point count location with ArcMap 10.0. The total number of removal events within 7 km, 15 km, or 25 km of a point count location were calculated for 3 and 6 months with ArcMap 10.0. I also calculated the number of removal events at landfills and other locations separately within 3 and 6 months. Removal events at landfills were calculated within 25 km under the assumption that ravens may be drawn into landfills from farther away, while non-landfill removal events were calculated at 7 km, 15 km, and 25 km from a point count location for 3 and 6 months excluding removal events at landfills. I report means (SE) of all removal event variables for removal and non-removal study sites (Table 4-3). I adapted the 7-km (153.9

$km^2$), 15-km (706.5 $km^2$), and 25-km (1962.5 $km^2$) search radii around point count locations to correspond to reported raven average home-range (California 0.3–45.8 $km^2$ [Linz et al. 1992], Minnesota 27.3–195 $km^2$ [Bruggers 1988]), average daily movements (Mojave Desert 4.5 km [Boarman et al. 1995], Idaho 6.9 km [>95% of movements within 12.5 km; Engel and Young 1992]), and documented roaming distances (Minnesota average 1,252 $km^2$ [Bruggers 1988], Maine >1,800 $km^2$ [Heinrich 1988], and Michigan average radius 27 km [range 3–147 km; Boarman and Heinrich 1999]). The smallest home-ranges correspond to breeding pairs, and larger distances correspond to non-breeding individuals.

**Vegetation Variables**

I sampled vegetation at sage-grouse nests in late-May to early-July 1 to 2 weeks after sage-grouse nests hatched or failed. I recorded the max height and the average canopy cover of the nest shrub. I quantified vegetation within 5 m surrounding sage-grouse nests by orienting 2 vegetation transects—each 10 m in length—at the cardinal directions and intersecting at a sage-grouse nest. Vegetation transects were conducted to measure average total shrub cover—including antelope bitterbrush, greasewood, rabbitbrush, sagebrush, Saskatoon serviceberry, and snowberry—using the line-intercept method (Canfield 1941). Average percent cover of shrubs was calculated by dividing the total shrub intercepted line length (cm) by the total line length (2000 cm) and then multiplying by 100. Gaps <3 cm were not recorded (Wambolt et al. 2006), and no section of shrub cover was measured more than once. I averaged the height of shrubs that

intersected the vegetation transect for average total shrub height; shrub heights excluded inflorescences. I calculated percent cover of grass, perennial grass, forbs, bare ground, and litter in six cover classes (1 = 0–1%, 2 = 1.1–5%, 3 = 5.1–25%, 4 = 25.1–50%, 5 = 50.1–75%, and 6 = 75.1–100%; Kirol et al. 2012) by averaging 9 20-cm × 50-cm quadrats placed along vegetation transects at 2 m, 4 m, 5 m, 6 m, and 8 m (Daubenmire 1959). Perennial grass height was measured by recording the maximum grown height (droop height) excluding flowering stalks within 1 m of the 9 quadrats. The lowest visible 5-cm section of a Robel pole—that was placed in the center of a sage-grouse nest—was recorded to provide an index of general line-of-sight obstruction (hereafter "visual obstruction"; Robel et al. 1970). I recorded Robel pole readings from 1 m off the ground and 5 m away at the 4 cardinal directions and averaged these values to report 1 visual obstruction measurement per site. I report means and standard errors (SE) for vegetation variables used in models for removal and non-removal study sites (Table 4-4).

**Data Analyses**

I implemented a spatiotemporal modeling strategy to evaluate general trends in 1) the effects of WS removal activities on raven abundance and 2) the effects of study site-level and sage-grouse nest-level raven abundance and microhabitat on sage-grouse nest success. A spatiotemporal strategy was implemented because many variables describing raven abundance and sage-grouse nest survival were exclusive to a given year or study site type (removal or non-removal). Modeling of raven abundance and sage-grouse nest

survival were conducted with an information theoretic approach (Anderson 2008), and I compared models with Akaike's information criterion adjusted for sample size ($AIC_c$) and Akaike weights ($w_i$; Burnham and Anderson 2002). I classified models <2 $AIC_c$ compared to the null model as having moderate support, and models with <4 $AIC_c$ compared to the null as having a greater degree of support (Burnham and Anderson 2002, Arnold 2010). To allow for direct comparison of raven and microhabitat variables, I reported all *a priori* models with explanations of non-informative variables as suggested by Arnold (2010). I evaluated goodness-of-fit of top selected $AIC_c$ models by computing a ratio of Zheng's (2000) proportional reduction of deviance (RDR) for covariate models to spatiotemporally saturated models (maximum proportional reduction in deviance; Iles 2012), which has been considered appropriate for generalized linear models (Zheng 2000, Aubry et al. 2011, Iles 2012). Deviance reduction for each spatiotemporally saturated model and top covariate models of interest were calculated relative to null models (time and study site type invariant):

$$D_{int} = 1 - (deviance_{interest}/deviance_{null}) \quad (1)$$

$$D_{sat} = 1 - (deviance_{saturated}/deviance_{null})$$

$$RDR = D_{int} / D_{saturated} \quad (2)$$

thus, the ratio gives an assessment of a covariate model's relative ability to explain spatiotemporal processes effecting raven abundance and sage-grouse nest survival. The ratio is 1 for the spatiotemporally saturated model and 0 for the null model (Iles 2012). I prevented multicollinearity by only including one variable of any pair of variables that co-varied in any model ($r$ >0.65) as determined with a Pearson's correlation matrix. In

this situation I eliminated one co-varying variable from further analysis by retaining the variable that made the most biological sense. Variance inflation factors (VIF) for all predictor variables were ≤5, which indicated that the variances of coefficient values were not drastically increased by the inclusion of any predictor variable; thus, collinearity was not a major problem.

*Raven density analysis.*– I used function 'distsamp' in package UNMARKED version 0.9-5 (Fiske and Chandler 2011) in R (R 2.14.2, www.r-project.org, accessed 15 Apr 2012) to model the effects of year, year trend, point count type (nest or random), and removal event variables on the abundance of ravens in removal and non-removal study sites. I assessed general annual raven abundance within removal and non-removal study sites by modeling year, year trend, and point count type. I compared year and year trend in additive models with point count type to assess which form of year best described raven density; thus, year and year trend were not combined in any single model.

For models describing WS removal events, I only included distance to the nearest removal event, number of removal events per area (total and landfill excluded), and landfill removal events that were calculated at the same temporal scale in all modeling. I did not include landfill removal event variables in models with total number of removal events. To assess WS removal effects, the top $AIC_c$ selected WS removal event variable model was compared to a spatiotemporally saturated model with RDR. The saturated model included year, point count type, and year × point count type for removal and non-removal study sites modeled separately. The 'distsamp' function fits a multinomial-Poisson mixture model (Royle et al. 2004) that allows for analysis of standard distance

sampling data (Ralph et al. 1995, Buckland et al. 2001, Thomas et al. 2010) at discrete distance intervals, while simultaneously modeling detection and abundance (Fiske and Chandler 2011).

For ‘distsamp’ analyses, raven detection distances were binned into 250-m intervals and right truncated at 1500 m. I chose distance intervals and truncation distances by determining the smallest interval and largest truncation that allowed for adequate fit of distance sampling models. I used 95% confidence intervals (CI) to compare parameter estimates from top $AIC_c$ selected ‘distsamp’ models. I generated CIs empirically using parameter estimates and SE from ‘distsamp’.

I fit half-normal, hazard-rate, uniform, and exponential key detection functions. I compared the fit of all possible key detection functions with detection held constant between point count types (random and nest) and allowing detection to vary between point count types. I selected the appropriate key detection function for removal and non-removal study sites separately using $AIC_c$. For removal and non-removal study sites, ‘distsamp’ models with hazard-rate key detection functions held constant were at least 10 $AIC_c$ lower than models with all other key detection functions and detection varying by point count type. This was not surprising, because all point counts were in sagebrush-dominated habitat. I adjusted ‘distsamp’ parameter estimates for survey effort (difference in the number of visits per point count location) by incorporating the number of visits per point count location as an offset, which is similar to the procedure used in Program DISTANCE (Thomas et al. 2010).

I used ‘distsamp’ to estimate observer effective detection radius (EDR), which

was defined as the distance from the observer that the number of detected ravens beyond EDR was equal to the undetected ravens within EDR (Thomas et al. 2002). 'Distsamp' does not allow fitting of observation specific covariates; thus, I was unable to compare models with detection varying among observers; however, I did not find differences in EDR among observers on data collected for the first 3 years of this study in Chapter 2. Thus, I did not incorporate differences in detection among observers into my 'distsamp' analyses.

*Sage-grouse nest success analysis.*– I analyzed daily survival rate (DSR) of sage-grouse nests by fitting generalized linear models of DSR using maximum likelihood in Program MARK (White and Burnham 1999). Model building was conducted in a two-step process to increase efficiency and avoid model dredging. For "Step 1," I evaluated the effect of year, year trend, study site type, a nesting sage-grouse's age (AGE), raven density at the study site-level, and raven density or occupancy at the sage-grouse nest-level on sage-grouse nest DSR. For "Step 2," I used the top $AIC_c$ selected model from Step 1 to evaluate raven abundance effects on sage-grouse nest DSR in comparison to microhabitat variables associated with the nest shrub and habitat directly surrounding the nest (5 m).

I calculated all raven variables from the raw count data within 550 m, which was the 'distsamp' estimated EDR. The raw densities were weighted by the number of visits to each point count location. Raven density at the study site-level was calculated at the study site-level by averaging the raven density at all random locations within each study site separately. I had noted through observation that relative changes in raven density

within many study sites had positive or negative effects on nest success of sage-grouse. I attributed this phenomenon to the possibility of ravens being more or less effective predators on sage-grouse nests depending on the study site due to overall characteristics of a particular study site (combination of individual raven behavior, topographic roughness, large scale cover, anthropogenic development, etc.). The combination of multiple large scale differences in study sites were not accounted for with the microhabitat variables that I used, such as shrub cover within 5 m around a nest. In addition to landscape raven densities, I calculated site-specific change in raven density—from random point count locations—as the increase or decrease in landscape raven density (annual density) relative to the raven density in a particular study site at the beginning of the study (2008). Thus, site-specific change in raven density was 0 for all study sites in 2008. The site-specific change in raven density variable was intended to look at relative change in risk of depredation within each study site (i.e., does site specific increase or decrease of raven densities effect nest success of sage-grouse). Thus, site-specific change in raven density was not quantifying the effect of the exact density of ravens on nest success of sage-grouse among all study sites. Rather, it was assessing site-specific change in exposure to ravens, which more directly related to the potential effects of WS reducing raven populations within a study site (reducing risk of raven depredation with a study site). Sage-grouse nest-level raven abundance was calculated from nest point counts as 1) raven density (hereafter "nest-level raven density") at the nest and 2) occupancy (0 or 1) of at least 1 raven during the last nest check when the sage-grouse hen was still on the nest (hereafter "raven occupancy"). In addition to additive models, I

included interactions between year × study site type and year trend × study site type to directly assess the effect of WS removal activities at removal study sites on DSR of sage-grouse nests; year and year trend were not included in models with raven variables because raven variables were temporally explicit to year. I did not include both nest-level raven density and raven occupancy in any model, because nest-level raven density and raven occupancy were measured at the same spatiotemporal scale.

I compared the top $AIC_c$ selected sage-grouse nest DSR models from Steps 1 and 2 to a spatiotemporally saturated model with RDR. The saturated model for sage-grouse nest DSR included year; study site type; max nest shrub, average total shrub, and average perennial grass height; average nest shrub, total shrub, grass, forb, bare ground, and litter cover; and visual obstruction. Grass and perennial grass cover were highly correlated ($r > 0.65$), and grass cover fit the data better than perennial grass cover; thus, I included grass cover in modeling instead of perennial grass cover.

*Spatial autocorrelation.*– Distance sampling estimates are known to be robust to spatial autocorrelation (Thomas et al. 2010); however, spatial autocorrelation violates the independence assumption for generalized linear models. Thus, I created an inverse weighted distance matrix to assess spatial autocorrelation among sage-grouse nests, where nest locations >12 km apart were not considered to be correlated. This distance was used to directly relate to the radius of my 24-km diameter study sites; however, 12 km was also larger than the home range size of breeding ravens (0.3–45.8 $km^{-2}$; Boarman and Heinrich 1999). Furthermore, I treated all sage-grouse nests, regardless of year, as correlated within 12 km with the degree of correlation related to the distance among

nests. I used function ‘moran.test’ in package SPDEP version 0.5-46 in R to calculate Moran’s *I* for Pearson residuals of top $AIC_c$ selected generalized linear models of sage-grouse nest success.

## RESULTS

### Raven Density

I conducted 3,842 point count surveys (1,621 at removal study sites and 2,221 at non-removal study sites) during 2008–2011 at 1,001 total point count locations with 341 sage-grouse nest locations and 660 random locations (Table 4-1). I counted 1179 ravens (687 at removal study sites and 492 at non-removal study sites), and ‘distsamp’ estimated EDR was 552 m. The number of detected ravens was greater than 60–80 detections, which Buckland et al. (1993) suggested was necessary for reliable density estimates.

I found that raven densities at removal study sites decreased over time, whereas raven densities at non-removal study sites increased over time (Tables 4-5 and 4-6; Fig. 4-2). For removal and non-removal study sites, raven densities at sage-grouse nests were lower than raven densities at random locations (Table 4-6). The average nearest removal event was 14.5 km (0.4 SE) and 39.3 km (1.0 SE) for removal study sites and non-removal study sites, respectively (Table 4-3).

For models describing general annual raven abundance, top $AIC_c$ ranked ‘distsamp’ models included year and point count type for both removal and non-removal study sites ($w_i = 0.65$ and $w_i = 0.45$, respectively; Table 4-5). In removal study sites, I found that 2009 raven densities were only moderately lower than 2009 (95% CI

overlapped 0; Table 4-6, Fig. 4-2); whereas, raven densities in 2010 and 2011 were lower than 2008 (Table 4-6, Fig. 4-2). The top removal study site model also included year × point count type (Table 4-5). The interaction between year and point count type indicated that raven density at sage-grouse nests was lower in all years but the difference in raven density at sage-grouse nests and random locations was not as large in 2011. Thus, the density of ravens at sage-grouse nests was similar for 2008 and 2011 and lower in 2009 and 2010 (Table 4-6).

For models describing removal events, I found that removal events calculated at 6 months fit better than removal events at 3 months. Decreases in raven density at removal study sites were best described by the parameter estimates of the number of landfill removal events (-0.073; 95% CI = -0.092 to -0.054), the number of non-landfill removal events within 15 km (-0.134; 95% CI = -0.188 to -0.080), and the distance to the nearest removal event (-0.002; 95% CI = -0.013 to 0.010; Table 4-7, Fig. 4-3). Increases in raven density at non-removal study sites were best described by the parameter estimate of the number of non-landfill removal events within 25 km (0.060; 95% CI = 0.031 to 0.089; Table 4-7, Fig. 4-4). Raven density at removal study sites was not affected by the distance to the nearest removal event, but the distance to the nearest removal event contributed to describing the data. There were 156 out of 593 point counts (26%) within non-removal study sites that had a number of non-landfill removal events within 25 km >0, whereas removal study sites had 358 out of 407 point counts (88%) >0. The top selected $AIC_c$ model for removal study sites ($w_i$ = 1.00) had RDR = 0.908, whereas, the top selected $AIC_c$ model for non-removal study sites ($w_i$ = 0.44) had RDR = 0.491. Thus,

removal event variables accounted for most of the reduction in deviance in removal study sites and approximately half of the deviance in non-removal study sites.

**Sage-grouse Nest Success**

In the four years of study (2008–2011), I found 121 sage-grouse nests in removal study sites with 52%, 35%, 50%, and 57% apparent nest success, respectively, and 220 sage-grouse nests in non-removal study sites with 54%, 57%, 45%, and 43% apparent nest success, respectively (Fig. 4-5). I did not find any differences in DSR of sage-grouse nests among year, year trend, study site type (removal or non-removal), and landscape raven density from Program MARK models; all models with year, year trend, study site type, and raven density at the study site-level had $AIC_c$ values greater than the null model (Table 4-8). However, I found that sage-grouse nest DSR was negatively impacted by site-specific change in raven density (study site-level) and raven occupancy (nest site-level), and microhabitat variables did not greatly improve the fit of DSR models (Tables 4-8 and 4-9). Average DSR for sage-grouse nests that were not occupied by a raven was 0.969 (± 0.003 SE), which yielded an estimated 41% (95% CI = 35% to 46%) nest survival using a 28-day incubation period. This estimate was lower than the apparent nest success of all but one year by study site combination, and highlighted the necessity to account for nests that were depredated or abandoned before I found them by using the nest survival model in Program MARK. Average DSR for sage-grouse nests that were occupied by a raven was 0.948 (± 0.010 SE), which yielded an estimated 22% (95% CI = 11% to 37%) nest survival using a 28-day incubation period. Spatial autocorrelation was

not a problem for the top $AIC_c$ selected sage-grouse nest DSR models (Moran's $I$: $P > 0.4$).

Step 1 of sage-grouse nest DSR modeling illustrated that raven occupancy fit the data better than nest-level raven density, and nest level (raven occupancy) and site-level (site-specific change in raven density) variables explained the sage-grouse nest success data better than models with year, year trend, study site type, year × study site type, year trend × study site type, or AGE (Table 4-8). Models with raven occupancy and site-specific change in raven density accounted for 45% and 33% of the cumulative $w_i$, respectively; whereas, models with year, year trend, study site type, or AGE accounted for lower $w_i$ (13%, 9%, 12%, and 4%, respectively; Table 4-8). Thus, the sage-grouse nest DSR model with raven occupancy + site-specific change in raven density was used in step 2 to compare with microhabitat variables. In step 2, all models that explained the data better than the null model included raven occupancy and site-specific change in raven density, and no microhabitat only model was better than the null (Table 4-9). The best model from Step 2 included raven occupancy, site-specific change in raven density, and average perennial grass height (Table 4-9). The parameter estimates of raven occupancy (-0.52; 95% CI = -0.96 to -0.07) and site-specific change in raven density (-1.27; 95% CI = -2.71 to 0.17) were negatively associated with sage-grouse nest DSR (Fig. 4-6), and the parameter estimate of average perennial grass height was positively associated with sage-grouse nest DSR (0.01; 95% CI = -0.01 to 0.03; Fig. 4-6). Site-specific change in raven density and average perennial grass height were imprecise predictors (95% CI overlapped zero); however, parameter estimates for site-specific

change in raven density (95% CI was slightly overlapping 0) had greater explanatory power than average perennial grass height (95% CI was drastically overlapping 0). The top $AIC_c$ model from Step 2 and the raven occupancy + site-specific change in raven density both had $w_i = 0.12$ (Table 4-9). The best Step 1 model had RDR = 0.54 versus RDR = 0.72 for the best Step 2 model; thus, average perennial grass height decreased the deviance but did not add much to $w_i$ or prediction of DSR.

## DISCUSSION

Sage-grouse nest success was negatively impacted by the presence of ravens near sage-grouse nests (local scale) and greater values of site-specific change in raven density (landscape scale); although, site-specific change in raven density was a slightly imprecise predictor. My sage-grouse nest success results suggest that sage-grouse nesting in areas with subsidized raven populations may have suppressed nest success, which may contribute to lower sage-grouse population growth rates. I did not find an overall difference in sage-grouse nest DSR between removal and non-removal study sites, which may indicate that all study sites had a similar sage-grouse nest DSR capacity. However, study site differences in raven abundance were accounted for by calculating the change in raven abundance relative to abundance within a study site at the start of the study. Alternatively, there may have been variability in sage-grouse nest DSR among study sites related to factors other than ravens and microhabitat, such as weather. The best sage-grouse nest DSR model had an RDR = 0.72, which indicated that a large proportion of spatiotemporal variability in sage-grouse nest success was not accounted for in my

models. The negative effect of ravens on the nest success of grouse has been well documented (Manzer and Hannon 2005, Bui et al. 2010, Coates and Delehanty 2010). For example sharp-tailed grouse (*Tympanuchus phasianellus*) in southern Alberta had 8-times greater nest success in landscapes with <3 corvids/km$^2$ as opposed to landscapes with ≥3 corvids/km$^2$ (Manzer and Hannon 2005). Around Jackson and Pinedale, Wyoming, Bui et al. (2010) found that higher occupancy rates of ravens were correlated with failed sage-grouse nests.

Although I could not test for spatial autocorrelation in 'distsamp' analyses, densities derived from distance sampling are robust to lack of independence of observation locations because distance sampling is setup to be a snap-shot in time (Thomas et al. 2010). My raven sampling was designed to count the greatest proportion of ravens within a study site each week as suggested by Ralph et al. (1995) and Thomas et al. (2010). Conducting all point counts within a study site in one day reduced the possibility of double-counting individual ravens during that week's visit. Counting the same individual raven during different weeks, regardless of the particular point count location, was properly scaled by accounting for survey effort. Replication of point counts by sampling multiple weeks was done to increase the proportion of ravens detected as suggested by Thomas et al. (2010). Spatial autocorrelation was not found to be a problem with nest success models.

Microhabitat variables did not substantially differ between successful and unsuccessful sage-grouse nests, which indicated that all sage-grouse selected nest-sites with relatively equal concealment cover (relative to the habitat that was available) and

microhabitat was not a limiting factor. Simultaneous comparison of raven and microhabitat vegetation variables accounted for differences among study sites in relation to sage-grouse nest-site selection. Thus, differences in nest success may be attributed to local and landscape scale raven abundance, local scale composition of other predators, weather, and habitat fragmentation (anthropogenic features).

Local predator densities can impact parental behavior, nest-site selection, and productivity of several prairie grouse species (Gregg et al. 1994, Schroeder and Baydack 2001, Manzer and Hannon 2005, Coates 2007). The presence of predators may induce changes in sage-grouse behavior associated with habitat usage. For instance, sage-grouse reduced time off of their nests when nesting in areas with high abundances of ravens (Coates and Delehanty 2008). Sage-grouse select nest sites at various scales. At the microhabitat scale, sage-grouse predominately choose nest sites in vegetation cover (Connelly et al. 2004). Several studies have reported that sage-grouse select nest sites based on a preference for different microhabitat characteristics, such as: sagebrush density (Wallestad and Pyrah 1974, Connelly et al. 2003), sagebrush cover (Doherty et al. 2010, Kirol et al. 2012), shrub height (Gregg et al. 1994), grass height (Gregg et al. 1994, Holloran et al. 2005, Kirol et al. 2012), and grass cover (Kaczor 2008, Kirol et al. 2012). Variability in reported microhabitat characteristic preferences of sage-grouse, with reference to nest-site selection, may indicate local differences in available microhabitat. Differences in available microhabitat among studies suggest that cover, in general, is important regardless of the type of vegetation cover that is available (e.g. sagebrush density, shrub height, or grass height). Alternatively, sage-grouse living in areas with

different predator compositions, such as avian or mammalian predators, may prefer different types of vegetation cover (Connelly et al. 2004, Coates and Delehanty 2010). Thus, the microhabitat characteristics upon which sage-grouse base their selection of nest-sites and the success of those nests may be a result of available vegetation and predator composition. For example, Coates and Delehanty (2010) found that microhabitat at sage-grouse nest-sites was correlated to nest failure depending on whether a raven or a badger depredated the nest (greater cover protected from ravens, but exposed sage-grouse to greater badger depredation and vice versa—predator facilitation). At the landscape scale, sage-grouse may avoid areas where there are high densities of ravens (Manzer and Hannon 2005, Mezquida et al. 2006; see Chapter 2).

I found that sage-grouse nested in areas with lower densities of ravens in both removal and non-removal study sites compared to random locations as predicted by the predator-avoidance hypothesis. Only 11% of sage-grouse nests had a raven detected during the last nest check with the hen on the nest. In Chapter 2, I found that in general sage-grouse nests had lower densities of avian predators, including ravens, compared to random locations in sagebrush habitat. This pattern of avoidance of avian predators was present when looking at average avian predator densities across years and study sites. My results from 'distsamp' for general annual raven abundance indicate that sage-grouse selected nest-sites with fewer ravens compared to the habitat available to them—within a removal or non-removal study site. By selecting habitat with lower raven densities, sage-grouse lower their exposure to avian predation, and risk of reproductive failure. In western Wyoming, Bui et al. (2010) claimed that raven density around sage-grouse

nesting and brood-rearing areas (1.0 ± 0.2 [SE] ravens/km$^2$) was marginally higher than raven densities in available sagebrush habitat (0.7 ± 0.2 [SE] ravens/km$^2$). The discrepancy between my results and Bui et al. (2010) may be a function of greater anthropogenic development and human activity in their study areas, or raven behavioral adaptations related to available resources (i.e., availability of nesting structure within sage-grouse nesting habitat and sage-grouse eggs).

Sage-grouse may avoid ravens indirectly by avoiding habitats with features that attract ravens (e.g., roads, livestock, rough topography, and tall structures) or directly by watching them; it is more likely that sage-grouse use both indirect and direct means. Arguments against only indirect avoidance include the fact that over half of my study sites had few anthropogenic structures (8 out of 12 study sites had <0.04 km$^{-2}$ of well infrastructure or communication towers). Yet, I found that sage-grouse avoided ravens in all of my study sites. Perhaps in addition to avoiding risky habitats (e.g., near anthropogenic features), sage-grouse also avoid nesting in areas where they see ravens. Clearly more research needs to be done before conclusions can be drawn about the mechanisms behind sage-grouse avoidance of ravens.

My spatiotemporal modeling strategy allowed me to evaluate the general effect of WS removal efforts on raven abundance and raven abundance on sage-grouse nesting success. By using Iles's (2012) ratio of deviance reduction, I was able to assess the relative explanatory power of covariates compared to spatial and temporal processes—fully saturated spatiotemporal models. Raven management conducted by WS during this study was not implemented as a regimented experiment—it was carried out where ravens

were causing problems for livestock operations; thus, some spatial locations of removal events changed among years, and DRC-1339 and the number of baits with toxicant were applied proportional to the number of ravens in an area. Thus, utilizing a modeling strategy that acknowledged and incorporated spatiotemporal processes into the evaluation of the data allowed for interpretation of the relative effect of WS raven management compared to annual and spatial variation. Proportional raven removal conducted by WS did not allow me to investigate variability in the concentration of DRC-1339, amount of DRC-1339 laced bait placed in an area, or the type of bait (e.g., meat or dog food). Even without rigorous implementation of WS raven management, my assessment of raven density and sage-grouse nest DSR was beneficial to assessing management as it can be provided from a practical logistics point-of-view.

Raven densities were reduced by WS up to 15 km from locations where WS was controlling ravens for the benefit of livestock (removal study sites; RDR = 0.908). The number of removal events conducted by WS within 15–25 km of non-removal study sites predicted higher raven densities; however, this only partially (RDR = 0.49) accounted for the change in the annual abundance of ravens. There was more anthropogenic development associated with natural gas extraction in non-removal study sites compared to removal study sites; thus, increases in raven density may have also been connected to human activity in non-removal study sites. Removal events were performed near areas with high densities of ravens (areas of raven conflict with livestock). Thus, my results indicate that higher densities of ravens in non-removal study sites were correlated with the point counts within non-removal study sites that were closer to areas with inherently

higher densities of ravens (a potential spill-over effect).

Coates (2007) studied the effect of raven removal on sage-grouse nest success at four study areas in Nevada—1 study area with raven removal and 3 study areas without raven removal. Ravens were removed with DRC-1339 treated egg baits (Coates 2007, Coates et al. 2007). With every 1 km increase in distance away from raven removal routes, Coates (2007) found that sage-grouse nests were 2.1% more likely to fail, and ravens were 13% more likely to be the culprit. This information provided a good indication that reduction of raven abundance by WS may provide a benefit for sage-grouse nesting in areas with subsidized raven populations. My study verified that WS raven management can reduce the abundance of ravens at a relatively large scale (15-km radius or 706.5 $km^2$, Fig. 4-2), and higher sage-grouse nest success was correlated with lower densities of ravens on the landscape (Fig. 4-6). Even though my year × study site type model did not fit the data well, site-specific change in raven density (density of ravens on the landscape) was lowest in study sites that had the greatest WS removal effort within a given year and those were the areas with the highest sage-grouse nest success.

Raven removal by WS during my study most likely removed transient ravens that traveled vast distances from roost to foraging sites. In removal study sites, average distance to the nearest removal event was 14.5 (0.4 SE) km with no removal event conducted <1.1 km from a point count location, which indicates that most breeding ravens (coastal California median home range radius = 0.62 km and Mojave Desert California average home range radius = 0.57 km [Boarman and Heinrich 1999]) were not

likely to have encountered removal events. Breeding pairs of ravens actively forage close to their nests, which entails relying on natural food sources (including sage-grouse eggs) more than food subsidies associated with human activities (road-kill, dead livestock, and landfills). Bui et al. (2010) hypothesized that higher densities of ravens near sage-grouse nesting areas were associated with breeding pairs of ravens, and occupancy of breeding pairs was negatively correlated with sage-grouse nest success. Increased anthropogenic structures in natural gas fields potentially allowed for greater overlap of breeding ravens and sage-grouse nesting areas (Bui et al. 2010). Coates (2007) results indicated that sage-grouse nests closer to removal routes had higher nest success, which may have been associated with a reduction in the number of raven breeding pairs. My results indicate that local scale and landscape scale raven abundance had negative consequences for sage-grouse nest success, which was likely correlated with breeding and non-breeding ravens. Kristan and Boarman (2003) found that breeding and non-breeding ravens were associated with increased predation of desert tortoises (*Gopherus agassizii*). Thus, both breeding and transient ravens may contribute to sage-grouse nest failure with greater abundances of transient ravens associated with incidental sage-grouse nest depredations.

Increased raven densities, regardless of breeding status, are likely to result in higher depredation rates on sage-grouse nests (Evans 2004, Bui et al. 2010, Coates and Delehanty 2010). As sagebrush habitat is developed, raven occupancy and density will increase in areas adjacent to and overlapping quality sage-grouse habitat. Increases in the human footprint have occurred and are likely to continue throughout most of the range of

sage-grouse (Leu et al. 2008). In addition, high-quality sagebrush habitat may become functionally unavailable to sage-grouse when raven densities are high (see Chapter 2). In removal study sites, I found that the density of ravens at sage-grouse nests was similar in 2008 and 2011; however, the density of ravens on the landscape was much less in 2011 (Table 4-6). This suggests that sage-grouse may have been utilizing a greater proportion of sagebrush habitat in 2011. Thus, habitat availability in removal study sites may not have been as limited in 2011 as opposed to 2008. Holloran and Anderson (2005) suggested that large intact sagebrush habitat with low sage-grouse nest densities was necessary to retain a viable sage-grouse population. In some areas, reductions in raven density at a landscape level may increase the amount of functional habitat for sage-grouse. Several studies on predator-avoidance in birds indicate that the presence of a predator has dramatic impacts on prey species use of habitat (Cresswell 2008). These non-lethal effects were found to be as great or greater than the effects of direct predation. Thus, quality nesting habitat for sage-grouse has become more limited from the loss of functional habitat, which has also resulted in more direct depredation of nests.

## MANAGEMENT IMPLICATIONS

The management of ravens may be a potential mitigating strategy for areas of low sage-grouse nest success. Coates (2007), Bui et al. (2010), and Hagen (2011) suggested that predator removal may provide a short-term release in predation rates within fragmented habitats and areas with subsidized predator populations. However, Hagen (2011) indicated that predator removal will not mitigate sage-grouse population declines

throughout the range of sage-grouse. I agree that the positive effects of raven removal for sage-grouse nest success are likely short-lived gains. I monitored WS raven management as it applied to livestock depredation; thus, targeted raven management to benefit sage-grouse may produce better results. However, identification of areas where sage-grouse may benefit from raven removal and implementation of a raven removal program targeted at benefitting sage-grouse will not be an easy task. Management of both breeding and transient ravens will be necessary, which will present many challenges. Predator removal may have a place in sage-grouse management when sage-grouse populations are subjected to high densities of ravens as an interim mitigation measure. However, low reproductive rates may persist in many areas due to compensatory predation by other predators (Coates 2007, Bui et al. 2010). Long-term solutions to reduce human-subsidized raven populations are necessary to address the growing raven and sage-grouse conflict. Reducing raven abundance may be possible through non-lethal means, such as reducing availability of supplemental food (road-kill, dead livestock, and garbage) and nesting and perching structures (oil and gas structures, power lines, telephone poles, communication towers, etc.; Jiménez and Conover 2001). More research needs to be focused on understanding raven population dynamics in sagebrush ecosystems, and how to reduce the utility of anthropogenic subsidies (food and nesting structure) for ravens.

## LITERATURE CITED

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence.

Springer Science, New York, New York, USA.

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794–804.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175–1178.

Aubry, L. M., E. Cam, D. N. Koons, J. -Y. Monnat, and S. Pavard. 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. Journal of Animal Ecology 80: 375–383.

Batterson, W. M., and W. B. Morse. 1948. Oregon sage grouse. Oregon Game Commission Fauna Service, Portland, USA.

Boarman, W. I. 1993. When a native predator becomes a pest: a case study. Pages 191–206 in S. K. Majumdar, E. W. Miller, D. E. Baker, E. K. Brown, J. R. Pratt, and R. F. Schmalz, editors. Conservation and resource management. Pennsylvania Academy of Science, Philadelphia, USA.

Boarman, W. I., R. J. Camp, M. Hagan, and W. Deal. 1995. Raven abundance at anthropogenic resources in the western Mojave Desert, California. Report to Edwards Air Force Base, California. National Biological Service, Riverside, California, USA.

Boarman, W. I., and B. Heinrich. 1999. Common raven (*Corvus corax*). Pages 1–31 *in* A. Poole and F. Gill, editors. The birds of North America, No. 476. The birds of North America, Philadelphia, Pennsylvania, USA.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the

problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139–156.

Bruggers, D. J. 1988. The behavior and ecology of the common raven in northeastern Minnesota. Dissertation, University of Minnesota, Minneapolis, USA.

Buckland, S. T., Anderson, D. R., Burnham, K. P., and Laake, J. L. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, New York, New York, USA.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, New York, New York, USA.

Bui, T. D., J. M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. Condor 112:65−78.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39:388–394.

Coates, P. S. 2007. Greater sage-grouse (*Centrocercus urophasianus*) nest predation and incubation behavior. Dissertation, Idaho State University, Pocatello, USA.

Coates, P. S., J. W. Connelly, and D. J. Delehanty. 2008. Predators of greater sage-grouse nests identified by video monitoring. Journal of Field Ornithology 79:421−428.

Coates, P. S., and D. J. Delehanty. 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. Condor 110:627−638.

Coates, P. S., and D. J. Delehanty. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. Journal of Wildlife Management. 74:240–248.

Coates, P. S., J. O. Spencer, Jr., and D. J. Delehanty. 2007. Efficacy of CPTH-treated egg baits for removing ravens. Human-Wildlife Conflicts 1:224–234.

Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53–67 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report, Cheyenne, Wyoming, USA.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station Bulletin 80, University of Idaho, Moscow, USA.

Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage grouse ecology. Idaho Department of Fish and Game Job Completion Report W-160-R-19, Boise, USA.

Cote, I. M., and W. J. Sutherland. 1997. The effectiveness of removing predators to

protect bird populations. Conservation Biology 11:395–405.

Cresswell, W. 2008. Non-lethal effects of predation in birds. Ibis 150:3−17.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Scientist 33:224–227.

Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

Engel, K. A., and L. S. Young. 1992. Daily and seasonal activity patterns of common ravens in southwestern Idaho. Wilson Bulletin 104:462–471.

Evans, K. L. 2004. A review of the potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.

Fiske, I., and R. B. Chandler. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetational cover and predation of sage-grouse nests in Oregon. Journal of Wildlife Management 58: 162–166.

Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effects. Pages 95–100 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian

Biology, University of California Press, Berkeley, USA.

Heath, B., R., Straw, S. H. Anderson, and J. Lawson. 1997. Sage grouse productivity, survival, and seasonal habitat use near Farson, Wyoming. Wyoming Game and Fish Department, Completion Report, Cheyenne, USA.

Heinrich, B. 1988. Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven (*Corvus corax*). Behavioral Ecology and Sociobiology 23:141–156.

Holloran, M. J. 1999. Sage-grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. Thesis, University of Wyoming, Laramie, USA.

Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638–649.

Iles, D. T. 2012. Drivers of nest success and stochastic population dynamics of the common eider (*Somateria mollissima*). Thesis, Utah State University, Logan, USA.

Jiménez, J. E., and M. R. Conover. 2001. Ecological approaches to reduce predation on ground-nesting gamebirds and their nests. Wildlife Society Bulletin 29:62–69.

Johnsgard, P. A. 2002. Grassland grouse and their conservation. Smithsonian Institution, Washington, D. C., USA.

Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection of greater

sage-grouse in northwestern South Dakota. Thesis, South Dakota State University, Brookings, USA.

Kirol, C. P. 2012. Quantifying habitat importance for greater sage-grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. Thesis, University of Wyoming, Laramie, USA.

Kirol, C. P., J. L. Beck, J. B. Dinkins, and M. R. Conover. 2012. Greater sage-grouse nesting and brood-rearing microhabitat selection in xeric big sagebrush. Condor 114:75–89.

Knight, R. L., and M. W. Call. 1980. The common raven. Bureau of Land Management, Technical Note No. 344. Bureau of Land Management, Denver, Colorado, USA.

Kristan, W. B., III, and W. I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoise. Ecology 84:2432–2443.

Larsen, K. H., and J. H. Dietrich. 1970. Reduction of a raven population on lambing grounds with DRC-1339. Journal of Wildlife Management 34:200–204.

Linz, G. M., C. E. Knittle, and R. E. Johnson. 1992. Home range of breeding common ravens in costal southern California. Southwestern Naturalist 37:199–202.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the west: a large scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Manzer, D. L., and S. J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. Journal of Wildlife Management 69:110–123.

Marzluff, J. M., and B. Heinrich. 1991. Foraging by common ravens in the presence and absence of territory holders: an experimental analysis of social foraging. Animal

Behavior 42:755–770.

Mezquida, E. T., S. J. Slater, and C. W. Benkman. 2006. Sage-grouse and indirect interactions: potential implication of coyote control on sage-grouse populations. Condor 108:747–759.

Patterson, R. L. 1952. The sage grouse of Wyoming. Sage Books, Denver, Colorado, USA.

Ralph, C. J., S. Droege, and J. R. Sauer. 1995. Managing and monitoring birds using point counts: standards and applications. USDA Forest Service Gen. Tech. Rep. PSW-GTR-149, Berkeley, California, USA.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–297.

Royle, J. A., D. K. Dawson, and S. Bates, 2004. Modeling abundance effects in distance sampling. Ecology 85:1591–1597.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2011. The North American breeding bird survey, results and analysis 1966–2010. Version 12.07.2011. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage grouse in North America. Condor

106:363–376.

Schroeder, M. A., and R. K. Baydack. 2001. Predation and the management of prairie grouse. Wildlife Society Bulletin 29:24–32.

Thomas, L., S. T. Buckland, K. P. Burnham, D. R. Anderson, J. L. Laake, D. L. Borchers, S. Strindberg. 2002. Distance sampling. Pages 544–552 *in* A.H. El-Shaarawi, and W. W. Piegorsch, editors. Encyclopedia of environmetrics. John Wiley and Sons, Chichester, England.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, R. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

U. S. Fish and Wildlife Service. 2010. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Federal Register 75:13909–14014.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

Wambolt, C. L., M. R. Frisina, S. J. Knapp, and R. M. Frisina. 2006. Effect of method, site, and taxon on line-intercept estimates of sagebrush cover. Wildlife Society Bulletin 34:440–445.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46:120–138.

Willis, M. J., G. P. Kiester, Jr., D. A. Immel, D. M. Jones, R. M. Powell, and K. R. Durbin. 1993. Sage grouse in Oregon. Oregon Department of Fish and Wildlife, Wildlife Research Report No.15. Portland, USA.

Zheng, B. 2000. Summarizing the goodness of fit of generalized linear models for longitudinal data. Statistics in Medicine 19:1265–1275.

Table 4-1. Summary of minimum, maximum, and mean distance (m) to nearest neighbor by location type (nest or random) reported by year. Data were collected in southwestern and south-central Wyoming, USA during 2008–2011.

| Year | Location Type | *n* | Min | Mean | Max | SD |
|---|---|---|---|---|---|---|
| | Nest | 63 | 241 | 2194 | 11812 | 2671 |
| 2008 | Random | 152 | 1000 | 2026 | 7216 | 1308 |
| | Nest | 85 | 103 | 1724.5 | 7195 | 1624 |
| 2009 | Random | 172 | 1000 | 2138 | 7073 | 1091 |
| | Nest | 83 | 107 | 2009 | 10011 | 2313 |
| 2010 | Random | 162 | 1031 | 2493 | 6136 | 1016 |
| | Nest | 109 | 124 | 1766 | 10086 | 1970 |
| 2011 | Random | 174 | 1061 | 2599 | 8450 | 1230 |

Table 4-2. Raven removal was conducted by USDA/APHIS Wildlife Services in southwest and south-central Wyoming during 2007–2011. Total number of removal events at raven foraging and roost sites around removal study sites. Number of removal events at landfills near removal study sites reported in parenthesis. Removal events quantified as the maximum number of events within 3 and 6 months prior to the last point count (sage-grouse nest or random) within a given year.

| Year | Number removal events 3 months | Number removal events 6 months |
|---|---|---|
| 2007 | 16 (0 landfill) | 16 (0 landfill) |
| 2008 | 6 (0 landfill) | 7 (0 landfill) |
| 2009 | 30 (6 landfill) | 44 (6 landfill) |
| 2010 | 33 (13 landfill) | 40 (15 landfill) |
| 2011 | 16 (1 landfill) | 27 (8 landfill) |

Table 4-3. Means and standard errors (SE) of variables used to model USDA/APHIS/Wildlife Services (WS) raven removal. Data were collected from 407 and 593 point count locations in removal and non-removal study sites, respectively, in southwestern and south-central Wyoming, USA during 2008–2011.

| | Removal study sites | | Non-removal study sites | |
|---|---|---|---|---|
| Variable description | mean | SE | mean | SE |
| Nearest (km) WS removal event within prior 3 mon | 15.8 | 0.4 | 39.7 | 1.0 |
| Nearest (km) WS removal event within prior 6 mon | 14.5 | 0.4 | 39.3 | 1.0 |
| Total # WS removal events within 7 km during prior 3 mon | 0.2 | 0.0 | 0.0 | 0.0 |
| Total # WS removal events within 7 km during prior 6 mon | 0.2 | 0.0 | 0.0 | 0.0 |
| Total # WS removal events within 15 km during prior 3 mon | 1.6 | 0.2 | 0.0 | 0.0 |
| Total # WS removal events within 15 km during prior 6 mon | 2.1 | 0.2 | 0.0 | 0.0 |
| Total # WS removal events within 25 km during prior 3 mon | 3.9 | 0.2 | 1.0 | 0.1 |
| Total # WS removal events within 25 km during prior 6 mon | 5.7 | 0.3 | 1.3 | 0.1 |

| | | | | |
|---|---|---|---|---|
| # WS removal events at landfills within 25 km during prior 3 mon | 2.4 | 0.2 | 0.1 | 0.0 |
| # WS removal events at landfills within 25 km during prior 6 mon | 3.3 | 0.3 | 0.1 | 0.1 |
| # WS removal events within 7 km during prior 3 mon | 0.2 | 0.0 | 0.0 | 0.0 |
| # WS removal events within 7 km during prior 6 mon | 0.2 | 0.0 | 0.0 | 0.0 |
| # WS removal events within 15 km during prior 3 mon | 1.3 | 0.1 | 0.0 | 0.0 |
| # WS removal events within 15 km during prior 6 mon | 1.6 | 0.1 | 0.0 | 0.0 |
| # WS removal events within 25 km during prior 3 mon | 2.2 | 0.2 | 0.9 | 0.1 |
| # WS removal events within 25 km during prior 6 mon | 3.3 | 0.2 | 1.2 | 0.1 |

Table 4-4. Means and standard errors (SE) of variables used to model sage-grouse nest daily survival rate (DSR). Data were collected from 121 and 220 sage-grouse nests at raven removal and non-removal study sites, respectively, in southwestern and south-central Wyoming, USA during 2008–2011.

| | Removal study sites | | Non-removal study sites | |
|---|---|---|---|---|
| Variable description | mean | SE | mean | SE |
| Max height of nest shrub (cm) | 61.8 | 1.8 | 60.8 | 1.3 |
| Average canopy cover of nest shrub (cm) | 109.6 | 3.5 | 113.7 | 4.7 |
| Total shrub cover (%) within 5 m | 42.1 | 1.3 | 45.0 | 1.0 |
| Sagebrush cover (%) at within 5 m | 36.0 | 1.3 | 37.0 | 1.0 |
| Average total shrub height (cm) within 5 m | 40.3 | 1.4 | 39.2 | 0.9 |
| Average sagebrush height (cm) within 5 m | 41.6 | 1.7 | 39.9 | 1.1 |
| Grass cover (%) within 5 m | 15.8 | 1.4 | 17.4 | 1.1 |
| Perennial grass cover (%) within 5 m | 12.1 | 0.8 | 15.5 | 0.7 |
| Average perennial grass height (cm) within 5 m | 21.5 | 0.9 | 23.0 | 0.6 |
| Forb cover (%) within 5 m | 6.9 | 0.7 | 8.6 | 0.6 |
| Bare ground cover (%) within 5 m | 29.2 | 1.6 | 21.9 | 1.0 |
| Litter cover (%) within 5 m | 38.3 | 1.8 | 36.9 | 1.3 |
| Horizontal visual obstruction (dm) | 3.2 | 0.2 | 3.3 | 0.1 |
| Raven density at the study site-level (no./ $km^2$) within | 0.2 | 0.2 | 0.11 | 0.1 |

| | | | | |
|---|---|---|---|---|
| 550 m of random locations | | | | |
| Site-specific change in raven density (no./km$^2$) within 550 m of random locations calculated as the change in raven density within a study site relative to 2008 | -0.1 | 0.0 | 0.0 | 0.0 |
| Raven density (no./km$^2$) within 550 m of a sage-grouse nest while sage-grouse on nest | 0.1 | 0.0 | 0.1 | 0.0 |
| Raven occupancy (0, 1) within 550 m of a sage-grouse nest during last nest check with hen on nest | N/A | N/A | N/A | N/A |
| Sage-grouse <1 or ≥1 year at time of capture (AGE) | N/A | N/A | N/A | N/A |

Table 4-5. Multinomial-Poisson mixture models assessing the effect of year, year trend, and point count type (sage-grouse nest or random) on raven densities using 'distsamp' in R. Models were analyzed separately for removal and non-removal study sites and then compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). Standard distance sampling data were collected at 250 m discrete distance intervals during May to early-Aug. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA ($n$ = 121 and 220 nests and $n$ = 287and 373 random point count locations for removal and non-removal study sites, respectively) during 2008–2011.

| Models | $k$ | $\Delta AIC_c$ | $w_i$ | Deviance |
|---|---|---|---|---|
| Removal study sites | | | | |
| Year+point count type+year×point count type[a] | 10 | 0.00 | 0.65 | 3326.24 |
| Year+point count type | 7 | 1.24 | 0.35 | 3333.76 |
| Year trend+point count type+year trend×point count type | 6 | 24.79 | 0.00 | 3359.38 |
| Year | 6 | 25.33 | 0.00 | 3359.92 |
| Year trend+point count type | 5 | 31.11 | 0.00 | 3367.76 |
| Year trend | 4 | 51.16 | 0.00 | 3389.86 |
| Point count type | 4 | 63.05 | 0.00 | 3401.76 |
| Null | 2 | 90.08 | 0.00 | 3430.82 |
| Non-removal study sites | | | | |
| Year+point count type[b] | 7 | 0.00 | 0.45 | 2721.74 |

| | | | | |
|---|---|---|---|---|
| Year trend+point count type | 5 | 1.57 | 0.20 | 2727.40 |
| Year+point count type+year×point count type | 10 | 2.25 | 0.15 | 2717.80 |
| Year trend+point count type+year trend×point count type | 6 | 2.92 | 0.10 | 2726.70 |
| Point count type | 4 | 3.05 | 0.10 | 2730.90 |
| Year | 6 | 13.41 | 0.00 | 2737.20 |
| Year trend | 4 | 16.72 | 0.00 | 2744.58 |
| Null | 2 | 18.43 | 0.00 | 2748.32 |

[a]$AIC_c$ = 3346.80

[b]$AIC_c$ = 2735.93

Table 4-6. Parameter estimates of raven density with *P*-values and 95% confidence intervals (CI) from top $AIC_c$ selected multinomial-Poisson mixture models using 'distsamp' in R. Raven densities were modeled with random locations as the reference. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA ($n$ = 121 and 220 nests and $n$ = 287 and 373 random point count locations for removal and non-removal study sites, respectively) during May to early-Aug, 2008–2011.

| | | | | | 95% CI | |
|---|---|---|---|---|---|---|
| Variable | Estimate[a] | SE | *Z* | *P* | Lower | Upper |
| Removal study sites | | | | | | |
| Intercept | -0.46 | 0.13 | -3.40 | <0.001 | -0.72 | -0.19* |
| Year 2009 | -0.12 | 0.11 | -1.12 | 0.26 | -0.34 | 0.09 |
| Year 2010 | -0.94 | 0.14 | -7.00 | <0.001 | -1.21 | -0.68* |
| Year 2011 | -0.57 | 0.12 | -4.71 | <0.001 | -0.80 | -0.33* |
| Point count type[a] | -0.82 | 0.26 | -3.13 | 0.002 | -1.33 | -0.31* |
| Year 2009×point count type [a] | -0.22 | 0.42 | -0.53 | 0.60 | -1.04 | 0.60 |
| Year 2010×point count type [a] | -0.01 | 0.47 | -0.02 | 0.99 | -0.93 | 0.92 |
| Year 2011×point count type [a] | 0.60 | 0.32 | 1.90 | 0.06 | -0.02 | 1.22 |
| Non-removal study sites | | | | | | |
| Intercept | -1.74 | 0.26 | -6.80 | <0.001 | -2.24 | -1.24* |
| Year 2009 | 0.51 | 0.20 | 2.59 | 0.01 | 0.12 | 0.90* |

| | | | | | | |
|---|---|---|---|---|---|---|
| Year 2010 | 0.41 | 0.20 | 2.03 | 0.04 | 0.01 | 0.80* |
| Year 2011 | 0.53 | 0.20 | 2.72 | 0.007 | 0.15 | 0.91* |
| Point count type[a] | -0.48 | 0.13 | -3.74 | <0.001 | -0.73 | -0.23* |

*Denotes a 95% confidence interval that does not include zero.

[a]Point count type (nest or random locations) with random point count locations coded as the reference category.

Table 4-7. Multinomial-Poisson mixture models assessing the effect of removal event variables on raven densities using 'distsamp' in R. Models were analyzed separately for removal and non-removal study sites and then compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). Only the top 10 models for removal and non-removal study sites were reported. Removal event variables used in modeling include removal distance, total removal events, removal events at landfills, and removal events other than at landfills. Removal events were analyzed at 7 km, 15 km, and 25 km. The temporal scale (3 or 6 months prior to nest fate or last point count at a random location) of each model is denoted in parenthesis. Standard distance sampling data were collected at 250 m discrete distance intervals during May to early-Aug. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA ($n$ = 407 and $n$ = 593 for removal and non-removal study sites, respectively) during 2008–2011.

| Models | $k$ | $\Delta AIC_c$ | $w_i$ | Deviance |
|---|---|---|---|---|
| Removal study sites | | | | |
| Removal 15k+removal dist+landfill removal (6 month)[a] | 6 | 0.00 | 1.00 | 3335.84 |
| Removal 25k+removal dist+landfill removal (6 month) | 6 | 29.36 | 0.00 | 3365.20 |
| Removal 15k+landfill removal (3 month) | 5 | 30.04 | 0.00 | 3367.92 |
| Removal 15k+removal dist+ landfill removal (3 month) | 6 | 30.52 | 0.00 | 3366.34 |
| Removal 25k+landfill removal (6 month) | 5 | 31.58 | 0.00 | 3369.48 |
| Removal 7k+removal dist+landfill removal (6 month) | 6 | 32.95 | 0.00 | 3368.78 |

| | | | | |
|---|---|---|---|---|
| Landfill removal (6 month) | 4 | 37.55 | 0.00 | 3377.50 |
| Removal 7k+landfill removal (6 month) | 5 | 39.10 | 0.00 | 3377.00 |
| Removal 25k+landfill removal (3 month) | 5 | 50.35 | 0.00 | 3388.24 |
| Removal 25k+removal dist+landfill removal (3 month) | 6 | 52.27 | 0.00 | 3388.10 |
| Non-removal study sites | | | | |
| Removal 25k (6 month)[b] | 4 | 0.00 | 0.44 | 2733.32 |
| Removal 25k+landfill removal (6 month) | 5 | 0.99 | 0.27 | 2732.26 |
| Removal 25k+removal dist+landfill removal (6 month) | 6 | 2.73 | 0.11 | 2731.96 |
| Removal 25k (3 month) | 4 | 3.57 | 0.07 | 2736.88 |
| Total removal 25k (6 month) | 4 | 4.91 | 0.04 | 2738.22 |
| Removal 25k+landfill removal (3 month) | 5 | 5.10 | 0.03 | 2736.38 |
| Total removal 25k+removal dist (6 month) | 5 | 6.98 | 0.01 | 2738.26 |
| Removal 25k+removal dist+landfill removal (3 month) | 6 | 7.09 | 0.01 | 2736.32 |
| Total removal 25k (3 month) | 4 | 7.57 | 0.01 | 2740.88 |
| Total removal 25k+removal dist (3 month) | 5 | 9.61 | 0.00 | 2740.88 |

[a] $AIC_c = 3348.04$

[b] $AIC_c = 2741.38$

Table 4-8. Generalized linear models assessing daily survival rate (DSR) of sage-grouse nests using Program MARK. Variables used in modeling include sage-grouse age (AGE), year, year trend, study site type (removal or non-removal), raven occupancy (raven occupancy) and density (raven density) at the sage-grouse nest level, and raven density (landscape raven density) and site-specific change in density of ravens at the study site-level. Models were compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). Data were collected from 121 and 220 sage-grouse nests at removal and non-removal study sites, respectively. Sage-grouse were located in eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA during 2008–2011.

| Models | $k$ | $\Delta AIC_c$ | $w_i$ | Deviance |
|---|---|---|---|---|
| Raven occupancy+site-specific change in raven density[a] | 3 | 0.00 | 0.25 | 811.58 |
| Raven occupancy | 2 | 0.39 | 0.20 | 813.97 |
| Site-specific change in raven density | 2 | 2.07 | 0.09 | 815.66 |
| Null | 1 | 2.14 | 0.09 | 817.72 |
| Year | 4 | 3.10 | 0.05 | 812.67 |
| Year+study site type+year×study site type | 8 | 3.11 | 0.05 | 804.67 |
| Year trend | 2 | 3.54 | 0.04 | 817.12 |
| Nest-level raven density | 2 | 3.63 | 0.04 | 817.22 |
| Study site type | 2 | 3.64 | 0.04 | 817.22 |
| AGE | 2 | 3.69 | 0.04 | 817.27 |

| | | | | |
|---|---|---|---|---|
| Landscape raven density | 2 | 4.14 | 0.03 | 817.72 |
| Year trend+study site type+year trend×study site type | 4 | 4.15 | 0.03 | 813.73 |
| Year+study site type | 5 | 4.77 | 0.02 | 812.34 |
| Year trend+study site type | 3 | 4.94 | 0.02 | 816.52 |

[a] $AIC_c = 817.59$

Table 4-9. Generalized linear models assessing sage-grouse nest daily survival rate (DSR) using Program MARK. Variables used in modeling include sage-grouse nest level (raven occupancy) and site-specific change in raven density (Δ site-level raven; site-level raven), max nest shrub height, average nest shrub canopy cover, Robel visual obstruction, total shrub cover, average total shrub height, grass cover, forb cover, bare ground cover, litter cover, and average perennial grass height. Models were compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). A fully saturated spatiotemporal model was included to assess goodness-of-fit; the fully saturated model included all microhabitat variables, year and study site type (removal and non-removal). Data were collected from 121 and 220 sage-grouse nests at removal and non-removal study sites, respectively. Sage-grouse were located in eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA during 2008–2011.

| Models | $k$ | $\Delta AIC_c$ | $w_i$ | Deviance |
|---|---|---|---|---|
| Raven occupancy+Δ site-level raven+perennial grass height | 4 | 0.00 | 0.12 | 809.54 |
| Raven occupancy+Δ site-level raven | 3 | 0.04 | 0.12 | 811.58 |
| Raven occupancy+Δ site-level raven+visual obstruction | 4 | 0.33 | 0.11 | 809.87 |
| Raven occupancy+Δ site-level raven+bare ground | 4 | 1.56 | 0.06 | 811.10 |
| Raven occupancy+Δ site-level raven+forb cover | 4 | 1.76 | 0.05 | 811.30 |
| Raven occupancy+Δ site-level raven+total shrub height | 4 | 1.77 | 0.05 | 811.31 |

| | | | | |
|---|---|---|---|---|
| Raven occupancy+Δ site-level raven+grass cover | 4 | 1.81 | 0.05 | 811.35 |
| Raven occupancy+Δ site-level raven+total shrub cover | 4 | 1.85 | 0.05 | 811.39 |
| Raven occupancy+Δ site-level raven+nest shrub cover | 4 | 1.87 | 0.05 | 811.41 |
| Raven occupancy+Δ site-level raven+litter | 4 | 1.99 | 0.05 | 811.53 |
| Raven occupancy+Δ site-level raven+nest shrub height | 4 | 2.01 | 0.05 | 811.55 |
| Null | 1 | 2.18 | 0.04 | 817.72 |
| Visual obstruction | 2 | 2.26 | 0.04 | 815.80 |
| Perennial grass height | 2 | 3.25 | 0.02 | 816.80 |
| Bare ground | 2 | 3.59 | 0.02 | 817.14 |
| Total shrub height | 2 | 3.78 | 0.02 | 817.32 |
| Forb cover | 2 | 3.98 | 0.02 | 817.53 |
| Nest shrub cover | 2 | 4.00 | 0.02 | 817.54 |
| Nest shrub height | 2 | 4.03 | 0.02 | 817.57 |
| Total shrub cover | 2 | 4.12 | 0.02 | 817.66 |
| Grass cover | 2 | 4.12 | 0.02 | 817.67 |
| Litter | 2 | 4.17 | 0.02 | 817.72 |
| Spatiotemporally saturated | 15 | 18.93 | 0.00 | 806.38 |

[a] $AIC_c = 817.55$

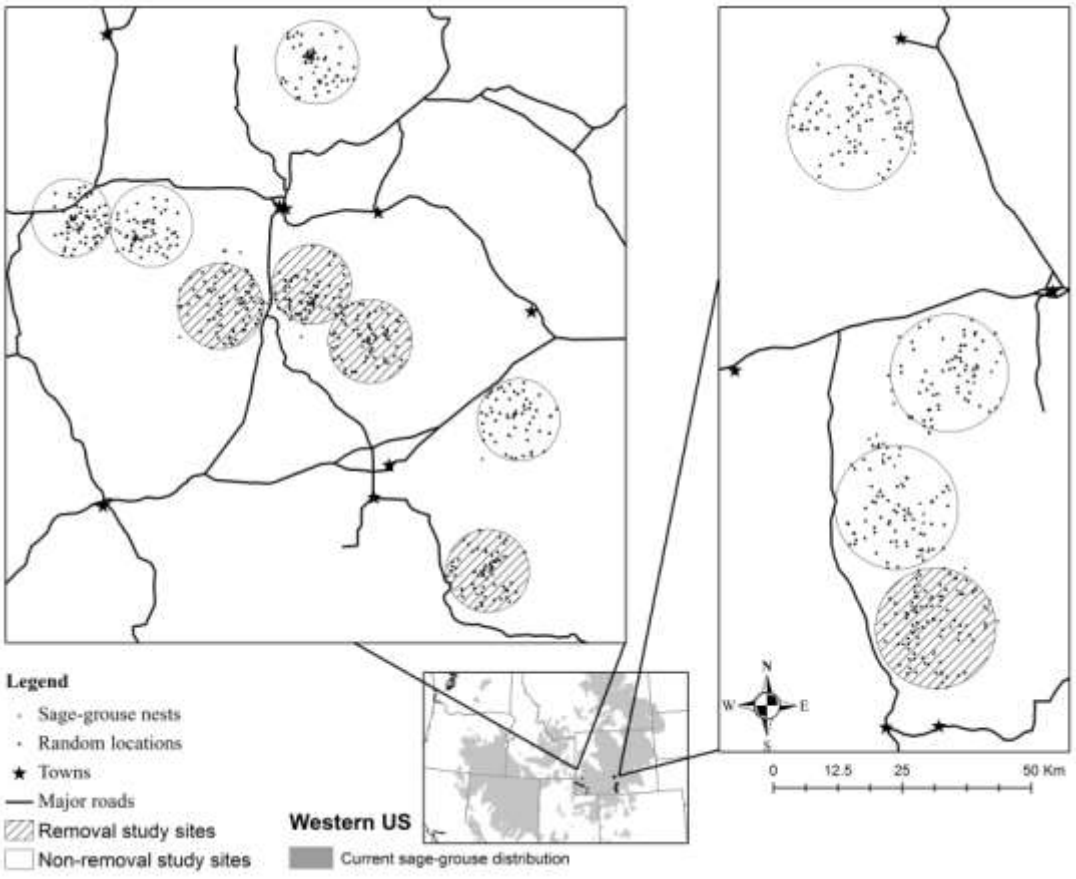



Figure 4-1. Location map of southern Wyoming depicting eight 16-km diameter and four 24-km diameter study sites, southwestern and south-central, Wyoming, USA, 2008–2011. Magnified sections correspond on left to southwest and on right to south-central Wyoming. Map includes locations of 2008–2011 sage-grouse nests, random locations, landfills, towns, and major roads.

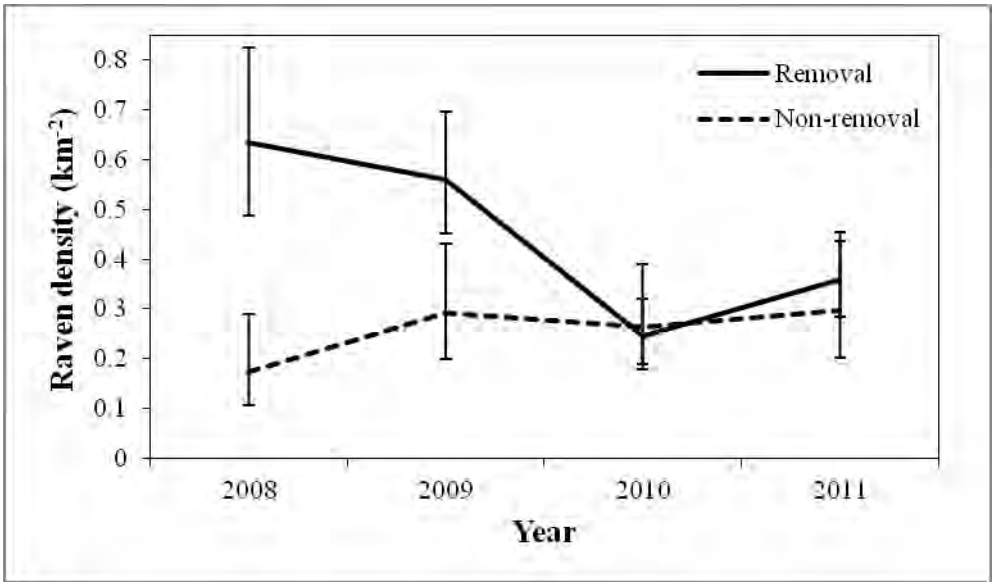



Figure 4-2. Raven density (no./km$^2$) estimates by year, 2008–2011, from the top AIC$_c$ selected multinomial-Poisson mixture models for removal and non-removal study sites. Estimates of raven density were modeled from 287 and 373 random locations in removal and non-removal study sites, respectively. Error bars indicate 95% confidence intervals. Data were collected from four 16-km and one 24-km removal study sites and four 16-km and three 24-km non-removal study sites in southwestern and south-central, Wyoming, USA.

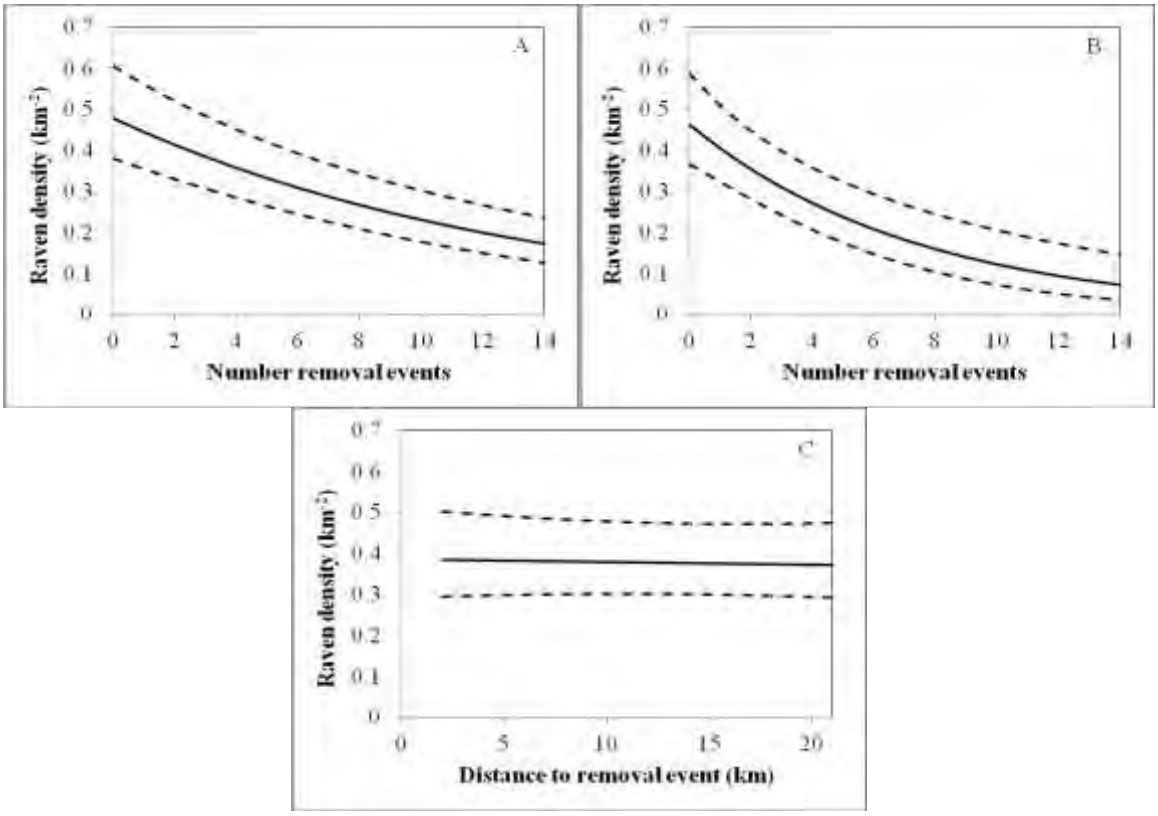



Figure 4-3. Predictions of raven density (no./km$^2$) from the top AIC$_c$ selected multinomial-Poisson mixture model of USDA/APHIS/Wildlife Services (WS) removal events at removal study sites with 95% confidence intervals. Predicted effects of the number of landfill (A; within 25 km) and non-landfill (B; within 15 km) based removal events conducted by WS and the effect of distance to nearest removal event (C). All variables calculated within six months of the fate of a sage-grouse nest or last recorded point count at a random location. Data were collected from four 16-km and one 24-km study sites in southwestern and south-central, Wyoming, USA ($n$ = 121 sage-grouse nests and $n$ = 287 random locations), 2008–2011.

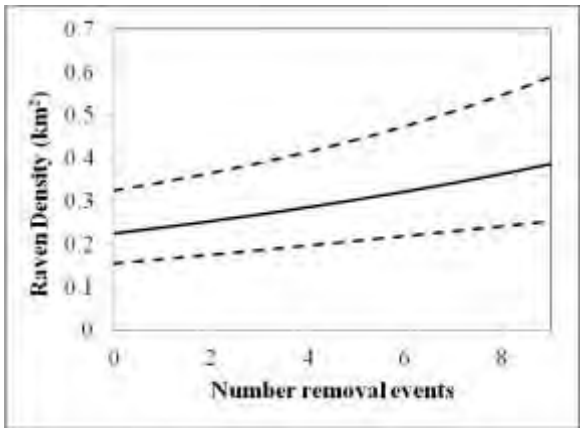



Figure 4-4. Predictions of raven density (no./km$^2$) from the top AIC$_c$ selected multinomial-Poisson mixture model of USDA/APHIS/Wildlife Services (WS) removal events at non-removal study sites with 95% confidence intervals. Predicted effects of the number of removal events conducted by WS between 15 and 25 km and within six months of the fate of a sage-grouse nest or last recorded point count at a random location. Data were collected from four 16-km and three 24-km study sites in southwestern and south-central, Wyoming, USA ($n$ = 220 sage-grouse nests and $n$ = 373 random locations), 2008–2011.

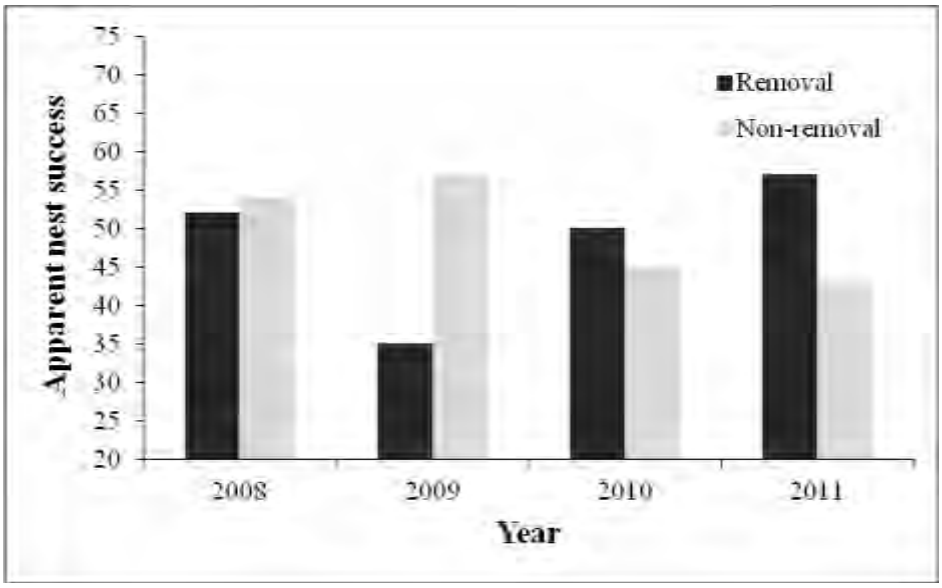



Figure 4-5. Apparent nest success (%) of 341 sage-grouse nests found in removal and non-removal study sites. Apparent nest success was calculated as the number of hatched nests divided by the total number of nests found. Removal study sites had 23, 28, 28, and 42 nests in 2008–2011, respectively. Non-removal study sites had 41, 57, 55, and 67 nests found during 2008–2011, respectively. Data were collected from four 16-km and one 24-km removal study sites and four 16-km and three 24-km non-removal study sites in southwestern and south-central, Wyoming, USA.

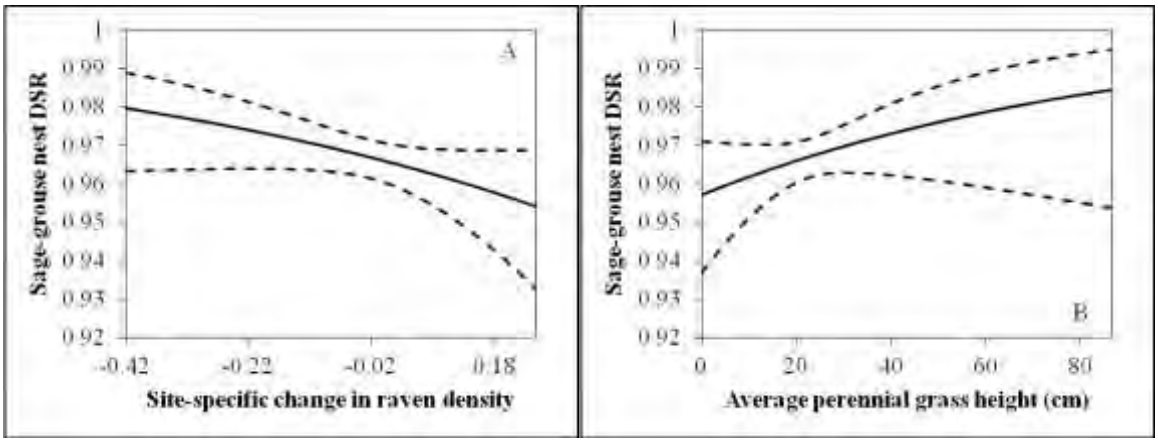



Figure 4-6. Predictions of daily survival rate (DSR) of sage-grouse nests from the top $AIC_c$ selected generalized linear model using Program MARK at removal and non-removal study sites with 95% confidence intervals. Predicted effects of site-specific change in raven density (no./km$^2$) at a study site relative to 2008 (A) and average perennial grass height within 5 m (B) on sage-grouse nest DSR. Raven variables calculated within EDR (550 m) of 'distsamp'. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA ($n$ = 341 sage-grouse nests), 2008–2011.

# CHAPTER 5

# GREATER SAGE-GROUSE NEST SUCCESS IN RELATION TO CORVIDS, PROXIMITY TO ANTHROPOGENIC AND LANDSCAPE FEATURES, AND MICROHABITAT IN SOUTHERN WYOMING

**ABSTRACT** Nest success of greater sage-grouse (*Centrocercus urophasianus*: hereafter "sage-grouse") has been well studied, but the effects of anthropogenic and landscape features on nest success have not been evaluated simultaneously with the potential effects of predators. Depredation of sage-grouse nests can be an influential factor limiting their productivity, and most failed sage-grouse nests are depredated by predators. Black-billed magpies (*Pica hudsonia*: hereafter "magpie") and common ravens (*Corvus corax*: hereafter "raven") have been verified with video as predators of ground nests, and the negative effect of ravens on the nest success of sage-grouse has been well documented. I collected nest success data from 341 sage-grouse nests in eight study sites (16 km diameter each) and four study sites (24 km diameter each) in southern Wyoming, USA during 2008–2011. I used the nest survival model in Program MARK to evaluate the effects of 4 covariate sets including corvid densities (nest-level and study site-level), anthropogenic features, landscape features, and microhabitat on sage-grouse nest success. Interactions between study site-level corvid densities (raven and magpie independently) and variables within all other covariate sets were also assessed. I tested the hypothesis that the negative effects of corvids would be amplified in areas closer to potential perches and areas with subsidized food resources. I did not find any evidence that anthropogenic

features or magpies had a negative impact on sage-grouse nest success. I found that nest success was positively correlated with rugged habitat measured at 1-km radius ($TRI_{1.0}$), and negatively impacted by the presence of ravens. My results highlight the necessity to assess habitat and predator community dynamics concurrently when designing management plans.

## INTRODUCTION

Several studies have suggested that quantity and condition of breeding habitat is the most important factor that dictates the productivity of sage-grouse (Connelly et al. 1994, Braun 1998, Schroeder and Baydack 2001, Connelly et al. 2011, Hagen 2011). However, even in excellent sage-grouse habitat, most greater sage-grouse (*Centrocercus urophasianus*: hereafter "sage-grouse") nests are lost to predators such as red fox (*Vulpes vulpes*), badgers (*Taxidea taxus*), coyotes (*Canis latrans*), black-billed magpies (*Pica hudsonia*: hereafter "magpie" ), and common ravens (*Corvus corax*: hereafter "ravens"; Willis et al. 1993, Gregg et al. 1994, Heath et al. 1997, Holloran 1999, Connelly et al. 2004, Baxter et al. 2007). Sage-grouse are a species of conservation concern, because their distribution and abundance in western North America has declined over the last century (Gregg et al. 1994, Johnsgard 2002, Connelly et al. 2004), and many factors have been attributed to this decline including predation, habitat loss, and habitat fragmentation (Braun 1998).

Johnson and Braun (1999) and Taylor et al. (2012) found, that along with chick and adult survival, nest success was an important demographic parameter for population

growth of sage-grouse. Nest success in relation to predator communities has not been the focus of sage-grouse research and conservation. However, nest success related to predator communities was not likely to have been a problem during pre-European settlement, because sage-grouse co-evolved with the predator communities present in sagebrush ecosystems (Schroeder et al. 1999, Schroeder et al. 2001). There are currently no predators that specialize on sage-grouse during any life history stage (egg, chick, or adult; Hagen 2011, Connelly et al. 2011). Thus, Hagen (2011) suggested that in general predation is not limiting sage-grouse populations; he also indicated that predators may only negatively affect sage-grouse populations in fragmented habitats and areas with human-subsidized predator populations. However, these areas of habitat fragmentation and areas with human-subsidized predator populations have drastically increased in the recent past (Leu et al. 2008); mostly via human endeavors in sagebrush steppe. For example, red fox and common raccoon (*Procyon lotor*) have increased in abundance in sage-grouse habitat, especially near human activities (Connelly et al. 2000, Baxter et al. 2007, Hagen 2011), and densities of ravens have increased in Wyoming and throughout the historic range of sage-grouse (Larsen and Dietrich 1970, Andrén 1992, Engel and Young 1992, Boarman et al. 1995, Sauer et al. 2011).

Increased habitat fragmentation has brought a range of new stresses to sage-grouse including increased predation rates (Schroeder and Baydack 2001, Connelly et al. 2004). Corvids, specifically ravens and magpies, have been known to utilize fragmented habitats with anthropogenic structures and features that provide subsidized food resources (anthropogenic features for ease of discussion; Andrén 1992, Vander Haegen 2002). For

example, Bui et al. (2010) found that higher raven occupancy of the landscape was correlated with a greater frequency of failed sage-grouse nests around Jackson and Pinedale, Wyoming. Bui et al. (2010) suggested that increased raven occupancy could have been attributed to increased availability of nest structure for ravens from anthropogenic structures in sagebrush habitat; over half of their study was located in an intensely developed natural gas field. Videos have verified that magpies and ravens are predators of ground nests (Vander Haegen et al. 2002); they found that both species depredated nests in fragmented habitat more often than intact shrubsteppe habitat (magpies especially utilized fragmented habitat). Furthermore, passerine nest success in fragmented habitat was shown to be lower than intact shrubsteppe habitat (Vander Haegen et al. 2002). In addition to the direct negative effect of corvid abundance on sage-grouse nest success, there are potentially additive impacts of anthropogenic features on sage-grouse nest success, such as increased hunting efficiency, increased number of nesting structures, and increased carrying capacity of corvids within sage-grouse breeding habitat. Sources of perch and nesting structure for corvids include oil and gas related structures, residential houses (on buildings or in trees associated with houses), communication towers, and power lines (Engel et al. 1992, Knight and Kawashima 1993, Trost 1999, Lammers and Collopy 2007, Prather and Messmer 2010, Slater and Smith 2010); whereas, sources of reliable food subsidies include residential houses, campgrounds, landfills, and roads, which provide road-kill, dead livestock, and garbage (Knight and Call 1980, Boarman 1993, Knight and Kawashima 1993, Boarman et al. 1995, Trost 1999, Kristan et al. 2004, Marzluff and Neatherlin 2006).

Corvid depredation of sage-grouse nests has been implicated as a potential factor limiting sage-grouse productivity, especially in fragmented habitats (Batterson and Morse 1948, Willis et al. 1993, Gregg et al. 1994, Schroeder and Baydack 2001, Vander Haegen 2002, Coates and Delehanty 2010, Bui et al. 2010). Yet, it is unclear why anthropogenic features affect corvid depredation of sage-grouse nests.

Connelly et al. (2011) recommended that conservation efforts for sage-grouse should include research to quantify predator communities in relation to sage-grouse demographic rates (including nest success) and potential additive effects of predators and anthropogenic features. Increased size of corvid populations, especially ravens, in areas with subsidized resources has been anecdotally documented in southwest and south-central Wyoming associated with human activities (e.g., livestock and natural gas development; R. J. Merrell, United States Department of Agriculture Animal and Plant Health Inspection Service Wildlife Services, personal communication), and raven abundance has increased in Wyoming during the past decade, 2001–2010 (Sauer et al. 2011). Thus, I recorded corvid densities associated with sage-grouse nesting and brood-rearing areas from 2008–2011 to determine if corvids were important sage-grouse nest predators. I hypothesized that sage-grouse nest success would be lower in areas and years with greater abundance of corvids, specifically, ravens and magpies. In addition, I hypothesized that this effect would be intensified in areas closer to potential perches and areas with food subsidies, such as oil and gas structures, power lines, houses, roads, towns, and landfills. To test these hypotheses, I assessed sage-grouse nest success in relation to sage-grouse exposure to corvids, potential perches, and proximity to areas

associated with human provided food subsidies. As secondary objectives, I evaluated the potential effects of landscape features and microhabitat in relation to corvid abundance. Similar to anthropogenic features, landscape features could be used as perches or nest structure by raptors, or could be areas with higher productivity that attract predators. Thus, I hypothesized that sage-grouse nest success would be lower in areas closer to forested and riparian habitat, rougher topography, and lower microhabitat quality.

## STUDY AREA

My study was conducted in southwest and south-central Wyoming. I had 12 circular study sites, eight were 16 km in diameter and four were 24 km in diameter. Study sites in southwest Wyoming were 16-km diameter and approximately centered around leks where hens were captured based on results found by Holloran and Anderson (2005). Study sites in south-central Wyoming were 24 km, because sage-grouse were captured at several nearby leks over a larger area. Five study sites were located in Lincoln County, two in Sweetwater County, two in Uinta County, and three in Carbon County. Study sites were chosen to provide a representation of overall sage-grouse nesting habitat in southern Wyoming. During 2007–2011, raven control (lethal removal) efforts of varying intensity were carried out by USDA/APHIS/Wildlife Services (WS) near five of the 12 study sites for the protection of livestock.

Removal and non-removal study sites had similar topographic features, weather, and vegetation. Elevation ranged from 1,950 m to 2,600 m among removal study sites

and 1,925 m to 2,550 m among non-removal study sites. Most of the land within all of the study sites was federally owned and administered by the U.S. Bureau of Land Management with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in the study sites. All study sites had anthropogenic development, which consisted mostly of unimproved 4-wheel drive roads. Conventional natural gas, coalbed methane natural gas, and/or conventional oil extraction activities were present in two of the removal study sites and four of the non-removal study sites.

The landscape at all study sites was dominated by sagebrush (*Artemisia* spp.); Wyoming big sagebrush (*A. tridentata wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) were the most common. Black sagebrush (*A. nova*) and dwarf sagebrush (*A. arbuscula*) were found on exposed ridges. Other common shrub species in the study sites included alderleaf mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), chokecherry (*Prunus virginiana*), common snowberry (*Symphoricarpos albus*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), Saskatoon serviceberry (*Amelanchier alnifolia*), and spiny hopsage (*Grayia spinosa*). Isolated stands of juniper (*Juniperus* spp.) and quaking aspen (*Populus tremuloides*) were found at the higher elevations on north-facing hillsides. Common forb species included arrowleaf balsamroot (*Balsamorhiza sagittata*), buckwheat (*Eriogonum* spp.), common yarrow (*Achillea millefolium*), dandelion (*Taraxacum* spp.), desert parsley (*Cymopterus* spp.), phlox (*Phlox* spp.), lupine (*Lupinus* spp.), sego lily (*Calochortus nuttallii*), and wild onion (*Allium* spp.). Common grass species included: bluegrasses (*Poa* spp.), bluebunch wheatgrass (Ps*eudoroegneria*

*spicata*), green needlegrass (*Nassella viridula*), needle and thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), and western wheatgrass (*Pascopyrum smithii*). Cheatgrass (*Bromus tectorum*) was present, but not widespread in any of the study sites.

## METHODS

### Sage-grouse Capture and Monitoring

From 2008 to 2011, I monitored sage-grouse hens during the nesting season (late-April to mid-July). Hens were captured, radio-collared, and released in April of each year. I captured hens at night using ATVs, spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992, Connelly et al. 2003). Sage-grouse hens were fitted with 17.5-g or 22-g (<1.5% body mass) necklace radio collars (Holohil Systems Ltd, RI-2D, Ontario, Canada or Advanced Telemetry Systems Inc, A4060, Isanti, MN, USA). I aged sage-grouse hens as yearlings or adults by examining outer primaries (Patterson 1952).

Between May 1 and July 15, I located hens weekly with VHF receivers (Communications Specialists, R-1000, Orange, CA, USA) and 3-way Yagi antennas (Communications Specialists, Orange, CA, USA). Potential nests were identified with binoculars from ~15 m by circling a radio-marked hen until she was visually spotted under a shrub. I used handheld global positioning system (GPS) units (eTrex, Garmin Inc., Olathe, KS) to record hen locations. Location accuracy on the GPS ranged from 2–8 m.

Nests were verified by triangulating the hen under the same shrub from ≥50 m

away or thoroughly searching the area of the potential nest when the hen was absent. I continued monitoring nests weekly until the nest hatched or failed. I assessed nest fate as successful or unsuccessful after a hen had left her nest. A successful nest was defined as having evidence that at least 1 egg hatched as determined by shell membrane condition (Wallestad and Pyrah 1974). I classified unsuccessful nests as abandoned (eggs not depredated or hatched) or depredated (at least one egg with evidence of depredation).

**Corvid Variables**

Between 1 May and 1 August of each year, I conducted point count surveys at sage-grouse nests and random locations within each study site to compare corvid densities. Ravens and magpies were quantified separately, but will be referred to as corvids for ease of discussion. To avoid disturbing an incubating hen, nest point counts were conducted 100–200 m away from a sage-grouse nest but within a line-of-sight of that sage-grouse nest. Random locations were selected in habitat considered to be available to sage-grouse for nesting within each study site. To restrict random locations to available nesting habitat, I used ArcMap 10.0 (ESRI Inc., Redlands, California) to generate random locations only in sagebrush-dominated habitat, which was classified by the Northwest ReGAP landcover data from 2008 (Lennartz 2007). Random locations were designated to be >1,000 m apart; however, random selection led to average nearest neighbor distances among random point count locations of >2,000 m (Chapter 2). I generated 12 random locations in each 16-km diameter study site and 18 random locations in each 24-km diameter study site per year. I generated a new set of random

locations each year to avoid spatial autocorrelation; thus, random locations among years were independent.

I used standard distance sampling techniques (Ralph et al. 1995, Buckland et al. 2001, Thomas et al. 2010), which entailed counting all corvids observed during point counts and recording each corvid's distance from the observer (when standing at the center of the point count location). I recorded distance as the distance from the observer to where a corvid was first located (Ralph et al. 1995, Thomas et al. 2010); this minimized possible bias associated with corvids being attracted to or flushed away from an observer. When a corvid was displaced from the center of a point count location as an observer approached (6% of all detected birds), I recorded distance from that corvid to the center of the point count location while the observer approached as suggested by Ralph et al. (1995). This was done when the approach of an observer resulted in a corvid moving away from the center of the point count location. A 1500–m rangefinder (American Technologies Network Corp., RE-1500 m, San Francisco, California) in conjunction with a GPS was used to estimate distances directly or to validate visually estimated distances.

Observers were trained and tested in corvid and raptor identification before conducting point counts. Point counts were 10 min in length, and I conducted them during daylight hours on a weekly basis at each study site. I visited each point count location 1 to 8 times with most locations visited ≥3 occasions. I did not survey for corvids in inclement weather (i.e., when raining or wind speeds greater than 25 km/h; Ralph et al. 1995). Unidentified birds were not included in analyses; these contributed

2% of detections within truncated observation distances. Nest point counts were performed after nests were initially located; thus, nest point counts were conducted in May to early-July. I performed random point counts May to 1 August each year.

I intermixed the sampling of nest and random point counts within each study site. To minimize observer bias, I changed the time of day and the observer that conducted individual point counts within a study site each week (i.e., each individual point count location regardless of type—nest or random—was conducted at a different time of day each week and by a different observer as best as possible). The observers conducting point counts within a particular study site changed each year.

All corvid variables were calculated from the raw count data within effective detection radii (EDR; 600 m for ravens and 300 m for magpies) estimated with DISTANCE, version 6.0 release 2 (Thomas et al. 2010) as specified in Chapter 2. The raw densities were weighted by the number of visits to each point count location. Raven and magpie study site-level variables were individually calculated from random point count locations. Sage-grouse nest-level corvid abundance was calculated from point counts at sage-grouse nests within species-specific EDRs as 1) raven density (number/km$^2$ and hereafter "nest-level raven density") or magpie density (number/km$^2$ and hereafter "nest-level magpie density") at the nest and 2) occupancy (0 or 1) of at least 1 raven or 1 magpie during the last nest check when the sage-grouse hen was still on her nest (hereafter: "raven occupancy" or "magpie occupancy"). I did not include both nest-level raven density and raven occupancy in any model, because nest-level raven density and raven occupancy were measured at the same spatiotemporal scale. Study site-level

corvid densities were calculated at each study site by averaging the raven or magpie densities at all random locations. I had noted through observation that relative changes in corvid densities within many study sites had positive or negative effects on nest success of sage-grouse. I attributed this phenomenon to the possibility of corvids being more or less effective predators on sage-grouse nests depending on the study site due to overall characteristics of a particular study site (combination of individual corvid behavior, topographic roughness, large scale cover, anthropogenic development, etc.). In addition to study site-level raven densities, I calculated site-specific change in corvid density—from random point count locations—as the increase or decrease in landscape corvid density (annual density) relative to the corvid density in a particular study site at the beginning of the study (2008). Thus, site-specific change in corvid density was 0 for all study sites in 2008. The site-specific change in corvid density variables were intended to look at relative change in risk of depredation within each study site (i.e., does site specific increase or decrease of corvid densities effect nest success of sage-grouse). Thus, site-specific change in corvid densities were not quantifying the effect of the exact density of corvids on nest success of sage-grouse among all study sites. Rather, they were assessing site-specific change in exposure to corvids.

**Anthropogenic and Landscape Feature Variables**

I calculated sage-grouse proximity to anthropogenic features that could be used as a perch by corvids, a nest structure by ravens, or had the potential to generate food subsidies that were provided by humans (e.g., road-kill, dead livestock, and garbage) with

ArcMap 10.0. Anthropogenic structures that were >2 m in height were considered available for perching or nesting by corvids. I quantified the distance from sage-grouse locations to the nearest oil and gas structure (energy well, compressor station, transfer station, refinery, or other energy extraction related buildings), major road, all roads, communication tower, house, town, landfill, and power line for each sage-grouse nest. Most (>95%) oil and gas structures were energy wells. Ongoing energy development was occurring in half of my study sites, which required me to assess the dates that energy related structures and roads were added or removed from the landscape. In distance calculations, I only included oil and gas structures and roads that were physically on the ground when each sage-grouse nest was located. I obtained information on oil and gas structures, including date construction started on the structure and date when wells were plugged and abandoned (date structure was removed), from the Wyoming Oil and Gas Conservation Commission (WOGCC; 2012). I verified the spatial location and existence of older structures with color aerial satellite imagery from summer 2006 and August 2009 obtained from the National Agriculture Imagery Program (NAIP; U.S. Department of Agriculture [USDA] 2010). Aerial imagery from NAIP was produced by the USDA on a 3-year rotation; thus, I used WOGCC data and on the ground GPS units to map energy development that occurred after August 2009. However, energy development reported to WOGCC after August 2009 had better reporting of location, spud date, and plug abandon date. I used 2009 NAIP imagery to digitize the location of major roads, all roads, communication towers, houses, towns, and landfills within a 5-km buffer around study sites; roads constructed between August 2009 and September 2011

were mapped on the ground with GPS units. Major roads included paved, improved gravel roads, and railroads; whereas, all roads included major roads and all unimproved 4-wheel drive roads. All transmission and distribution power lines within a 5-km buffer around study sites were mapped on the ground with GPS units; telephone lines not associated with a power line were included in power line mapping. Neither sage-grouse nor corvids were likely to discriminate between many of the different types of anthropogenic structures; thus, I created 2 anthropogenic structure variables that represented the nearest 1) distance to either an oil and gas structure, communication tower, or house (DIST_WCH); and 2) distance to either an oil and gas structure, communication tower, house, or power line (ANTH). This was in addition to distances from sage-grouse nests to individual types of anthropogenic structures. I report means and standard errors (SE) for distances to anthropogenic feature variables for successful and unsuccessful nests (Table 5-1).

Similar to anthropogenic features, landscape features could be used as perches or nest structures by corvids or could be areas with higher productivity that attract predators. For example, magpies have been associated with riparian habitats for food availability and nesting (Trost 1999). Thus, I used ArcMap 10.0 to calculate the distance from every sage-grouse nest to forest (deciduous and conifer stands) and riparian habitats. Tree stands and riparian habitat were identified with Northwest ReGAP landcover data from 2011 (Lennartz 2007), and verified with NAIP imagery from 2009. Topography with greater surface roughness has the potential to create topographic structures (e.g., hilltops, knolls, and cliff edges) that provide vantage points similar to perches, and sage-grouse

have been found to avoid rougher topography during nesting (Jensen 2006, Doherty et al. 2010). For sage-grouse nests, I used ArcMap 10.0 to extract topographic ruggedness index (TRI) values generated by Hanser et al. (2011) for the Wyoming Basins Ecoregion; TRI variables were developed using a moving window analysis at 0.27-km, 0.54-km, 1-km, and 3-km radii (0.23 $km^2$, 0.92 $km^2$, 3.14 $km^2$, and 28.26 $km^2$ scales, respectively). Riley et al. (1999) created TRI to describe the roughness of landscapes, and the index is quantified as the difference in elevation among adjacent pixels of a digital elevation map; the index is then averaged over a user defined area. I report means and standard errors (SE) for distances to landscape feature variables for successful and unsuccessful nests (Table 5-1).

**Microhabitat Variables**

I sampled vegetation at sage-grouse nests in late-May to early-July 1 to 2 weeks after sage-grouse nests hatched or failed. I recorded the maximum height and the average canopy cover of the nest shrub. I quantified vegetation within 5 m surrounding sage-grouse nests by orienting 2 vegetation transects—each 10 m in length—at the cardinal directions and intersecting at a sage-grouse nest. Vegetation transects were conducted to measure average total shrub cover—including antelope bitterbrush, greasewood, rabbitbrush, sagebrush, Saskatoon serviceberry, and snowberry (Canfield 1941). Average percent cover of shrubs was calculated by dividing the total shrub intercepted line length (cm) by the total line length (2000 cm) and then multiplying by 100. Gaps <3 cm were not recorded (Wambolt et al. 2006), and no section of shrub cover was measured more

than once. I averaged the height of shrubs that intersected the vegetation transect for average total shrub height; shrub heights excluded inflorescences. I calculated percent cover of grass, perennial grass, forbs, bare ground, and litter in six cover classes (1 = 0–1%, 2 = 1.1–5%, 3 = 5.1–25%, 4 = 25.1–50%, 5 = 50.1–75%, and 6 = 75.1–100%; Kirol et al. 2012) by averaging 9, 20-cm × 50-cm quadrats placed along vegetation transects at 2 m, 4 m, 5 m, 6 m, and 8 m (Daubenmire 1959). Perennial grass height was measured by recording the maximum grown height (droop height) excluding flowering stalks within 1 m of the 9 quadrats. The lowest visible 5-cm section of a Robel pole—that was placed in the center of a sage-grouse nest—was recorded to provide an index of general line-of-sight obstruction (hereafter "visual obstruction"; Robel et al. 1970). I recorded Robel pole readings from 1 m off the ground and 5 m away at the 4 cardinal directions and averaged these values to report 1 visual obstruction measurement per site. I report means and standard errors (SE) for vegetation variables used in models for successful and unsuccessful nests (Table 5-1).

**Data Analyses**

I analyzed daily survival rate (DSR) of sage-grouse nests by fitting generalized linear models of DSR using maximum likelihood in Program MARK (White and Burnham 1999). I evaluated the effect of a nesting sage-grouse's age (AGE), study site-level corvid densities, site-specific change in corvid densities, nest-level corvid occupancy or density, anthropogenic features, landscape features, and microhabitat on sage-grouse nest DSR. Modeling of sage-grouse nest DSR was conducted with an

information theoretic approach (Anderson 2008). I compared models with Akaike's information criterion corrected for small sample sizes ($AIC_c$) and Akaike weights ($w_i$; Burnham and Anderson 2002). I employed sequential $AIC_c$ modeling of covariate sets, which was suggested by Arnold (2010) as an appropriate approach for identifying and ranking the most parsimonious models. Non-informative covariates (85% confidence intervals [CIs] of parameter estimates overlapped 0) were eliminated within each covariate set before comparing top $AIC_c$ selected models among covariate sets (Arnold 2010).

Four covariate sets were evaluated sequentially, and consisted of 1) nest-level and site-specific change in corvid densities, 2) anthropogenic features, 3) landscape features, and 4) microhabitat variables. I evaluated the effect of a sage-grouse's age (AGE) on sage-grouse nest DSR within the sage-grouse corvid abundance covariate set. I included site-specific change in corvid densities × anthropogenic feature variables, site-specific change in corvid densities × landscape feature variables, and site-specific change in corvid densities × microhabitat as pairwise interactions within each respective covariate set. Pairwise interactions with site-specific change in corvid densities were included to assess whether negative effects of site-specific change in corvid densities were intensified in areas closer to potential perches or corvid nest structure, in areas closer to human provided food subsidies, or in areas with poorer quality microhabitat. I did not include DIST_WCH or ANTH with any other anthropogenic structure variable, because DIST_WCH and ANTH were derived from a combination of distance from sage-grouse nests to energy wells, communication towers, houses, and power lines. The best variable

describing the effect of anthropogenic structures on sage-grouse nest DSR was determined through $AIC_c$ selection within the anthropogenic feature covariate set. I compared models with individual TRI variables measured at 0.27 km, 0.54 km, 1 km, and 3 km radii with $AIC_c$ to choose the best spatial scale for the TRI variable to be used in the landscape feature covariate set; the TRI variable scale with the lowest $AIC_c$ was used in all further modeling. As the final modeling step, I compared all top $AIC_c$ selected models from every covariate set (models within 2 $AIC_c$ of the top model within each covariate set) among each other and as additive models with combinations of all 4 covariate sets. I based my inference on models within 2 $AIC_c$ of the top selected model (Burnham and Anderson 2002). I prevented multicollinearity by only including one variable of any pair of variables that co-varied in any model ($r$ >0.65) as determined with a Pearson's correlation matrix. In this situation I eliminated one co-varying variable from further analysis by retaining the variable that made the most biological sense. Variance inflation factors (VIF) for all predictor variables were ≤5, which indicated that the variances of coefficient values were not drastically increased by the inclusion of any predictor variable; thus, collinearity was not a major problem.

In addition to $AIC_c$ model comparison, I implemented a spatiotemporal modeling strategy to evaluate general trends in sage-grouse nest DSR in relation to site-specific change in corvid densities, anthropogenic features, landscape features, and microhabitat. A spatiotemporal strategy was implemented because many variables describing raven abundance and sage-grouse nest survival were exclusive to a given year or type of study site (removal or non-removal). I assessed goodness-of-fit of top $AIC_c$ selected models by

computing a ratio of Zheng's (2000) proportional reduction of deviance (RDR) for covariate models to spatiotemporally saturated models (maximum proportional reduction in deviance; Iles 2012), which has been considered appropriate for generalized linear models (Zheng 2000, Aubry et al. 2011). Deviance reduction for each spatiotemporally saturated model and top $AIC_c$ selected models were calculated relative to null models (time and study site invariant):

$$D_{int} = 1 - (deviance_{interest}/deviance_{null}) \quad (1)$$

$$D_{sat} = 1 - (deviance_{saturated}/deviance_{null})$$

$$RDR = D_{int} / D_{saturated} \quad (2)$$

thus, the ratio gives an assessment of a covariate model's relative ability to explain spatiotemporal processes effecting sage-grouse nest DSR. The ratio is 1 for the spatiotemporally saturated model and 0 for the null model (Iles 2012). I compared the top $AIC_c$ selected models of sage-grouse nest DSR to a spatiotemporally saturated model with RDR. The saturated model for sage-grouse nest DSR included year; type of study site; max nest shrub, average total shrub, and average perennial grass heights; average nest shrub, total shrub, grass, forb, bare ground, and litter cover; visual obstruction; distance to town, landfill, energy well, communication tower, house, power line, all road, and riparian and forested habitat; and the top selected TRI variable.

Spatial autocorrelation violates the independence assumption for generalized linear models. Thus, I created an inverse weighted distance matrix to assess spatial autocorrelation among sage-grouse nests, where nest locations >12 km apart were not considered to be correlated. This distance was used to directly relate to the radius of my

24-km diameter study sites; however, 12 km was also larger than the home range size of breeding ravens (0.3–45.8 ravens/km$^2$; Boarman and Heinrich 1999). Furthermore, I treated all sage-grouse nests within 12km of each other, regardless of year, as correlated with the degree of correlation related to the distance among nests. I used function 'moran.test' in package SPDEP version 0.5-46 in R to calculate Moran's *I* for Pearson residuals of top AIC$_c$ selected generalized linear models of sage-grouse nest success.

**RESULTS**

I found 341 sage-grouse nests (170 hatched [50.0%], 5 abandoned [1.5%], and 166 failed [48.5%]). Average annual DSR for all sage-grouse nests was estimated at 0.968 (± 0.003 SE) from Program MARK, which yielded an estimated 40% (95% CI = 34% to 48%) nest survival using a 28-day incubation period. This estimate differed from the apparent nest success of 49.9%, and highlighted the necessity to account for nests that were depredated or abandoned before I found them by using the nest survival model in Program MARK. To assess the effect of corvid abundance on sage-grouse nest success, I conducted 3,842 point count surveys during 2008–2011 at 1,001 total point count locations with 341 sage-grouse nest locations and 660 random locations. I counted 559 ravens and 121 magpies within species-specific EDR (600 m and 300 m, respectively). Spatial autocorrelation was not a problem for the top AIC$_c$ selected sage-grouse nest DSR model (Moran's *I*: $P > 0.5$).

Nest-level raven occupancy negatively affected sage-grouse nest success, but I

did not find any effects of magpies on nest success of sage-grouse (parameter estimates for magpie occupancy and site-level magpie density had 85% CI that overlapped 0). No anthropogenic variable described differences in sage-grouse nest DSR (parameter estimates with 85% CI that overlapped 0). I found that $TRI_{1.0}$ (1-km radius) from the landscape feature covariate set described sage-grouse nest DSR best. Thus, the top $AIC_c$ selected model included raven occupancy and $TRI_{1.0}$ (Table 5-2, Fig 5-1), which had $w_i = 0.26$ and RDR = 0.37. The second $AIC_c$ ranked model had $w_i = 0.25$ and $\Delta AIC_c = 0.01$. I will only discuss the top model for parsimony, because the second $AIC_c$ ranked model was a more complicated version of the top model. The parameter estimate of $TRI_{1.0}$ was positively associated with sage-grouse nest DSR (0.02; 95% CI = 0.01 to 0.04; Table 5-3), which indicated that sage-grouse had better nest success in more rugged terrain. The parameter estimate of raven occupancy (-0.45; 95% CI = -0.89 to -0.02) was negatively associated with sage-grouse nest DSR (Table 5-3).

## DISCUSSION

Nest success of sage-grouse was negatively impacted by the presence and abundance of ravens (nest-level and site-level; Chapter 4). I did not find any evidence that magpies had a negative impact on sage-grouse nest success regardless of microhabitat characteristics near the nest or proximity to anthropogenic or landscape features. Similar to Aldridge and Boyce (2007) and Kirol (2012), I did not find any significant correlations between nest success and proximity to anthropogenic development, and there was no evidence of interactive effects between microhabitat or

anthropogenic or landscaped features and corvid densities. Although the landscape features that I assessed represented riskier habitat, I found that nest success was positively correlated with relatively rugged habitat measured within 1 km from nests ($TRI_{1.0}$). My sage-grouse nest success results suggest that sage-grouse nesting in areas with elevated raven populations may have suppressed nest success. The best sage-grouse nest success model had RDR = 0.37, which indicated that a large proportion of spatiotemporal variability in sage-grouse nest success was not accounted for in my models. Thus, there may have been variability in sage-grouse nest DSR among study sites related to factors such as weather or different predator communities. The positive correlation between rugged terrain and increased nest success of sage-grouse was counterintuitive because Kirol 2012 found that rugged terrain was negatively correlated with adult hen survival, which is the most important factor affecting sage-grouse population growth (Taylor et al. 2012).

Corvids have been found to use anthropogenic structures as perches and nesting structure (Trost 1999, Lammers and Collopy 2007, Prather and Messmer 2010, Slater and Smith 2010). Several studies have demonstrated that sage-grouse avoided habitat with man-made features, such as oil and gas infrastructure, while nesting (Holloran 2005, Kaiser 2006, Aldridge and Boyce 2007, Holloran et al. 2010, Kirol 2012). Man-made structures are potential perches, nest structure, or provide reliable food subsidies for corvids. I did not find any sage-grouse study that found a direct decrease in sage-grouse nest success in relation to proximity to potential perches. However, sharp-tailed grouse (*Tympanuchus phasianellus*) nest success was correlated to the distance from potential

perch sites for corvids and raptors (i.e. nests that were >75 m away from a potential perch were more successful; Manzer and Hannon 2005). Kirol (2012) and I (Chapter 3) found that sage-grouse avoided oil and gas wells while nesting. Sage-grouse may be avoiding man-made structures to reduce risk of nest depredation and predation from corvids and raptors (i.e., sage-grouse may treat anthropogenic features as riskier areas); anthropogenic features do not directly cause any depredations of sage-grouse nests, but anthropogenic features are likely stressors that elevate predation risk in previously suitable habitat. Thus, I hypothesized that sage-grouse nest success would be lower near anthropogenic features and that this effect would be amplified when there was also greater values of site-specific change in corvid densities. However, I did not find support for this hypothesis, because neither independent anthropogenic feature variables nor anthropogenic features in conjunction with site-specific change in corvid densities had an effect on sage-grouse nest success. This indicates that anthropogenic features do not necessarily predict riskier habitat either because sage-grouse avoidance of anthropogenic features masked any effects on nest success or anthropogenic disturbance was not greater than a potential threshold. Proximity to an anthropogenic feature may not be indicative of lower nest success, but rather the quantity of anthropogenic features in close proximity.

In Chapter 4, I did not look at interactive effects of site-specific change in raven density with aspects of habitat (including microhabitat), because I was interested in evaluating direct effects of ravens on sage-grouse nest success in the context of reduction of raven density as a management tool. Simultaneous comparison of the main effects of

raven and microhabitat vegetation variables in Chapter 4 was intended to account for differences among study sites in relation to sage-grouse nest-site selection. Thus, differences in nest success could be attributed to local and landscape scale raven abundance. It was possible that the microhabitat at a nest site impacted a nest's success (Holloran et al. 2005, Moynahan et al. 2007) in fragmented habitat.

The negative effect of ravens on the nest success of sharp-tailed and sage grouse has been well documented (Manzer and Hannon 2005, Bui et al. 2010, Coates and Delehanty 2010, Chapter 4). Coates and Delehanty (2010) found that sage-grouse nests were more likely to be depredated by a raven when nesting in relatively lower total shrub cover (50 $m^2$ scale), but sage-grouse nests in relatively high visual obstruction (presumably higher total shrub cover) were more likely to be depredated by a badger. This indicates that microhabitat conditions near a sage-grouse nest have different effects on nest success depending on the predator composition of an area, and the presence of different types of predators may induce changes in sage-grouse behavior associated with habitat usage. For instance, sage-grouse reduced time off of their nests when nesting in areas with high abundances of ravens (Coates and Delehanty 2008), which may reduce a sage-grouse's risk of nest depredation. Sometimes visual predators find nests of ground-nesting birds, including sage-grouse, by watching hens leave or return to nests (Manzer and Hannon 2005, Coates 2007). Sage-grouse also predominately choose nest sites in vegetation cover at the microhabitat scale (Connelly et al. 2004). Several studies have reported that sage-grouse select nest sites based on a preference for different microhabitat characteristics, such as: sagebrush density (Wallestad and Pyrah 1974, Connelly et al.

2003), sagebrush cover (Doherty et al. 2010, Kirol et al. 2012), shrub height (Gregg et al. 1994), grass height (Gregg et al. 1994, Holloran et al. 2005, Kirol et al. 2012), and grass cover (Kaczor 2008, Kirol et al. 2012). Sage-grouse living in areas with different predator compositions, such as avian or mammalian predators, may prefer different types of vegetation cover (Connelly et al. 2004, Coates and Delehanty 2010). Thus, I hypothesized that higher percent concealment cover and vegetation height (microhabitat characteristics) would have a greater positive effect on nest success when there was higher corvid abundance (interactive effect). However, I did not find any evidence of interactive effects of microhabitat variables and site-specific change in corvid densities on sage-grouse nest success. Interactive mechanisms effecting sage-grouse nest success between predators and habitat characteristics are difficult to detect, but are commonly cited as potential factors effecting nest success; thus, there clearly needs to be more research before conclusions are made.

Magpies have been found to depredate sage-grouse nests (Holloran and Anderson 2003), and magpies have been found to be effective nest depredators in fragmented habitats (Andrén 1992, Vander Haegen et al. 2002). I found a slight negative effect of magpie occupancy (parameter estimate -0.25; 95% CI: -1.27 to 0.77) on sage-grouse nest success, but the magpie occupancy model in the corvid covariate set was below the null model. Thus, I did not find any evidence for increased depredation of sage-grouse nests in areas with greater values of site-specific change in magpie density. Magpie populations may have been too stable to detect direct negative effects of magpie abundance on sage-grouse nest success (i.e., there may not have been enough temporal

variation in the values of site-specific change in magpie density to detect differences in sage-grouse nest success). Sage-grouse may have reduced the risk of nest depredation by magpies by not nesting near areas used by magpies (see Chapter 2). Magpies are known to be associated with riparian areas but also forage in sagebrush habitats (Trost 1999). In Chapter 3, I also found that sage-grouse placed their nests away from riparian habitat; therefore, sage-grouse may avoid magpies and the habitat that most frequently has magpies. However, this could also indicate that sage-grouse and magpies select different habitat (differential habitat selection). Within the range of proximity to riparian habitat where sage-grouse nested, the proximity of a sage-grouse's nest to riparian habitat did not affect nest success. Sage-grouse nest success may not have had detectible negative effects from proximity to riparian habitat, because sage-grouse placement of nests was beyond a threshold distance from riparian habitat.

The only landscape feature predictive of sage-grouse nest success was $TRI_{1.0}$, and sage-grouse hens nesting in more rugged habitat at a relatively large scale (1-km radius) were more likely to succeed. I hypothesized that rugged terrain would be riskier habitat and high corvid densities would intensify this effect, because hilltops, knolls, and cliff edges associated with rugged terrain would act as perches for corvids. In addition, moderately rugged terrain may be correlated to greater risk of predation from olfactory predators (mammalian predators), which have been known to hunt in areas such as drainage bottoms. Thus, rugged terrain would correlate with greater exposure to nest depredation from corvids and mammalian predators. Contrary to my hypothesis, I found a positive effect of $TRI_{1.0}$ (Table 5-3). Two potential explanations for this finding include

1) rugged topography may provide some refugia from visual predators (e.g., ravens and magpies), because topographic features such as slight depressions may decrease the effective distance that a corvid can detect a sage-grouse on the ground; and 2) rugged terrain creates atmospheric turbulence, and higher turbulence decreases an olfactory predator's ability to detect prey (Conover 2007). However, Conover et al. (2010) found that sage-grouse use nest locations that hide their nests from visual but not olfactory predators. Even though sage-grouse do not generally nest in locations that provide concealment from olfactory predators, sage-grouse that tend to nest in more rugged topography may experience less nest depredation by olfactory predators. The relationship of topography related to corvid and mammalian depredation of sage-grouse nests was beyond the scope of my study, and more research is needed before conclusions can be drawn about the impact of interactions between landscape features and predator community dynamics on sage-grouse nest success.

## MANAGEMENT IMPLICATIONS

A diverse array of generalist predators have encroached into sagebrush steppe habitats throughout the western United States. These generalist predators have been able to sustain elevated populations by capitalizing on structural and forage resources associated with habitat fragmented by humans. Thus, their densities are not limited by the density of a particular species of prey (Schroeder and Baydack 2001, Evans 2004, Manzer and Hannon 2005, Coates 2007). Ravens, magpies, red foxes, and coyotes are generalist predators that use different hunting strategies to obtain prey, and they can

suppress the breeding success of ground-nesting birds (Evans 2004). These factors produce complex predator community dynamics that interact with prey species behavior including selection of available habitat. For this reason, management agencies need to understand how interactions among anthropogenic and landscape features, microhabitat, and the predator community relate to sage-grouse demographic rates (e.g., nest success). The aspects of habitat (anthropogenic and landscape features) that present riskier areas for prey species are confounded by the predator composition that reside in those areas. For example, the effect of concealment cover on nest success of sage-grouse can be dependent upon the species of predator near nests (Coates and Delehanty 2010). Likewise, it was unclear how rugged topography related to the risk of nest depredation. Prey species select habitat that reduces the risk of predation; however, selecting nesting habitat that provides them some protection against one predator species may increase their vulnerability to another predator species. Thus, selection of habitat to protect against visual predators may force sage-grouse to nest in riskier habitats with respect to mammalian predators. However, sage-grouse have been found to select habitat that provides concealment from visual and not olfactory predators (Conover et al. 2010). It is imperative to understand the anthropogenic and landscape feature and predator community conditions that reduce sage-grouse exposure to all predators while nesting. My results highlight the necessity to assess habitat and predator community dynamics concurrently when designing management plans.

**LITERATURE CITED**

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer Science, New York, New York, USA.

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794–804.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175–1178.

Aubry, L. M., E. Cam, D. N. Koons, J. -Y. Monnat, and S. Pavard. 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. Journal of Animal Ecology 80:375–383.

Batterson, W. M., and W. B. Morse. 1948. Oregon sage grouse. Oregon Game Commission Fauna Service, Portland, USA.

Baxter, R. J., K. D. Bunnell, J. T. Flinders, and D. L. Mitchell. 2007. Impacts of predation on greater sage-grouse in Strawberry Valley, Utah. Transactions of the 72nd North American Wildlife and Natural Resources Conference 72:258–269.

Boarman, W. I. 1993. When a native predator becomes a pest: a case study. Pages 191–206 *in* S. K. Majumdar, E. W. Miller, D. E. Baker, E. K. Brown, J. R. Pratt, and R. F. Schmalz, editors. Conservation and resource management. Pennsylvania Academy of Science, Philadelphia, USA.

Boarman, W. I., R. J. Camp, M. Hagan, and W. Deal. 1995. Raven abundance at anthropogenic resources in the western Mojave Desert, California. Report to Edwards Air Force Base, California. National Biological Service, Riverside, USA.

Boarman, W. I., and B. Heinrich. 1999. Common raven (*Corvus corax*). Pages 1–31 *in* A. Poole and F. Gill, editors. Birds of North America, No. 476. Birds of North America, Philadelphia, Pennsylvania, USA.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139–156.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, New York, New York, USA.

Bui, T. D., J. M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. Condor 112:65−78.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39:388–394.

Coates, P. S. 2007. Greater sage-grouse (*Centrocercus urophasianus*) nest predation and

incubation behavior. Dissertation, Idaho State University, Pocatello, USA.

Coates, P. S., and D. J. Delehanty. 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. Condor 110:627−638.

Coates, P. S., and D. J. Delehanty. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. Journal of Wildlife Management 74:240–248.

Connelly, J. W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000. Effects of predation and hunting on adult sage grouse (*Centrocercus urophasianus*) in Idaho. Wildlife Biology 6:227–232.

Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53–67 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report, Cheyenne, Wyoming, USA.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station Bulletin 80, University of Idaho, Moscow, USA.

Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer.

1994. Sage grouse ecology. Idaho Department of Fish and Game Job Completion Report W-160-R-19, Boise, USA.

Conover, M. R. 2007. Predator−prey dynamics: the use of olfaction. Taylor and Francis, Boca Raton, Florida, USA.

Conover, M. R., J. S. Borgo, R. E. Dritz, J. B. Dinkins, and D. K. Dahlgren. 2010. Greater sage-grouse select nest sites to avoid visual predators but not olfactory predators. Condor 112:331−336.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Scientist 33:224–227.

Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

Engel, K. A., and L. S. Young. 1992. Daily and seasonal activity patterns of common ravens in southwestern Idaho. Wilson Bulletin 104:462–471.

Evans, K. L. 2004. A review of the potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetational cover and predation of sage-grouse nests in Oregon. Journal of Wildlife Management 58:162–166.

Hanser, S. E., M. Leu, S. T. Knick, and C. L. Aldridge. 2011. Sagebrush ecosystem

conservation and management: ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, Kansas, USA.

Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effects. Pages 95–100 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Heath, B., R., Straw, S. H. Anderson, and J. Lawson. 1997. Sage grouse productivity, survival, and seasonal habitat use near Farson, Wyoming. Wyoming Game and Fish Department, Completion Report, Cheyenne, USA.

Holloran, M. J. 1999. Sage-grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. Thesis, University of Wyoming, Laramie, USA.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Holloran, M. J., and S. H. Anderson. 2003. Direct identification of northern sage-grouse (*Centrocercus urophasianus*) nest predators using remote sensing cameras. Canadian Field-Naturalist 117:308–310.

Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638–649.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Iles, D. T. 2012. Drivers of nest success and stochastic population dynamics of the common eider (*Somateria mollissima*). Thesis, Utah State University, Logan, USA.

Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection of greater sage-grouse in northwestern South Dakota. Thesis, South Dakota State University, Brookings, USA.

Kaiser, R. C. 2006. Recruitment by greater sage-grouse in association with natural gas development in western Wyoming. Thesis, University of Wyoming, Laramie, USA.

Kirol, C. P. 2012. Quantifying habitat importance for greater sage-grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. Thesis, University of Wyoming, Laramie, USA.

Kirol, C. P., J. L. Beck, J. B. Dinkins, and M. R. Conover. 2012. Greater sage-grouse nesting and brood-rearing microhabitat selection in xeric big sagebrush. Condor 114:75–89.

Knight, R. L., and M. W. Call. 1980. The common raven. Bureau of Land Management, Technical Note No. 344. Bureau of Land Management, Denver, Colorado, USA.

Knight, R. L., and J. Y. Kawashima. 1993. Responses of ravens and red-tailed hawk populations to linear right-of-ways. Journal of Wildlife Management 57:266–271.

Kristan, W. B. III, W. I. Boarman, and J. J. Crayon. 2004. Diet composition of common ravens across the urban-wildland interface of the West Mojave Desert. Wildlife Society Bulletin 32:244–253.

Jensen, B. M. 2006. Migration, transition range, and landscape use by greater sage-grouse (*Centrocercus urophasianus*). Thesis, University of Wyoming, Laramie, USA.

Johnsgard, P. A. 2002. Grassland grouse and their conservation. Smithsonian Institution, Washington, D. C., USA.

Johnson, K. H., and C. E. Braun. 1999. Viability and conservation of an exploited sage grouse population. Conservation Biology 13:77–84.

Lammers, W. M., and M. W. Collopy. 2007. Effectiveness of avian predator perch deterrents on electric transmission lines. Journal of Wildlife Management 71:2752–2758.

Larsen, K. H., and J. H. Dietrich. 1970. Reduction of a raven population on lambing grounds with DRC-1339. Journal of Wildlife Management 34:200–204.

Lennartz, S. 2007. USGS Gap Analysis Program (GAP) species distribution model. Sanborn Map Corporation. Portland, Oregon, USA.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the West: a large scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Manzer, D. L., and S. J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. Journal of Wildlife Management 69:110–123.

Marzluff, J. M., and E. A. Neatherlin. 2006. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. Biological

Conservation 130:301–314.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in northcentral Montana. Journal of Wildlife Management 71:1773–1783.

Patterson, R. L. 1952. The sage grouse of Wyoming. Sage Books, Denver, Colorado, USA.

Prather, P. R., and T. A. Messmer. 2010. Raptor and corvid response to power distribution line perch deterrents in Utah. Journal of Wildlife Management 74:796–800.

Ralph, C. J., S. Droege, and J. R. Sauer. 1995. Managing and monitoring birds using point counts: standards and applications. USDA Forest Service General Technical Report PSW-GTR-149, Berkeley, California, USA.

Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:1–4.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–297.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2011. The North American breeding bird survey, results and analysis 1966–2010. Version 12.07.2011. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schroeder, M. A., and R. K. Baydack. 2001. Predation and the management of prairie

grouse. Wildlife Society Bulletin 29:24–32.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). *In* A. Poole and F. Gill, editors. Birds of North America. Birds of North America, Philadelphia, Pennsylvania, USA.

Slater, S. J., and J. P. Smith. 2010. Effectiveness of raptor perch deterrents on an electrical transmission line in southwestern Wyoming. Journal of Wildlife Management 74:1080–1088.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336−347.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, R. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Trost, C. H. 1999. Black-billed magpie (*Pica hudsonia*). *In* A. Poole and F. Gill, editors. Birds of North America, No. 398. Philadelphia, Pennsylvania, USA.

Vander Haegen, W. M., M. A. Schroeder, and R. M. DeGraaf. 2002. Predation on real and artificial nests in shrubsteppe landscapes fragmented by agriculture. Condor 104:496–506.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

Wambolt, C. L., M. R. Frisina, S. J. Knapp, and R. M. Frisina. 2006. Effect of method, site, and taxon on line-intercept estimates of sagebrush cover. Wildlife Society Bulletin 34:440–445.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138.

Willis, M. J., G. P. Kiester, Jr., D. A. Immel, D. M. Jones, R. M. Powell, and K. R. Durbin. 1993. Sage grouse in Oregon. Oregon Department of Fish and Wildlife, Wildlife Research Report No.15. Portland, USA.

Wyoming Oil and Gas Conservation Commission (WOGCC). 2012. WOGCC homepage. [Online.] Available at http://wogcc.state.wy.us.

Zheng, B. 2000. Summarizing the goodness of fit of generalized linear models for longitudinal data. Statistics in Medicine 19:1265–1275.

Table 5-1. Means and standard errors (SE) of variables used to model sage-grouse nest daily survival rate (DSR) for successful and unsuccessful nests. Data were collected from 341 sage-grouse nests at eight 16-km and four 24-km diameter study sites in southwestern and south-central Wyoming, USA during 2008–2011.

| | Successful | | Unsuccessful | |
|---|---|---|---|---|
| Variable description | Mean | SE | Mean | SE |
| Max height of nest shrub (cm) | 60.34 | 1.47 | 61.90 | 1.48 |
| Average canopy cover of nest shrub (cm) | 112.62 | 5.93 | 111.90 | 2.72 |
| Total shrub cover (%) within 5 m | 43.47 | 1.21 | 44.38 | 1.02 |
| Average total shrub height (cm) within 5 m | 38.90 | 1.10 | 40.34 | 1.07 |
| Grass cover (%) within 5 m | 20.31 | 1.11 | 19.88 | 1.17 |
| Perennial grass cover (%) within 5 m | 14.17 | 0.70 | 14.32 | 0.86 |
| Average perennial grass height (cm) within 5 m | 22.81 | 0.83 | 22.15 | 0.65 |
| Forb cover (%) within 5 m | 7.90 | 0.65 | 8.06 | 0.62 |
| Bare ground cover (%) within 5 m | 25.46 | 1.24 | 23.50 | 1.26 |
| Litter cover (%) within 5 m | 36.96 | 1.46 | 37.76 | 1.52 |
| Horizontal visual obstruction (dm) | 3.12 | 0.13 | 3.34 | 0.12 |
| Site-level raven density (no./$km^2$) within 550 m of random locations | 0.15 | 0.13 | 0.15 | 0.13 |
| Site-specific change in raven density (no./$km^2$) within 550 m of random locations calculated as the | -0.04 | 0.01 | -0.02 | 0.01 |

| | | | | |
|---|---|---|---|---|
| change in raven density within a study site relative to 2008 | | | | |
| Site-level magpie density (no./km$^2$) within 550 m of random locations | 0.14 | 0.19 | 0.16 | 0.20 |
| Site-specific change in magpie density (no./km$^2$) within 550 m of random locations calculated as the change in raven density within a study site relative to 2008 | -0.09 | 0.02 | -0.10 | 0.02 |
| Raven occupancy (0, 1) within 550 m of a sage-grouse nest during last nest check with hen on nest | N/A | N/A | N/A | N/A |
| Magpie occupancy (0, 1) within 300 m of a sage-grouse nest during last nest check with hen on nest | N/A | N/A | N/A | N/A |
| Sage-grouse <1 or ≥1 year old at time of capture (AGE) | N/A | N/A | N/A | N/A |
| Distance (km) from sage-grouse nest to nearest oil and gas structure (energy well, compressor station, transfer station, refinery, or other energy extraction related buildings) | 5.71 | 0.39 | 5.00 | 0.33 |
| Distance (km) from sage-grouse nest to nearest major road including paved roads, railroad, and improved gravel roads | 1.41 | 0.10 | 1.33 | 0.09 |

| | | | | |
|---|---|---|---|---|
| Distance (km) from sage-grouse nest to nearest road including paved roads, railroad, improved gravel roads, and unimproved 4-wheel drive roads | 0.34 | 0.02 | 0.33 | 0.02 |
| Distance (km) from sage-grouse nest to nearest communication tower | 10.16 | 0.63 | 10.04 | 0.63 |
| Distance (km) from sage-grouse nest to nearest residential house | 7.41 | 0.43 | 7.49 | 0.47 |
| Distance (km) from sage-grouse nest to nearest overhead line (transmission or distribution power lines, or telephone line) | 7.93 | 0.39 | 8.11 | 0.39 |
| Distance (km) from sage-grouse nest to nearest anthropogenic perch (ANTH; oil and gas structure, communication tower, residential house, or power lines) | 3.11 | 0.18 | 2.97 | 0.18 |
| Distance (km) from sage-grouse nest to nearest town | 3.46 | 0.19 | 3.27 | 0.19 |
| Distance (km) from sage-grouse nest to nearest landfill | 23.77 | 0.59 | 24.14 | 0.52 |
| Distance (km) from sage-grouse nest to nearest oil and gas structure, communication tower, or residential house (DIST_WCH) | 28.16 | 0.82 | 28.07 | 0.70 |
| Distance (km) from sage-grouse nest to nearest | 2.61 | 0.24 | 3.15 | 0.28 |

| | | | | |
|---|---|---|---|---|
| forested habitat including deciduous and conifer stands | | | | |
| Distance (km) from sage-grouse nest to nearest riparian habitat | 1.70 | 0.11 | 1.55 | 0.10 |
| Topographic ruggedness index within 0.27-km radius (0.23 $km^2$ scale) | 19.66 | 1.03 | 16.36 | 0.80 |
| Topographic ruggedness index within 0.54-km radius (0.92 $km^2$ scale) | 19.68 | 0.93 | 16.70 | 0.73 |
| Topographic ruggedness index within 1-km radius (3.14 $km^2$ scale) | 20.63 | 0.86 | 17.66 | 0.69 |
| Topographic ruggedness index within 3-km radius (28.26 $km^2$ scale) | 22.00 | 0.72 | 21.33 | 0.63 |

Table 5-2. Generalized linear models assessing sage-grouse nest daily survival rate using Program MARK. Variables used in modeling included sage-grouse nest-level occupancy and site-specific change in corvid densities (study site-level), anthropogenic and landscape features, and microhabitat. Models were compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). A fully saturated spatiotemporal model was included to assess goodness-of-fit; the saturated model included year; study site type; distance to town, landfill, energy well, communication tower, house, power line, all road, and riparian and forested habitat; topographic ruggedness at 1 km radius ($TRI_{1.0}$) variable; and all microhabitat variables.

| Models | $k$ | $\Delta AIC_c$ | $w_i$ | Deviance |
|---|---|---|---|---|
| Raven occupancy, $TRI_{1.0}$ [a] | 3 | 0.00 | 0.26 | 806.51 |
| Raven occupancy, site-level raven, $TRI_{1.0}$ | 4 | 0.10 | 0.25 | 804.61 |
| $TRI_{1.0}$ | 2 | 1.76 | 0.11 | 810.27 |
| Raven occupancy, site-level raven, forest distance, $TRI_{1.0}$ | 5 | 1.81 | 0.11 | 804.31 |
| Site-level raven, $TRI_{1.0}$ | 3 | 2.10 | 0.09 | 808.61 |
| Raven occupancy, forest distance | 3 | 2.57 | 0.07 | 809.08 |
| Raven occupancy, site-level raven, forest distance | 4 | 3.60 | 0.04 | 808.10 |
| Raven occupancy, site-level raven | 3 | 5.07 | 0.02 | 811.58 |
| Forest distance | 2 | 5.31 | 0.02 | 813.82 |
| Raven occupancy | 2 | 5.46 | 0.02 | 813.97 |

| | | | | |
|---|---|---|---|---|
| Site-level raven | 2 | 7.15 | 0.01 | 815.66 |
| Null | 1 | 7.21 | 0.01 | 817.72 |
| Fully saturated | 25 | 25.13 | 0.00 | 787.36 |

[a]$AIC_c$ = 812.51

Table 5-3. Parameter estimates with 95% confidence intervals (CI) from the top $AIC_c$ selected generalized linear model (see Table 5-2) assessing sage-grouse nest daily survival rate (DSR) using Program MARK. Sage-grouse nest-level raven (raven occupancy) was recorded as raven occupancy during last nest check with sage-grouse on her nest, and topographic ruggedness index at 1 km radius ($TRI_{1.0}$) was quantified as the difference in elevation among adjacent pixels of a digital elevation map.

| | | | 95% CI | |
|---|---|---|---|---|
| Variable | Estimate[a] | SE | Lower | Upper |
| Intercept | 3.02 | 0.17 | 2.69 | 3.34* |
| Raven occupancy | -0.45 | 0.22 | -0.89 | -0.02* |
| $TRI_{1.0}$ | 0.02 | 0.01 | 0.01 | 0.04* |

*Denotes a 95% confidence interval that does not include zero.

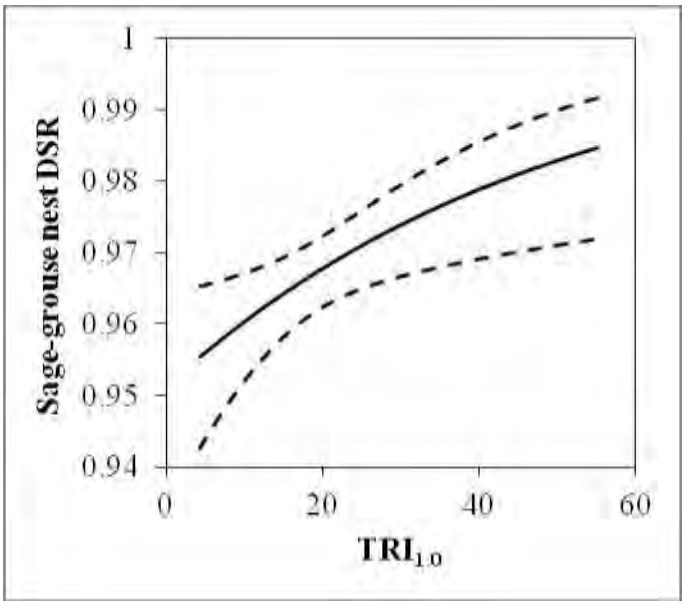



Figure 5-1. Predictions of daily survival rate (DSR) of sage-grouse nests from the top $AIC_c$ selected generalized linear model using Program MARK with 95% confidence intervals. Predicted effects of topographic ruggedness calculated at 1 km radius ($TRI_{1.0}$) on DSR of sage-grouse nests. Data were collected from eight 16-km and four 24-km study sites in southwestern and south-central, Wyoming, USA ($n$ = 341 sage-grouse nests), 2008–2011.

# CHAPTER 6

# GREATER SAGE-GROUSE HEN SURVIVAL: EFFECTS OF RAPTORS, ANTHROPOGENIC AND LANDSCAPE FEATURES, AND HEN BEHAVIOR

**ABSTRACT** Survival of breeding-age hens is the most important demographic parameter driving greater sage-grouse (*Centrocercus urophasianus*: hereafter "sage-grouse") populations. Effects of anthropogenic and landscape features on survival of sage-grouse hens have not been evaluated in the context of predator communities. In addition, management agencies would benefit from more information on the effects of parental investment and anti-predation strategies on sage-grouse survival. During 2008–2011, I collected survival data for 427 sage-grouse hens at 12 study sites (eight 16-km diameter sites and four 24-km diameter sites) in southern Wyoming, USA. Between 1 May and 31 August each year, there were 132, 162, 156, and 165 hens monitored, respectively. Cox proportional hazard (Cox PH) models were used to assess the effects of four covariate sets including: raptor densities, anthropogenic features, landscape features, and sage-grouse behavior on sage-grouse hen survival. Cox PH models were analyzed in two separate steps; 1) parental investment analysis and 2) anti-predation strategy analysis. Data for the parental investment analysis included 3,523 survival intervals with 380 nests and 162 broods; whereas, data for the anti-predation strategy analysis included 2,304 survival intervals from non-reproductive sage-grouse hens. I found that sage-grouse summer survival was correlated with landscape features that represented riskier habitat,

especially risk of predation from raptors. Breeding season survival of sage-grouse was negatively associated with proximity to trees (deciduous and coniferous), topographic ruggedness at a 0.27 km scale ($TRI_{0.27}$), and site-specific change in golden eagle (*Aquila chrysaetos*) density (site-specific change in golden eagle density was calculated as the increase or decrease in study site-level golden eagle density [annual density] relative to the raptor density in a particular study site at the beginning of the study [2008]). However, site-specific change in golden eagle density was negatively associated with sage-grouse survival only when taking $TRI_{0.27}$ into context (interactive effect). This interaction indicated that the negative effect of both site-specific change in golden eagle density and $TRI_{0.27}$ was dampened in areas with higher $TRI_{0.27}$ and greater values of site-specific change in golden eagle density. My sage-grouse survival results indicated that survival of non-reproductive hens was greater than brooding or nesting hens. Hens that stayed in intermediate-size flocks and yearling hens had higher survival than hens in small or large flocks and hens >2 years old. Topographic ruggedness in conjunction with site-specific change in golden eagle density had a dynamic effect on sage-grouse survival, which illustrates the importance of considering predator communities in tandem with habitat components.

## INTRODUCTION

Survival of breeding age birds in direct relation to predator communities has not been a main focus of greater sage-grouse (*Centrocercus urophasianus*: hereafter "sage-grouse") research. Survival related to predator communities was not likely to have been a

problem during pre-European settlement because sage-grouse co-evolved with the predator communities present in sagebrush ecosystems (Schroeder et al. 1999, Schroeder et al. 2001). There are currently no predators that specialize on sage-grouse during any life history stage (egg, chick, or adult; Connelly et al. 2011). Thus, Hagen (2011) indicated that predators may only be negatively affecting sage-grouse populations in fragmented habitats and areas with human-subsidized predator populations. However, these areas of habitat fragmentation and areas with human-subsidized predator populations have drastically increased in the recent past (Leu et al. 2008). For example, red fox (*Vulpes vulpes*) and common raccoon (*Procyon lotor*) have increased in abundance in sage-grouse habitat, especially near human activities (Connelly et al. 2000b, Baxter et al. 2007, Hagen 2011). In addition, golden eagles (*Aquila chrysaetos*) use anthropogenic structures as perches and nesting structure (Lammers and Collopy 2007, Prather and Messmer 2010, Slater and Smith 2010).

Recent research has indicated that sage-grouse hen survival may be the most important demographic parameter driving sage-grouse productivity (Johnson and Braun 1999, Taylor et al. 2012). Taylor et al. (2012) found that sage-grouse hen survival was the most influential demographic rate on population growth, and Johnson and Braun (1999) found that adult and juvenile sage-grouse survival were the most limiting demographic parameters for a population in northern Colorado. This should not be surprising, because sage-grouse are relatively long-lived ground-nesting birds with low productivity (Connelly et al. 2000b, Holloran et al. 2005, Connelly et al. 2011). Thus, many aspects of recruiting new individuals into a population are connected to sage-

grouse hens (i.e., nest success and chick survival). Juvenile survival may also be partially connected to learned behaviors from when an individual sage-grouse was a chick (Thompson 2012).

Sage-grouse hens have been known to have high annual survival (48–78% in Wyoming; Holloran 2005, Connelly et al. 2011) with the breeding season having the lowest seasonal survival rate for sage-grouse hens (Connelly et al. 2000a). There has been little published on seasonal survival estimates for female sage-grouse (Connelly et al. 2011); however, Connelly et al. (2000a) found that 52% of sage-grouse hen mortalities occurred in spring and summer. Sage-grouse are a species of conservation concern because their distribution and abundance in western North America have declined over the last century (Gregg et al. 1994, Johnsgard 2002, Connelly et al. 2004); many factors have been attributed to this decline including predation, habitat loss, and habitat fragmentation (Braun 1998). Research designed to evaluate potential factors affecting summer survival of sage-grouse in relation to predators and habitat quality will help guide management practices. Furthermore, low productivity of sage-grouse in combination with increased predation rates in fragmented habitats has the potential to decrease or extirpate local sage-grouse populations.

Increasing levels of human development in sage-grouse habitat have brought a range of new stresses to sage-grouse from habitat fragmentation to predation (Connelly et al. 2004, Doherty et al. 2010, Kirol 2012). Potentially additive impacts of human development on sage-grouse survival include increased hunting efficiency of raptors (perches), number of nesting structures, and carrying capacity of generalist predators.

Sources of perch and nesting structure for raptors include oil and gas structures, residential houses, communication towers, power lines, trees, and rugged terrain.

Although raptors have been reported to prey on sage-grouse, raptor densities have not been directly correlated to sage-grouse survival rates or population growth. Golden eagles have been suggested as the major sage-grouse predator (Willis et al. 1993, Connelly et al. 2000a, Danvir 2002, Dahlgren 2006, Mezquida et al. 2006), and high golden eagle abundance was associated with decreased sage-grouse survival (Danvir 2002). However, no sage-grouse study has directly related site-specific densities of raptors to sage-grouse hen survival. I recorded raptor densities associated with sage-grouse nesting and brood-rearing areas from 2008–2011 to determine if raptors were important sage-grouse predators and impact sage-grouse hen survival during the summer. I hypothesized that sage-grouse hen survival would be greater in areas and years with fewer raptors, specifically, golden eagles, *Buteo* hawks (*Buteo* spp.), and northern harriers (*Circus cyaneus*; hereafter "harrier"). In addition, I hypothesized that this effect would be intensified in areas closer to potential perches, such as oil and gas structures, power lines, houses, trees, and rougher topography. To test these hypotheses, I assessed sage-grouse hen survival in relation to sage-grouse exposure to raptors, potential raptor perches, and proximity to areas associated with natural or human provided food subsidies. As secondary objectives, I evaluated differences between yearling and adult sage-grouse hen survival, and the effect of sage-grouse hen behavior (parental investment, weekly movement, and flock size) in relation to survival. I hypothesized that

lower parental investment, shorter weekly movements, and an optimal flock size would increase hen survival.

## STUDY AREA

My study was conducted in southwest and south-central Wyoming. I chose 12 circular study sites, each 16 or 24 km in diameter (eight study sites of 16-km diameter and four study sites of 24-km diameter). Study sites in southwest Wyoming were 16-km diameter and approximately centered around leks where hens were captured based on results found by Holloran and Anderson (2005). Study sites in south-central Wyoming were 24 km in diameter, because sage-grouse were captured at several nearby leks over a larger area. Five study sites were located in Lincoln County, two in Sweetwater County, two in Uinta County, and three in Carbon County. Study sites were chosen to provide a representation of overall sage-grouse nesting habitat in southern Wyoming. Elevation of study sites ranged from 1,925 m – 2,550 m. Most of the land within all of the study sites was federally owned and administered by the Bureau of Land Management with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in the study sites. All study sites had anthropogenic development, which consisted mostly of unimproved 4-wheel drive roads. Conventional natural gas, coalbed methane natural gas, and/or conventional oil extraction activities were present in six (50%) of the study sites; well density within study sites averaged 0.12 ± 0.22 (SD) wells $km^{-2}$ (range = 0.0–0.64 wells $km^{-2}$).

The landscape at all study sites was dominated by sagebrush (*Artemisia* spp.);

Wyoming big sagebrush (*A. tridentata wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) were the most common. Black sagebrush (*A. nova*) and dwarf sagebrush (*A. arbuscula*) were found on exposed ridges. Other common shrub species in the study sites included alderleaf mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), chokecherry (*Prunus virginiana*), common snowberry (*Symphoricarpos albus*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), Saskatoon serviceberry (*Amelanchier alnifolia*), and spiny hopsage (*Grayia spinosa*). Isolated stands of juniper (*Juniperus* spp.) and quaking aspen (*Populus tremuloides*) were found at the higher elevations on north-facing hillsides. Common forb species included arrowleaf balsamroot (*Balsamorhiza sagittata*), buckwheat (*Eriogonum* spp.), common yarrow (*Achillea millefolium*), dandelion (*Taraxacum* spp.), desert parsley (*Cymopterus* spp.), phlox (*Phlox* spp.), lupine (*Lupinus* spp.), sego lily (*Calochortus nuttallii*), and wild onion (*Allium* spp.). Common grass species included: bluegrasses (*Poa* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), green needlegrass (*Nassella viridula*), needle and thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), and western wheatgrass (*Pascopyrum smithii*). Cheatgrass (*Bromus tectorum*) was present, but not widespread in any of the study sites.

## METHODS

### Sage-grouse Capture and Monitoring

From 2008 to 2011, I monitored sage-grouse hen survival during late spring and summer (May through August). Hens were captured, radio-collared, and released in April

of each year. I captured hens at night using ATVs, spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992, Connelly et al. 2003) and fitted them with 17.5-g or 22-g (<1.5% body mass) necklace radio collars (Holohil Systems Ltd, RI-2D, Ontario, Canada or Advanced Telemetry Systems Inc, A4060, Isanti, MN, USA). Collars were equipped with motion-sensors (pulse rate of transmitter increased after 8 hours without bird movement), which allowed me to detect mortalities from a distance. I aged sage-grouse hens at the time of capture as yearlings or >2 years of age by examining outer primaries feathers (Patterson 1952).

I visually located hens weekly with VHF receivers (Communications Specialists, R-1000, Orange, CA, USA) and 3-way Yagi antennas (Communications Specialists, Orange, CA, USA) to locate and monitor nests. To assess the effects of parental investment on survival, I classified sage-grouse hen status as nesting, brooding, or non-reproductive each week (hen status was a surrogate for differences in parental investment). Potential nests were identified with binoculars from ~15 m by circling a radio-marked hen until she was visually spotted under a shrub. Nests were verified by triangulating the hen under the same shrub from ≥50 m away or thoroughly searching the area of the potential nest when the hen was absent. After 1 July, I continued to visually locate brooding hens weekly; whereas, non-reproductive hens were visually located bi-weekly. Brood hens were identified by either visually detecting chicks or observing hen behavior that indicated the presence of a brood (e.g., hesitation to flush, feigning injury, or clucking). I classified a sage-grouse hen as a brood hen if there was evidence of at least 1 chick with that hen. A non-reproductive hen was a hen that never nested, her nest

failed, or her brood failed. I reclassified a brooding hen as non-reproductive when I did not detect evidence of a brood during 2 consecutive telemetry visits. The reproductive status of an individual sage-grouse hen was re-assessed every time a hen was visually located. I documented sage-grouse hen survival with telemetry equipment from a distance when a visual location was not possible, and telemetry signal from a distance was used as often as possible to identify mortality dates; thus, a live or dead signal for most sage-grouse was obtained >1 per week. I used handheld global positioning system (GPS) units (eTrex, Garmin Inc., Olathe, KS, USA) to record hen locations. Location accuracy on the GPS ranged from 2–8 m.

**Sage-grouse Behavior Variables**

I used visual sage-grouse locations to record minimum flock size and minimum weekly movements. Both of these metrics were collected as indicators of exposure to predation. The minimum flock size each week was recorded as the number of adult sage-grouse near (within ~50 $m^2$) a radio-collared hen including the radio-collared hen. I considered this count a minimum flock size, because there were probably individuals that were not detected during each count. Flock size was averaged across all visits for each individual hen during a summer. Movement distances between a sage-grouse's sequential locations were calculated using Geospatial Modeling Environment version 0.7.1.0 (Spatial Ecology LLC, Marshfield, WI, USA) and ArcMap version 10.0 (ESRI Inc., Redlands, CA, USA). I standardized movement distance between sequential visits to minimum weekly movement distances by dividing each distance between telemetry

locations by the number of days that had elapsed between telemetry locations, I then averaged all weekly movement distances for each sage-grouse. This produced a minimum distance, because sage-grouse movements between telemetry locations were unknown.

**Raptor Variables**

From May 1 – August 1 of each year, I conducted point count surveys at random locations within each study site to compare raptor densities. Random locations were selected in habitat considered to be available to sage-grouse hens during the summer within each study site. To restrict random locations to available nesting habitat, I used ArcMap 10.0 to generate random locations only in sagebrush-dominated habitat, which was classified by the Northwest ReGAP landcover data from 2008 (Lennartz 2007). Random locations were designated to be ≥1000 m apart, but average nearest neighbor distances among random point count locations was >2000 m after random selection. I generated 12 random locations in each 16-km diameter study site and 18 random locations in each 24-km diameter study site per year. I generated a new set of random locations each year to avoid spatial autocorrelation; thus, random locations among years were independent.

I used standard distance sampling techniques (Ralph et al. 1995, Buckland et al. 2001, Thomas et al. 2010), which entailed counting all raptors observed during point counts and recording each raptor's distance from the observer (when standing at the center of the point count location). Observers recorded the distance from the observer to

where a raptor was first located (Ralph et al. 1995, Thomas et al. 2010); this minimized possible bias associated with raptors being attracted to or flushed away from an observer. When a raptor was displaced from the center of a point count location as an observer approached (6% of all detected birds), I recorded distance from that raptor to the center of the point count location while the observer approached as suggested by Ralph et al. (1995). A 1500–m rangefinder (American Technologies Network Corp., RE-1500 m, San Francisco, CA, USA) in conjunction with a GPS was used to estimate distances directly or to validate visually estimated distances.

Observers were trained and tested in raptor identification before conducting point counts. Point counts were 10 minutes in length, and we conducted them during daylight hours on a weekly basis at each study site. We visited each point count location 1–8 times with most locations visited ≥3 occasions. We did not survey for raptors in inclement weather (i.e., when raining or wind speeds were greater than 25 km/h; Ralph et al. 1995). Unidentified birds were not included in analyses; these contributed to 2% of detections within truncated observation distances. To minimize observer bias, I changed the time of day and the observer that conducted individual point counts within a study site each week. The observers conducting point counts within a particular study site changed each year.

I calculated average annual densities of raptors at the study site-level (number / 100 $km^2$). All raptor variables were calculated from the raw count data within Program DISTANCE estimated effective detection radii (EDR) as specified in Chapter 2. Study site-level density of golden eagles, *Buteo* hawks, and harriers were individually

calculated within species-specific EDRs (1000 m, 450 m, and 350 m, respectively) of each random point count location within a study site (see Chapter 2 for further details). I had noted through observation that relative changes in raptor densities within many study sites had positive or negative effects on survival of sage-grouse. I attributed this phenomenon to the possibility of raptors being more or less effective predators on sage-grouse depending on the study site due to overall characteristics of a particular study site (combination of individual raptor behavior, topographic roughness, large scale cover, anthropogenic development, etc.). In addition to study site-level raptor densities, I calculated site-specific change in raptor densities—from random point count locations—as the increase or decrease in study site-level raptor density (annual density) relative to the raptor density in a particular study site at the beginning of the study (2008). Thus, site-specific change in raptor density was 0 for all study sites in 2008. These site-specific change in raptor density variables were intended to look at relative change in risk of predation within each study site (i.e., does site specific increase or decrease of raptor densities effect survival of sage-grouse). Thus, site-specific change in raptor densities were not quantifying the effect of the exact density of raptors on survival of sage-grouse among all study sites. Rather, they were assessing site-specific change in exposure to raptors.

**Anthropogenic and Landscape Feature Variables**

I calculated sage-grouse proximity to anthropogenic features that could be used as perch or nest sites by raptors or could provide food subsidies with ArcMap 10.0.

Anthropogenic structures that were >2 m in height were considered available for perching or nesting by raptors. I quantified the distance from sage-grouse locations to the nearest oil and gas structure (energy well, compressor station, transfer station, refinery, or other energy extraction related buildings), major road, all roads, communication tower, house, and power line for each sage-grouse location. Most (>95%) oil and gas structures were energy wells. Ongoing energy development was occurring in half of my study sites, which required me to assess the dates that energy related structures and roads were added or removed from the landscape.

In distance calculations, I only included oil and gas structures and roads that were physically on the ground when each sage-grouse was located. I obtained information on oil and gas structures, including date construction started on the structure and date when wells were plugged and abandoned (date structure was removed), from the Wyoming Oil and Gas Conservation Commission (WOGCC; 2012). I verified the spatial location and existence of older structures with color aerial satellite imagery from summer 2006 and August 2009 obtained from the National Agriculture Imagery Program (NAIP; U.S. Department of Agriculture [USDA] 2010). Aerial imagery from NAIP is produced by the USDA on a 3-year rotation; thus, I used WOGCC data and on the ground GPS units to map energy development that occurred after August 2009. However, energy development reported to WOGCC after August 2009 had better reporting of location, spud date, and plug abandon date.

I used 2009 NAIP imagery to digitize the location of major roads, all roads, communication towers, and houses within a 5-km buffer around study sites; roads

constructed between August 2009 and September 2011 were mapped on the ground with GPS units. Major roads included paved, improved gravel roads, and railroads; whereas, all roads included major roads and all unimproved 4-wheel drive roads. All transmission and distribution power lines within a 5-km buffer around study sites were mapped on the ground with GPS units; telephone lines not associated with a power line were included in power line mapping.

Neither sage-grouse nor raptors were likely to discriminate between many different types of anthropogenic structures. Thus, I created 2 anthropogenic structure variables that represented the nearest 1) distance to either an oil and gas structure, communication tower, or house (DIST_WCH); and 2) distance to either an oil and gas structure, communication tower, house, or power line (ANTH). This was in addition to distances from sage-grouse locations to individual types of anthropogenic structures. I report means and standard errors (SE) for distances to anthropogenic feature variables (Table 6-1).

Similar to anthropogenic features, landscape features could be used as perches or nest structure by raptors, or could be areas with higher productivity that attract predators. Thus, I used ArcMap 10.0 to calculate the distance from every sage-grouse location to forested (deciduous and conifer stands) and riparian habitats. Stands of trees and riparian habitat were identified with Northwest ReGAP landcover data from 2011 (Lennartz 2007), and verified with NAIP imagery from 2009. Topography with greater surface roughness has the potential to create topographic structures (e.g., hilltops, knolls, and cliff edges) that provide vantage points similar to perches. For every sage-grouse

location, I used ArcMap 10.0 to extract topographic ruggedness index (TRI) values generated by Hanser et al. (2011) for the Wyoming Basins Ecoregion; TRI variables were developed using a moving window analysis at 0.27-km ($TRI_{0.27}$), 0.54-km ($TRI_{0.54}$), 1-km ($TRI_1$), and 3-km ($TRI_3$) radii (0.23-$km^2$, 0.92-$km^2$, 3.14-$km^2$, and 28.26-$km^2$ scales, respectively). Riley et al. (1999) created TRI to describe the roughness of landscapes, and the index is quantified as the difference in elevation among adjacent pixels of a digital elevation map; the index is then averaged over a user defined area. I report means and standard errors (SE) for distances to landscape feature variables in Table 6-1.

**Data Analyses**

I analyzed sage-grouse hen survival with the Anderson-Gill formulation of the Cox proportional hazard (Cox PH) model using function 'coxph' in package SURVIVAL version 2.36-14 in R (R 2.14.2, www.r-project.org, accessed 15 Apr 2012). Cox PH models are robust semi-parametric models that are commonly used to analyze time-to-event data (Cox 1972), such as survival obtained from telemetry. The risk of mortality (hazard ratio [$h(t|x_t)$]) is a function of the non-parametric baseline hazard ($h_0(t)$) and the parametric covariates (x's) affecting survival (Hosmer and Lemeshow 1999) with the Cox PH equation expressed as:

$$h(t|x_t) = h_0(t) \times \exp(\beta_1 x_{i1} + \beta_2 x_{i+} \beta_k x_{ik}) \quad (1)$$

Coefficient values were expressed as mortality hazard; thus, positive values would be associated with greater risk of mortality and lower survival.

Data can be left censored for individuals entering the study at different times and right censored for individuals that did not die during the study. In Cox PH models, fixed (time-independent; average exposure for an individual) and time-dependent (exposure of individual during each survival interval) covariates can be fit to assess their effect on survival (Hosmer and Lemeshow 1999). The baseline hazard is allowed to vary with time in Cox PH, and time-dependent variables are included by constructing time intervals for each unique individual (Therneau and Grambsch 2000). However, covariates in Cox PH models are assumed to have proportional mortality hazard over time (proportional hazard assumption; Hosmer and Lemeshow 1999). Thus, I used function 'cox.zph' in package SURVIVAL in R (Therneau and Grambsch 2000) to test the proportional hazard assumption for each covariate in all models; the proportionality of each covariate was validated with $P > 0.05$ for each covariate.

In addition, I calculated dfbetas (statistic that measures the scaled change in each parameter estimate by iteratively deleting each observation) and generated leverage plots to evaluate if there were any influential observations; no observations were omitted as a result of high influence. I prevented multicollinearity by only including one variable of any pair of variables that co-varied in any Cox PH model ($r > 0.65$) as determined with a Pearson's correlation matrix; thus, I eliminated one co-varying variable from further analysis by retaining the variable that made the most biological sense. Variance inflation factors (VIF) for all predictor variables were ≤5, which indicated that the variances of coefficient values were not drastically increased by the inclusion of any predictor variable; thus, collinearity was not a major problem.

I constructed time intervals for each individual sage-grouse hen by calculating the day that corresponded to halfway between each time that I located a sage-grouse. Unless mortality date could be more accurately assessed by evidence from a carcass, mortality date was estimated as the time equal to halfway between the last date the hen was known to be alive and the date mortality was detected. During each year, time was started at t = 0 upon the first visual location of each sage-grouse hen that was relocated at least 2 weeks after radio-collaring. I did not include survival data collected directly after radio-collaring, because survival may have been affected by trapping stress or the bird adjusting to the collar (Winterstein et al. 2001); this excluded 4 birds from analyses. There were approximately 110 days of exposure time for each sage-grouse per summer (i.e., summer survival was assessed from t = 0 to t = 110, which corresponded to 1 May to 31 August).

I included study site-level raptor densities and site-specific change in raptor densities as fixed variables (average exposure to raptors over a summer), and anthropogenic and landscape feature variables as time-dependent variables (calculated from all sage-grouse locations where the hen was visually located). Study site-level raptor densities and site-specific change in raptor densities were defined as fixed variables, because raptor variables were quantified as annual densities (across an entire summer) at the study site-level. Anthropogenic and landscape features were incorporated as time-dependent variables, because the effect of these variables on survival was likely different depending on the bird's location relative to these features, which changed as the bird moved through its environment over time. The distance to houses and forested

habitat were highly correlated ($r > 0.65$), and distance to forested habitat fit the data better than distance to houses; thus, I included distance to forested habitat in modeling instead of distance to houses. However, distance to houses was incorporated into the DIST_WCH and ANTH variables.

Modeling of sage-grouse survival was conducted with an information theoretic approach (Anderson 2008). I compared Cox PH models with Akaike's information criterion corrected for small sample sizes ($AIC_c$) and Akaike weights ($w_i$; Burnham and Anderson 2002) with function 'aictab' in package AICCMODAVG version 1.25 in R. I employed sequential $AIC_c$ modeling of covariate sets, which was suggested by Arnold (2010) as an appropriate approach for identifying and ranking the most parsimonious models. Non-informative covariates (85% confidence intervals [CI] of parameter estimates overlapped 0) were eliminated within each covariate set before comparing top $AIC_c$ selected models among covariate sets (Arnold 2010). I classified models within 2 $AIC_c$ of the null model as being non-competitive (Burnham and Anderson 2002); thus, any model <2 $AIC_c$ of the null was omitted from further analyses. Four covariate sets were evaluated sequentially: 1) raptor variables, 2) anthropogenic features, 3) landscape features, and 4) sage-grouse behavior. Cox PH models with raptor variables were compared as single variable models for each raptor species individually with $AIC_c$ to choose which type (study site-level or site-specific change in density) of raptor variable fit the data best; thus, the raptor variable type with the lowest $AIC_c$ was used in all further modeling. I evaluated the effect of a sage-grouse's age (AGE) on survival within the sage-grouse behavior covariate set. I included raptor variables × anthropogenic structure

variables and raptor variables × landscape feature variables as pairwise interactions within anthropogenic and landscape feature covariate sets. Pairwise interactions with raptor variables were included to assess whether negative effects of raptor variables were intensified in areas closer to potential perches or nest structure or in areas closer to natural or human provided food subsidies. I did not include DIST_WCH or ANTH with any other anthropogenic structure variable, because DIST_WCH and ANTH were derived from a combination of distance from sage-grouse locations to energy wells, communication towers, houses, and power lines. The best variable describing the effect of anthropogenic structures on survival was determined through $AIC_c$ selection within the anthropogenic feature covariate set. I compared Cox PH models with individual TRI variables measured at 0.27-km, 0.54-km, 1-km, and 3-km radii with $AIC_c$ to choose the best spatial scale for the TRI variable to be used in the landscape feature covariate set; the TRI variable scale with the lowest $AIC_c$ was used in all further modeling. As the final modeling step, I compared all top $AIC_c$ selected models from every covariate set (models within 2 $AIC_c$ of the top model within each covariate set) among each other and as additive models with combinations of all 3 covariate sets. I based my inference on Cox PH models within 2 $AIC_c$ of the top selected model (Burnham and Anderson 2002).

The effects of sage-grouse behavior on survival in relation to raptors and anthropogenic and landscape features had to be analyzed as 2 separate Cox PH analysis steps. The sequential modeling procedure described above was applied to both the Cox PH analysis steps. In “Step 1” (parental investment analysis), I evaluated parental

investment (hen status) with raptors and anthropogenic and landscape features by using all sage-grouse locations (nesting, brooding, and roosting locations). However, I excluded potential anti-predation behaviors (average weekly movement and average flock size) from Step 1 model building, because all variables that potentially described an anti-predation behavior were constant for 2 of 3 of the parental investment categories (nesting and brooding). In "Step 2" (anti-predation strategy analysis), I used non-reproductive locations to evaluate the effects of weekly movements and average flock size with raptors and anthropogenic and landscape features on sage-grouse survival. Average flock size was compared as a linear and quadratic variable in the sage-grouse behavior covariate set to assess the possibility of an optimal flock size. In Step 2, I included an interaction between average flock size and AGE to assess if yearling sage-grouse in larger flocks had higher survival.

In addition to $AIC_c$ model comparison, I implemented a spatiotemporal modeling strategy to evaluate general trends in sage-grouse hen survival in relation to raptor variables, anthropogenic features, landscape features, and sage-grouse behavior. A spatiotemporal strategy was implemented to Cox PH model evaluation because many variables describing sage-grouse survival were exclusive to a given year or study site. I assessed goodness-of-fit of the top Cox PH models by computing a ratio of Zheng's (2000) proportional reduction of deviance (RDR) for covariate models to spatiotemporally saturated models (maximum proportional reduction in deviance; Iles 2012), which has been considered appropriate for Cox PH models (Zheng 2000, Aubry et al. 2011). Deviance reduction for each spatiotemporally saturated model and top

covariate models of interest were calculated relative to null models (time and study site invariant):

$$D_{int} = 1 - (deviance_{interest}/deviance_{null}) \quad (2)$$

$$D_{sat} = 1 - (deviance_{saturated}/deviance_{null})$$

$$RDR = D_{int} / D_{saturated} \quad (3)$$

thus, the ratio gives an assessment of a covariate model's relative ability to explain spatiotemporal processes effecting sage-grouse survival. The ratio is 1 for the spatiotemporally saturated model and 0 for the null model (Iles 2012). I compared the top $AIC_c$ selected Cox PH models of sage-grouse survival from Step 1 and 2 to a spatiotemporally saturated model with RDR. The saturated model for sage-grouse survival included year; study site; distance to energy well, communication tower, house, power line, all road, and tree stand; the top selected TRI variable; and distance to riparian habitat.

Although I could not test for spatial autocorrelation in Cox PH analyses, raptor densities derived from distance sampling techniques are robust to lack of independence of observation locations because distance sampling is setup to be a snap-shot in time (Thomas et al. 2010). My raptor sampling was designed to count the greatest proportion of raptors within a study site each week while not counting the same raptor more than once per week as suggested by Ralph et al. (1995) and Thomas et al. (2010). Conducting all point counts within a study site in one day reduced the possibility of double-counting individual raptors during that week's visit. Counting the same individual raptor during different weeks, regardless of the particular point count location, was properly scaled by

accounting for survey effort. Replication of point counts by sampling multiple weeks was done to increase the proportion of raptors detected as suggested by Thomas et al. (2010). Furthermore, study site-level and site-specific change in raptor densities were averaged by study site and year; thus, the lowest unit of measurement was at the study site-level annually. Time-dependent variables for Cox PH analyses were not subject to spatial autocorrelation, because Cox PH treats each time interval as a separate observation (Hosmer and Lemeshow 1999).

**RESULTS**

During 2008–2011, I captured 427 sage-grouse hens that were included in my Cox PH analyses because they were available to monitor (i.e., they did not go missing or die within 2 weeks of radio-collaring). Fifty, 76, and 69 sage-grouse hens survived into a subsequent year, 2009, 2010, and 2011, respectively; thus, there were 132, 162, 156, and 165 sage-grouse hens in 2008, 2009, 2010, and 2011, respectively. From 1 May – 31 August, I found 88 sage-grouse hen mortalities (22 nesting, 19 brooding, and 47 non-reproductive sage-grouse), which yielded apparent summer survival estimates of 81–89% annually. There were 3,523 time intervals for analyzing survival (402 nesting, 817 brooding, and 2,304 non-reproductive locations). I monitored 380 nesting sage-grouse and 162 brooding sage-grouse. The proportional hazards assumption was not violated for any model within 2 $AIC_c$ of the top selected model.

To evaluate the effect of raptor densities on sage-grouse survival, I conducted 2,948 point count surveys during 2008–2011 at 660 total random point count locations. I

counted 252 golden eagles, 138 *Buteo* hawks, and 57 harriers within species-specific EDRs (see Chapter 2). Neither study site-level nor site-specific change in golden eagle, *Buteo* hawk, and harrier densities had an individual effect on sage-grouse summer survival (all main effects of raptor variables had 85% CIs that overlapped 0). Variables describing site-specific changes in raptor densities fit the data better than landscape densities of raptors; thus, I used site-specific change in raptor densities in interactive models.

I found that landscape variables and sage-grouse behavior variables described summer sage-grouse survival best for both the parental investment and anti-predation analyses. I found that TRI at the 0.27-km radius ($TRI_{0.27}$) fit the data best for all analyses. No anthropogenic variable described differences in summer survival of sage-grouse hens (parameter estimates had 85% CI that overlapped 0) for either the parental investment or anti-predation analyses. In the parental investment analysis, I found that the top $AIC_c$ selected Cox PH model included AGE, sage-grouse hen status (nesting, brooding, or non-reproductive), and site-specific change in golden eagle density × $TRI_{0.27}$ (Table 6-2), which had $w_i = 0.96$ and RDR = 0.82. The anti-predation strategy analysis had 3 models within 2 $AIC_c$ (Table 6-2). However, the top 2 $AIC_c$ ranked models had $w_i = 0.38$ and $w_i = 0.32$, respectively, and the third $AIC_c$ ranked model had $w_i = 0.17$ (Table 6-2); thus, I will only discuss the top 2 models. Both top $AIC_c$ ranked models included average flock size, quadratic effect of flock size, AGE, AGE × average flock size, distance to forested habitat, and $TRI_{0.27}$ (Table 6-2). In addition, I found that the top $AIC_c$ ranked model for the anti-predator strategy analysis included the site-specific change in golden eagle

density × $TRI_{0.27}$ interaction and had RDR = 0.98 (Table 6-2). Whereas, the simpler second $AIC_c$ ranked model for the anti-predator strategy analysis had RDR = 0.90. The near 1 values of RDR for all top $AIC_c$ selected models indicated that a high proportion of the maximum explainable deviance for sage-grouse summer survival was accounted for in my top selected models.

Topographic ruggedness index at 0.27 km radius was the landscape feature variable that most consistently explained sage-grouse summer survival. I found that higher $TRI_{0.27}$ values were correlated with lower sage-grouse summer survival (Tables 6-3 and 6-4). In the anti-predator analysis, there was support for lower survival of sage-grouse closer to forested habitat at non-reproductive locations from all top $AIC_c$ ranked models from the anti-predator strategy analysis (Tables 6-2 and 6-4, Fig. 6-1). Parameter estimates for distance to forested habitat were -0.15 (0.08 SE; 95% CI = -0.31 to 0.02) and -0.15 (0.08 SE; 95% CI = -0.31 to 0.01) for the top and second $AIC_c$ ranked models, respectively (Table 6-4).

Even though raptor densities (study site-level and site-specific change) by themselves did not describe sage-grouse survival, I found that the interaction between site-specific change in golden eagle density and $TRI_{0.27}$ was highly explanative of sage-grouse summer survival (Tables 6-3 and 6-4). Site-specific change in golden eagle density was negatively associated with sage-grouse summer survival only when taking $TRI_{0.27}$ into context. When site-specific change in golden eagle density was relatively high and sage-grouse were in areas with more rugged terrain, I found that the negative effect of site-specific change in golden eagle density and $TRI_{0.27}$ were dampened (Fig. 6-

2). The site-specific change in golden eagle density × $TRI_{0.27}$ parameter estimate was -0.01 (0.00 SE; 95% CI = -0.01 to -0.00) and -0.01 (0.00 SE; 95% CI = -0.02 to -0.00) for the parental investment analysis and anti-predation analyses, respectively (Tables 6-3 and 6-4).

For variables describing the effect of sage-grouse behavior on sage-grouse summer survival, I found that non-reproductive sage-grouse had marginally higher survival than nesting (parameter estimate 0.45 [0.27 SE]; 95% CI = -0.09 to 0.99) or brooding (parameter estimate 0.51 [0.28 SE]; 95% CI = -0.04 to 1.07) sage-grouse hens in the parental investment analysis (Table 6-3). In the anti-predation strategy analysis, I found that non-reproductive adults that flocked in intermediate numbers had higher survival (Table 6-4, Fig. 6-3A); thus, sage-grouse hens in small flocks (by themselves or another hen) and large flocks had lower summer survival. Average flock size parameter estimates were -0.55 (0.18 SE; 95% CI = -0.89 to -0.20) with quadratic 0.03 (0.01 SE; 95% CI = 0.01 to 0.05) for the top $AIC_c$ ranked model, and -0.55 (0.18 SE; 95% CI = -0.90 to -0.21) for the second $AIC_c$ ranked model with the same quadratic parameter estimate as the top $AIC_c$ ranked model. All top $AIC_c$ ranked Cox PH models included AGE. However, yearling sage-grouse hens had higher survival (parameter estimate -0.69 [0.30 SE]; 95% CI = -1.27 to -0.11) in the parental investment analysis, but marginally lower survival (parameter estimates: top model = 1.26 [0.78 SE]; 95% CI = -0.28 to 2.80; and second model = 1.23 [0.78 SE]; 95% CI = -0.28 to 2.80) in both of the top $AIC_c$ selected models from the anti-predation strategy analysis when a yearling hen was in a flock of <3 birds (Table 6-4, Fig. 6-3B). In the anti-predation strategy analysis, I also

found the AGE × average flock size interaction term was marginally significant for the top 2 $AIC_c$ selected models, which indicated that yearlings that on average chose to flock in greater numbers had greater survival (interaction parameter estimates: top model = -0.86 [0.48 SE]; 95% CI = -1.80 to 0.08; and second model = -0.87 [0.48 SE]; 95% CI = -1.81 to 0.07).

## DISCUSSION

I found that sage-grouse summer survival was negatively correlated with landscape features that represented riskier habitat, especially risk of predation from raptors. Breeding season survival of sage-grouse was negatively impacted by proximity to trees (deciduous and coniferous) and greater values of $TRI_{0.27}$ and site-specific change in golden eagle density (study site relative change in golden eagle density among years). Kirol (2012) also found that terrain roughness was negatively correlated with sage-grouse summer survival in south-central Wyoming. His study indicated that proximity to anthropogenic features had no effect on sage-grouse survival, and I found no evidence of an interactive effect between anthropogenic features and raptor densities. My results also suggest that survival was greater for non-reproductive hens, hens that stayed in intermediate size flocks, and yearling hens. The best sage-grouse survival models had RDR = 0.82 to 0.98, which indicated that a large proportion of spatiotemporal variability in sage-grouse survival was accounted for in my models. My apparent late spring and summer survival rate was 79%, which was within estimated annual survival rates in Wyoming (Connelly et al. 2011). Thus, landscape features in conjunction with site-

specific change in golden eagle density and sage-grouse behavior had dynamic effects on survival.

It was possible that distance variables associated with time intervals for mortalities were biased due to a predator moving a sage-grouse carcass. However, I did not find summer mortalities with evidence of drastic predator movements (>1 km), and sage-grouse carcasses were typically found close to the last location where the sage-grouse was known to be alive. For example, sage-grouse killed while nesting were found on average 0.38 km from their nest, and only 2 of 22 (9%) were found >1 km away from their nest. The average distance from sage-grouse nest to mortality location (0.38 km) was within the 0.54 km diameter of the $TRI_{0.27}$ variable, and topographic ruggedness variables at 0.27 km, 0.54 km, 1 km, and 3 km radii all had a negative effect on sage-grouse survival.

Previous research has shown that most sage-grouse mortalities in the spring and summer can be attributed to predation (Connelly et al. 2011), but other possible sources of mortality include collisions with vehicles, fences, and power lines (Braun 1998, Connelly et al. 2000a, Connelly et al. 2004, Beck et al. 2006); and West Nile virus (Naugle et al. 2004, Walker et al. 2007b, Walker and Naugle 2011). I did not find evidence of any sage-grouse colliding with a fence or power line (no carcasses near fences or under power lines). West Nile virus was not likely to have killed many birds in this study, because West Nile virus was not known to be prominent in my study sites during this study (Walker and Naugle 2011). In addition, mortalities from West Nile virus usually occur July to mid-September (Walker et al. 2007b, Walker and Naugle

2011), and I only found 17 of the 88 mortalities after 5 July. Sage-grouse survival has been documented to be lowest from March to June and relatively higher after July (Connelly et al. 2000a, Connelly et al. 2011, Walker and Naugle 2011); thus the timing of mortalities in my study coincides with typical sage-grouse summer survival.

Golden eagle, *Buteo* hawk, and harrier densities (study site level or site-specific change) did not independently predict sage-grouse survival. Raptor populations may have been too stable over time for me to detect direct negative effects of raptor abundance on sage-grouse survival. However, I found moderate support for lower sage-grouse survival when sage-grouse were exposed to a greater density of golden eagles within a study site (site-specific change in golden eagle density) while simultaneously taking $TRI_{0.27}$ into account (site-specific change in golden eagle density × $TRI_{0.27}$; Tables 6-3 and 6-4), and high values of $TRI_{0.27}$ negatively affected sage-grouse survival. Marzluff et al. (1997) found that golden eagles in sagebrush habitat selected areas with more rock outcrops and cliffs in southern Idaho. I hypothesized that rugged terrain would be riskier habitat and high raptor densities would intensify this effect because hilltops, knolls, and cliff edges associated with rugged terrain would act as perch or nesting structure for raptors. Thus, rugged terrain would correlate with greater exposure to predation from raptors. Contrary to my hypothesis, I found that the negative effect of $TRI_{0.27}$ and site-specific change in golden eagle density was dampened by the combination of greater rugged terrain and greater values of site-specific change in golden eagle density (Tables 6-3 and 6-4). Two potential explanations for this finding include; 1) rugged topography may provide some refugia from visual predators (e.g., golden eagles), because topographic features such as

slight depressions may decrease the effective distance that a raptor can detect a sage-grouse on the ground; and 2) greater abundance of golden eagles in rugged topography (risky habitat) may competitively exclude other predators. Golden eagles and coyotes are known to be the top predators in sagebrush ecosystems (Mezquida et al. 2006, Hagen 2011), and presence of golden eagles may reduce the hunting efficiency of mammalian predators. I found that nesting and brooding sage-grouse selected locations with lower topographic ruggedness compared to the landscape at random in Chapter 3, which has been verified by other sage-grouse research (Jensen 2006, Doherty et al. 2010, Hanser et al. 2011, Kirol 2012); thus, sage-grouse avoided extremely rugged terrain. The moderately rugged topography (relative to the landscape) where sage-grouse had higher mortality may have been correlated to greater risk of predation from olfactory predators (mammalian predators), which have been known to hunt in areas such as drainage bottoms (Conover 2007).

Other landscape features such as forested and riparian habitats have the potential to pose a higher risk of predation for sage-grouse. Sage-grouse avoidance of forested habitat, especially pinyon (*Pinus* spp.)-juniper (*Juniperus* spp.), has been documented (Doherty et al. 2010), but there has been little research looking at the impact of proximity to forested areas on sage-grouse survival. I found that proximity to trees was negatively related to the survival of non-reproductive hens; although distance from sage-grouse locations to forested habitat was an imprecise predictor (95% CI overlapped 0; Table 6-4). There has been some documentation of the negative effect of proximity to trees on sage-grouse survival, but this topic clearly needs more study. For example, Commons et

al. (1999) found higher spring counts of male Gunnison sage-grouse (*Centrocercus minimus*) on leks after removal of pinyon-juniper in southwestern Colorado; they attributed this to lower densities of raptors after pinyon-juniper was removed. Nesting and early brood-rearing sage-grouse avoid riparian habitat (Doherty et al. 2010, Chapter 3), presumably due to increased risk of predation. However, I did not find a connection of low hen survival and proximity to riparian habitats.

Several studies have demonstrated that sage-grouse avoid habitat with man-made features, such as oil and gas infrastructure (Aldridge 2005, Holloran 2005, Walker et al. 2007a, Kirol 2012), power-lines (Hanser et al. 2011), and roads (Holloran 2005, Aldridge and Boyce 2007), which are potential perches or nest structure for raptors or provide reliable food subsidies. In fact, golden eagles, red-tailed hawks (*Buteo jamaicensis*), ferruginous hawks (*Buteo regalis*), and Swainson's hawks (*Buteo swainsoni*) have been found to use power lines for perch sites and areas around power lines for foraging (Lammers and Collopy 2007, Prather and Messmer 2010 , Slater and Smith 2010). Holloran (2005) found that annual survival of adult female sage-grouse was lower in a natural gas field, and collisions with vehicles are known to cause sage-grouse mortalities (Braun 1998). Thus, I hypothesized that sage-grouse survival would be lower near anthropogenic features and that this effect would be amplified when there were also high densities of raptors. However, I did not find support for this hypothesis indicating that anthropogenic features do not necessarily predict riskier habitats or sage-grouse avoidance of anthropogenic features masked any effects on survival.

Behaviors associated with parental investment and anti-predation strategies have

the potential to influence survival rates of animals. Increased experience, quantified as age, should also be positively correlated with survival. However, yearling sage-grouse have been found to have higher survival than adults ≥2 years of age (Zablan et al. 2003, Holloran 2005, Connelly et al. 2011). For example, Zablan et al. (2003) found 77% and 59% survival for yearling and adult female sage-grouse in Colorado, respectively. Connelly et al. (1993), Holloran (2005), and Moynahan et al. (2007) documented that yearling sage-grouse hens initiated nests and re-nested less often than adult hens. I found similar results with 56% and 60% apparent nest initiation for yearling and adult hens, respectively, and 11 of 14 re-nesting events were from adult hens. Adult sage-grouse hens have higher nest success compared to yearlings, which indicates that adults are more likely to have a brood (Connelly et al. 2011). I found broods with 19% and 30% of yearling and adult sage-grouse hens, respectively, and I found that sage-grouse hens that were nesting or brooding had lower survival than hens without a nest or brood (Table 6-3). Thus, yearling sage-grouse hens may have had higher survival, because they were less likely to be incubating or tending a brood. This provides some evidence that differential behavior related to parental investment may account for higher survival rates of yearling sage-grouse hens.

In contrast, Moynahan et al. (2006) found nesting sage-grouse in Montana had higher survival than non-nesting hens. They attributed their findings to better physical condition of nesters versus non-nesters, increased visibility of non-nesting hens, or both. The apparent inconsistency with Moynahan et al. (2006) and my results most likely arises from differences in analyses. Moynahan et al. (2006) compared survival of hens that had

initiated a nest within a summer versus hens that did not initiate a nest within a summer. On the other hand, I allowed the nesting status (nesting, brooding, or non-reproductive) of each hen to change over time with a time-dependent Cox PH variable; thus, I assigned each mortality to a time-dependent breeding status. In light of my results, Moynahan et al. (2006) results more likely relate to the better physical condition or experience of hens that attempted to nest.

My results from the anti-predation strategy analysis suggested that survival was greater for non-reproductive hens that stayed in intermediate size flocks (Fig. 6-3A). I did not find higher survival of yearlings versus adults when comparing survival of only non-reproductive hens (i.e., the main effect of AGE was not significant; Table 6-4), and yearling hen survival was connected to average flock size (interaction AGE × average flock size; Tables 6-2 and 6-4). In fact, survival of yearling sage-grouse hens was lower than adults when yearlings were in flocks of <3 grouse on average (Fig. 6-3B, Table 6-4). However, the interaction between AGE and average flock size indicated that yearlings that chose to stay in larger groups had higher survival.

I hypothesized that sage-grouse would have higher survival in optimally sized flocks, because small and very large flocks would represent increased risk of predation. Small flocks would decrease the benefits of sentinel behavior (i.e., sage-grouse detecting a predator) and the dilution effect, and large flocks would increase a predator's probability of detecting a flock of sage-grouse. The dilution effect predicts that an individual in a larger flock will have a lower probability of being eaten. Intermediate flock sizes would allow individual sage-grouse to benefit from the dilution effect and

sentinel behavior, while avoiding detection by predators. I found support for an optimally sized flock for non-reproductive sage-grouse, which my top $AIC_c$ selected Cox PH model predicted around 3–14 birds (Fig. 6-3A). I also predicted that increased movement distances would be negatively related to survival, because there would be a greater risk of being detected by a visual predator for hens moving greater distances. However, I did not find support for a negative effect of weekly movement distance. This may be attributed to no effect or a lack of detailed information on movements from telemetry techniques. I was only able to record minimum linear movements, which ignore daily movements within a smaller area.

Raptors including golden eagles, *Buteo* hawks, and harriers have been identified as significant threats to sage-grouse survival (Schroeder et al. 1999, Schroeder and Baydack 2001). However, I found that natural abundances of raptors, even in the presence of anthropogenic features, did not seem to adversely affect sage-grouse survival. This may be attributed to sage-grouse avoiding raptors, avoidance of risky habitats, and habitat condition; negative effects of high raptor densities may also have been masked by other spatiotemporal processes such as weather. Dinkins et al. (2012) found that nesting and brooding sage-grouse avoided raptors, and many researchers have found that sage-grouse avoid risky habitats (Aldridge 2005, Holloran 2005, Aldridge and Boyce 2007, Walker et al. 2007a, Doherty et al. 2010, Hanser et al. 2011, Kirol 2012).

## MANAGEMENT IMPLICATIONS

Many authors have suggested that ground-nesting bird survival, including sage-

grouse, is connected to quantity and quality of habitat, and the presence of adequate sagebrush habitat minimizes predator effects on sage-grouse survival (Connelly et al. 1994, Braun 1998, Aldridge et al. 2008, Connelly et al. 2011). I agree with this, but there needs to be careful consideration of interactive effects of anthropogenic and landscape features and predator community dynamics (risk of predation). For example, sage-grouse hens avoided conventional and natural gas wells (Kirol 2012; Chapter 3), which placed them in areas with higher $TRI_{0.27}$. In addition, areas with higher $TRI_{0.27}$ had lower sage-grouse survival, which was dampened by high densities of golden eagles. However, the overall sage-grouse survival in areas with higher $TRI_{0.27}$ was lower. This indicates that changes in sage-grouse selection of habitat in response to anthropogenic features (fragmentation of habitat) can have dynamic consequences for sage-grouse survival, especially when considering differences in predator compositions. Thus, habitat fragmentation of sagebrush habitats has complex effects on sage-grouse use of the landscape, which in turn can have complex impacts on survival.

## LITERATURE CITED

Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation, University of Alberta, Edmonton, Canada.

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

Aldridge, C. L., S. E. Nielson, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range wide patterns of greater sage-grouse persistence. Diversity and Distributions 14:983–994.

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer Science, New York, New York, USA.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175–1178.

Aubry, L. M., E. Cam, D. N. Koons, J. -Y. Monnat, and S. Pavard. 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. Journal of Animal Ecology 80:375–383.

Baxter, R. J., K. D. Bunnell, J. T. Flinders, and D. L. Mitchell. 2007. Impacts of predation on greater sage-grouse in Strawberry Valley, Utah. Transactions of the 72nd North American Wildlife and Natural Resources Conference 72:258–269.

Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070–1078.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139–156.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, New York, New York, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Commons, M. L., R. K. Baydack, and C. E. Braun. 1999. Sage-grouse response to pinyon-juniper management. Pages 238–239 *in* S. B. Monsen, and R. Stevens, editors. Proceedings, ecology and management of pinyon-juniper communities within the Interior West. United States Department of Agriculture, Forest Service, RMRS-P-9, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Connelly, J. W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000a. Effects of predation and hunting on adult sage grouse (*Centrocercus urophasianus*) in Idaho. Wildlife Biology 6:227–232.

Connelly, J. W., R. A. Fischer, A. D. Apa, K. P. Reese, and W. L. Wakkinen. 1993. Renesting of sage-grouse in southeastern Idaho. Condor 95:1041–1043.

Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53–67 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report, Cheyenne, Wyoming, USA.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-

grouse habitats and populations. College of Natural Resources Experiment Station Bulletin 80, University of Idaho, Moscow, USA.

Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage grouse ecology. Idaho Department of Fish and Game Job Completion Report W-160-R-19, Boise, USA.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000b. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Conover, M. R. 2007. Predator−prey dynamics: the use of olfaction. Taylor and Francis, Boca Raton, Florida, USA.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society Series B-Statistical Methodology 34:187–220.

Dahlgren, D. K. 2006. Greater sage-grouse ecology and response to experimental management of mountain big sagebrush on Parker Mountain, Utah. Thesis, Utah State University, Logan, Utah, USA.

Danvir, R. E. 2002. Sage grouse ecology and management in northern Utah sagebrush-steppe. Deseret Land and Livestock Wildlife Research Report, Deseret Land and Livestock Ranch and the Utah Foundation for Quality Resource Management, Woodruff, Utah, USA.

Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetational cover and predation of sage-grouse nests in Oregon. Journal of Wildlife Management 58:162–166.

Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effects. Pages 95–100 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Hanser, S. E., M. Leu, S. T. Knick, and C. L. Aldridge. 2011. Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, Kansas, USA.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638–649.

Hosmer, D. W., and S. Lemeshow. 1999. Applied logistic regression. Second edition. John Wiley and Sons, New York, New York, USA.

Iles, D. T. 2012. Drivers of nest success and stochastic population dynamics of the common eider (*Somateria mollissima*). Thesis, Utah State University, Logan, USA.

Jensen, B. M. 2006. Migration, transition range and landscape use by greater sage-grouse (*Centrocercus urophasianus*). Thesis, University of Wyoming, Laramie, USA.

Johnsgard, P. A. 2002. Grassland grouse and their conservation. Smithsonian Institution, Washington, D. C., USA.

Johnson, K. H., and C. E. Braun. 1999. Viability and conservation of an exploited sage-grouse population. Conservation Biology 13:77–84.

Kirol, C. P. 2012. Quantifying habitat importance for greater sage-grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. Thesis, University of Wyoming, Laramie, USA.

Lammers, W. M., and M. W. Collopy. 2007. Effectiveness of avian predator perch deterrents on electric transmission lines. Journal of Wildlife Management 71:2752–2758.

Lennartz, S. 2007. USGS Gap Analysis Program (GAP) species distribution model. Sanborn Map Corporation. Portland, Oregon, USA.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the West: a large scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Marzluff, J. M., S. T. Knick, M. S. Vekasy, L. S. Schueck, and T. J. Zarriello. 1997. Spatial use and habitat selection of golden eagles in southwestern Idaho. Auk 114:673–687.

Mezquida, E. T., S. J. Slater, and C. W. Benkman. 2006. Sage-grouse and indirect interactions: potential implication of coyote control on sage-grouse populations. Condor 108:747–759.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in northcentral Montana. Journal of Wildlife Management 71:1773–1783.

Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2006. Factors contributing to process variance in annual survival of female greater sage-grouse in Montana. Ecological Applications 16:1529–1538.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: pending crisis for greater sage-grouse. Ecology Letters 7:704–713.

Patterson, R. L. 1952. The sage grouse of Wyoming. Sage Books, Denver, Colorado, USA.

Prather, P. R., and T. A. Messmer. 2010. Raptor and corvid response to power distribution line perch deterrents in Utah. Journal of Wildlife Management 74:796–800.

Ralph, C. J., S. Droege, and J. R. Sauer. 1995. Managing and monitoring birds using point counts: standards and applications. USDA Forest Service General Technical Report PSW-GTR-149, Berkeley, California, USA.

Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:1–4.

Schroeder, M. A., and R. K. Baydack. 2001. Predation and the management of prairie grouse. Wildlife Society Bulletin 29:24–32.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). *In* A. Poole, and F. Gill, editors. Birds of North America. Birds of North America, Philadelphia, Pennsylvania, USA.

Slater, S. J., and J. P. Smith. 2010. Effectiveness of raptor perch deterrents on an electrical transmission line in southwestern Wyoming. Journal of Wildlife Management 74:1080–1088.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336−347.

Therneau, T. M., and P. M. Gambsch. 2000. Modeling survival data: extending the Cox model. Springer-Verlag, New York, New York, USA.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, R. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Thompson, T. R. 2012. Dispersal ecology of greater sage-grouse in northwestern Colorado: evidence from demographic and genetic methods. Dissertation,

University of Idaho, Moscow, USA.

U.S. Department of Agriculture. 2010. 2009 NAIP survey: summary report. Farm Service Agency, Aerial Photography Field Office, Salt Lake City, Utah, USA.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

Walker, B. L., and D. E. Naugle. 2011. West Nile virus ecology in sagebrush habitat and impacts on greater sage-grouse populations. Pages 127–141 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007a. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2007b. West Nile virus and greater sage-grouse: estimating infection rate in a wild bird population. Avian Diseases 51:691–696.

Willis, M. J., G. P. Kiester, Jr., D. A. Immel, D. M. Jones, R. M. Powell, and K. R. Durbin. 1993. Sage grouse in Oregon. Oregon Department of Fish and Wildlife, Wildlife Research Report No.15. Portland, USA.

Winterstein, S. R., K. H. Pollock, and C. M. Bunck. 2001. Analysis of survival data from radiotelemetry studies. Pages 352–380 *in* J. J. Millspaugh, and J. M. Marzluff,

editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Wyoming Oil and Gas Conservation Commission (WOGCC). 2012. WOGCC homepage. <http://wogcc.state.wy.us/>. Accessed 15 January 2012.

Zablan, M. A., C. E. Braun, and G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal of Wildlife Management 67:144–154.

Zheng, B. 2000. Summarizing the goodness of fit of generalized linear models for longitudinal data. Statistics in Medicine 19:1265–1275.

Table 6-1. Descriptions, means, and standard errors (SE) of variables used to model sage-grouse survival with the Anderson-Gill formulation of the Cox proportional hazard model; means and SE were stratified by sage-grouse that survived the duration of the study and those that did not. Variables include raptor densities, anthropogenic features, and landscape features from 3,523 summer (1 May through 31 August) survival intervals. Sage-grouse behavior variables (average weekly movement and average flock size) were from non-reproductive 2,304 sage-grouse locations. Data were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011.

| | Survived | | | Mortality | | |
|---|---|---|---|---|---|---|
| Variable description | *n* | mean | SE | *n* | mean | SE |
| Study site-level golden eagle density (no./100 $km^2$) | 3435 | 1.91 | 2.73 | 88 | 2.22 | 2.84 |
| Study site-level *Buteo* hawk density (no./100 $km^2$) | 3435 | 6.59 | 7.44 | 88 | 7.66 | 8.42 |
| Study site-level harrier density (no./100 $km^2$) | 3435 | 7.02 | 8.19 | 88 | 6.41 | 6.92 |
| Distance (km) from sage-grouse location to nearest oil and gas structure (energy well, compressor station, transfer station, refinery, or other | 3435 | 7.55 | 0.12 | 88 | 7.38 | 0.62 |

| | | | | | | |
|---|---|---|---|---|---|---|
| energy extraction related buildings) | | | | | | |
| Distance (km) from sage-grouse location to nearest major road including paved roads, railroad, and improved gravel roads | 3435 | 1.51 | 0.02 | 88 | 1.71 | 0.13 |
| Distance (km) from sage-grouse location to nearest road including paved roads, railroad, improved gravel roads, and unimproved 4-wheel drive roads | 3435 | 0.33 | 0.01 | 88 | 0.38 | 0.03 |
| Distance (km) from sage-grouse location to nearest communication tower | 3435 | 10.13 | 0.13 | 88 | 10.55 | 0.78 |
| Distance (km) from sage-grouse location to nearest residential house | 3435 | 7.50 | 0.10 | 88 | 6.87 | 0.52 |
| Distance (km) from sage-grouse location to nearest overhead line (transmission or distribution power lines, or telephone line) | 3435 | 8.57 | 0.09 | 88 | 8.41 | 0.60 |
| Distance (km) from sage-grouse location to nearest anthropogenic perch (ANTH; oil and gas structure, | 3435 | 3.32 | 0.04 | 88 | 3.46 | 0.24 |

| | | | | | | |
|---|---|---|---|---|---|---|
| communication tower, residential house, or power lines) | | | | | | |
| Distance (km) from sage-grouse location to nearest oil and gas structure, communication tower, or residential house (DIST_WCH) | 3435 | 3.64 | 0.05 | 88 | 3.88 | 0.25 |
| Distance (km) from sage-grouse location to nearest forested habitat including deciduous and conifer stands | 3435 | 2.87 | 0.05 | 88 | 2.00 | 0.26 |
| Distance (km) from sage-grouse location to nearest riparian habitat | 3435 | 1.65 | 0.03 | 88 | 1.48 | 0.16 |
| Topographic ruggedness index at 0.27 km radii (0.23-$km^2$ scale) | 3435 | 16.48 | 0.19 | 88 | 21.76 | 1.55 |
| Topographic ruggedness index at 0.54 km radii (0.92-$km^2$ scale) | 3435 | 17.06 | 0.18 | 88 | 21.62 | 1.38 |
| Topographic ruggedness index at 1 km radii (3.14-$km^2$ scale) | 3435 | 18.01 | 0.17 | 88 | 21.82 | 1.28 |
| Topographic ruggedness index at 3 km radii (28.26-$km^2$ scale) | 3435 | 20.65 | 0.16 | 88 | 23.74 | 1.04 |
| Average weekly sage-grouse movement distance (km) | 2257 | 1.17 | 0.05 | 47 | 0.99 | 0.14 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | | | | | 257 |
| Average flock of sage-grouse | 2257 | 3.71 | 0.06 | 47 | 2.07 | 0.34 |

Table 6-2. Model comparison of Cox proportional hazard (Cox PH) models from the parental investment and anti-predator strategy analyses. Models assessed the effects of 4 covariate sets including site-specific change in raptor densities, anthropogenic features, landscape features, and sage-grouse behavior on sage-grouse hen survival. Models were compared with Akaike's information criterion (adjusted for small sample sizes; $AIC_c$) and Akaike weights ($w_i$). Data were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA. A total of 427 sage-grouse hens were monitored during 2008–2011.

| Models [a,d] | $k$ | $\Delta AIC_c$ | $w_i$ | Deviance |
|---|---|---|---|---|
| Parental investment | | | | |
| AGE, status, GOEA×$TRI_{0.27}$ [b] | 6 | 0.00 | 0.96 | 1039.30 |
| GOEA×$TRI_{0.27}$ | 3 | 6.44 | 0.04 | 1051.76 |
| AGE, status | 3 | 13.71 | 0.00 | 1059.02 |
| Null | 0 | 22.83 | 0.00 | 1074.16 |
| Fully saturated | 22 | 24.47 | 0.00 | 1031.50 |
| Anti-predation strategy | | | | |
| Flock^2, flock×AGE, forest distance, GOEA×$TRI_{0.27}$ [c] | 8 | 0.00 | 0.38 | 479.86 |
| Flock^2, flock×AGE, forest distance, $TRI_{0.27}$ | 6 | 0.36 | 0.32 | 484.24 |
| Flock^2, forest distance, GOEA×$TRI_{0.27}$ | 6 | 1.63 | 0.17 | 485.52 |
| Flock^2, forest distance, $TRI_{0.27}$ | 4 | 2.14 | 0.13 | 490.06 |
| Flock^2, flock×AGE | 4 | 14.31 | 0.00 | 502.22 |

| | | | | |
|---|---|---|---|---|
| Flock^2 | 2 | 15.27 | 0.00 | 507.20 |
| Forest distance, GOEA×$TRI_{0.27}$ | 4 | 21.71 | 0.00 | 509.62 |
| Forest distance, $TRI_{0.27}$ | 2 | 22.75 | 0.00 | 514.68 |
| Fully saturated | 22 | 27.03 | 0.00 | 478.50 |
| Null | 0 | 39.04 | 0.00 | 534.96 |

[a]Models with interaction terms included all individual variables within the interactions.

[b]$AIC_c$ = 1051.32

[c]$AIC_c$ = 495.93

[d]Variables included in final Cox PH model selection included sage-grouse age (AGE), sage-grouse parental investment status (status), average flock size (flock), quadratic of average flock size (flock^2), site-specific change in golden eagle density (GOEA), topographic ruggedness index at 0.27-km radius ($TRI_{0.27}$), and distance to forested habitat (deciduous and conifer stands). The saturated model for sage-grouse survival included year; study site; distance to energy well, communication tower, house, power line, all road, and riparian and forested habitats; and the top selected TRI variable.

Table 6-3. Parameter estimates of sage-grouse survival (as hazard ratios—depicting risk of mortality) from top $AIC_c$ selected Cox proportional hazard model for parental investment analysis with *P*-values and 95% confidence intervals. Data were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011. A total of 427 sage-grouse hens were monitored during 2008–2011.

| | | | | | 95% CI | |
|---|---|---|---|---|---|---|
| Variable [c] | Estimate | SE | Z | *P* | Lower | Upper |
| AGE | -0.69 | 0.30 | -2.3 | 0.02 | -1.27 | -0.11* |
| Status brooding [a] | 0.51 | 0.28 | 1.8 | 0.07 | -0.04 | 1.07 |
| Status nesting [b] | 0.45 | 0.27 | 1.6 | 0.10 | -0.09 | 0.99 |
| GOEA | 0.14 | 0.08 | 1.7 | 0.09 | -0.02 | 0.31 |
| $TRI_{0.27}$ | 0.02 | 0.01 | 2.2 | 0.03 | 0.00 | 0.04* |
| GOEA×$TRI_{0.27}$ | -0.01 | 0.00 | -2.6 | 0.01 | -0.01 | -0.00* |

*Denotes a 95% confidence interval that does not include zero.

[a]Sage-grouse survival comparing brooding to non-reproductive hens.

[b]Sage-grouse survival comparing nesting to non-reproductive hens.

[c]Variables included in top $AIC_c$ selected Cox PH model include sage-grouse age (AGE), sage-grouse parental investment status (status), site-specific change in golden eagle density (GOEA), and topographic ruggedness index at 0.27-km radius ($TRI_{0.27}$).

Table 6-4. Parameter estimates of sage-grouse survival (as hazard ratios—depicting risk of mortality) from top 2 $AIC_c$ selected Cox proportional hazard models for anti-predation strategy analysis with *P*-values and 95% confidence intervals. Data were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011. A total of 427 sage-grouse hens were monitored during 2008–2011.

| | | | | | 95% CI | |
|---|---|---|---|---|---|---|
| Variable [a] | Estimate | SE | Z | *P* | Lower | Upper |
| Top selected | | | | | | |
| Flock | -0.55 | 0.18 | -3.11 | <0.01 | -0.89 | -0.20* |
| Flock^2 | 0.03 | 0.01 | 3.17 | <0.01 | 0.01 | 0.05* |
| AGE | 1.26 | 0.78 | 1.60 | 0.11 | -0.28 | 2.80 |
| GOEA | 0.15 | 0.12 | 1.26 | 0.21 | -0.08 | 0.38 |
| $TRI_{0.27}$ | 0.02 | 0.01 | 1.61 | 0.11 | -0.01 | 0.05 |
| Forest distance | -0.15 | 0.08 | -1.76 | 0.08 | -0.31 | 0.02 |
| Flock×AGE | -0.86 | 0.48 | -1.79 | 0.07 | -1.80 | 0.08 |
| GOEA×$TRI_{0.27}$ | -0.01 | 0.00 | -2.13 | 0.03 | -0.02 | -0.00* |
| Second selected | | | | | | |
| Flock | -0.55 | 0.18 | -3.11 | <0.01 | -0.90 | -0.21* |
| Flock^2 | 0.03 | 0.01 | 3.21 | <0.01 | 0.01 | 0.05* |
| AGE | 1.23 | 0.78 | 1.57 | 0.12 | -0.31 | 2.76 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Forest distance | -0.15 | 0.08 | -1.79 | 0.07 | -0.31 | 0.01 |
| $TRI_{0.27}$ | 0.03 | 0.01 | 2.72 | 0.01 | 0.01 | 0.05* |
| Flock×AGE | -0.87 | 0.48 | -1.81 | 0.07 | -1.81 | 0.07 |

*Denotes a 95% confidence interval that does not include zero.

[a]Variables included in top 2 $AIC_c$ selected Cox PH models include sage-grouse age (AGE), average flock size (flock), quadratic of average flock size (flock^2), site-specific change in golden eagle density (GOEA), topographic ruggedness index at 0.27-km radius ($TRI_{0.27}$), and distance to forested habitat (deciduous and conifer stands).

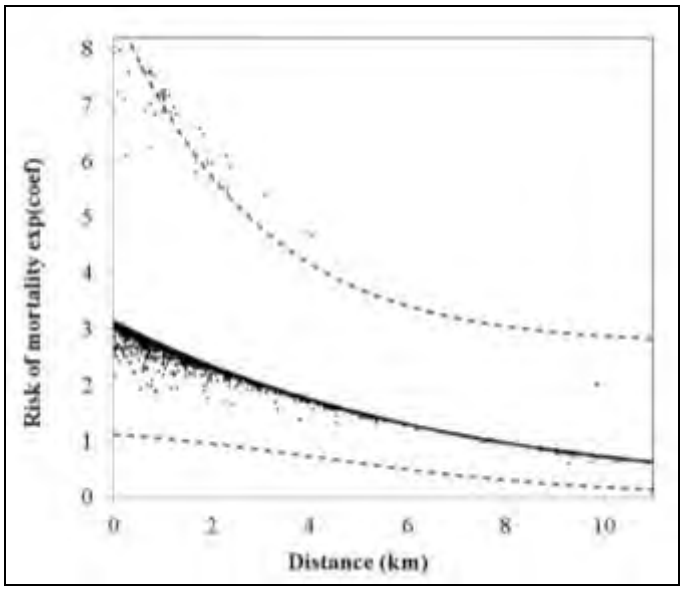



Figure 6-1. Predicted effect with 95% confidence intervals of distance to forested habitat (deciduous and conifer) on sage-grouse hen survival from the top $AIC_c$ selected Cox proportional hazard model from the anti-predation strategy analysis. Predicted effects displayed as the risk of mortality with the y-axis units plotted as exp(coefficient values). All other parameters were held at the mean value. Partial residuals were overlaid on predicted effect plots as solid points. Data from 427 sage-grouse hens were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011.

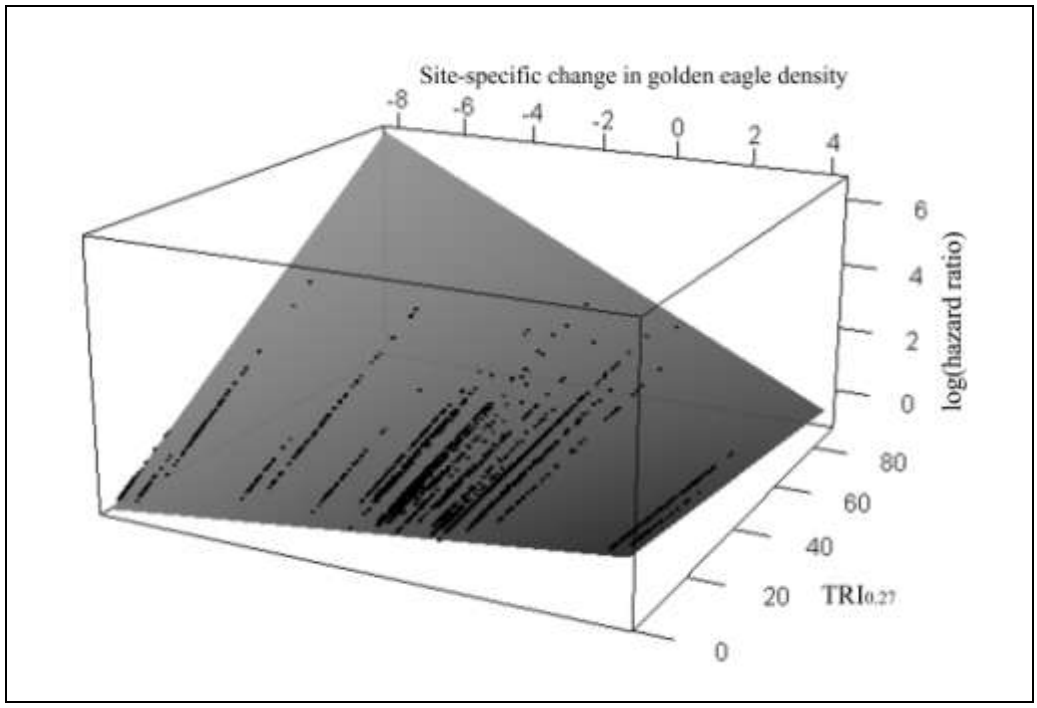



Figure 6-2. Interactive effect of site-specific change in golden eagle density and topographic ruggedness index at 0.27-km radius ($TRI_{0.27}$) on sage-grouse hen survival (as a hazard ratio—depicting risk of mortality) from the parental investment analysis. Predicted effects from the top $AIC_c$ selected Cox proportional hazard model displayed as the risk of mortality with the y-axis units plotted as exp(coefficient values). All other parameters were held at their mean value. Solid points represent observed data overlaid on the predicted surface. Data from 427 sage-grouse hens were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011.

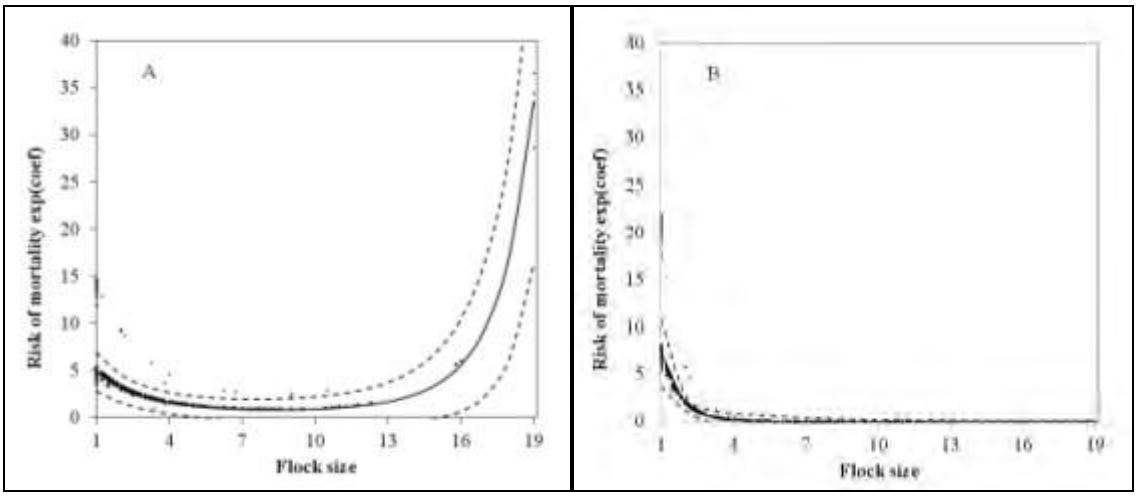



Figure 6-3. Predicted effect of average flock size of sage-grouse hens with 95% confidence intervals from the top $AIC_c$ selected Cox proportional hazard model (from the anti-predation strategy analysis) of sage-grouse hen survival. The model included a quadratic of average flock size and an interaction between flock size and sage-grouse age (adult or yearling). Predicted effects of the average flock size of sage-grouse during the summer for adult (A) and yearling (B) hens. Predicted effects displayed as risk of mortality with the y-axis units plotted as exp(coefficient values). Partial residuals were overlaid on predicted effect plots. Data from 427 sage-grouse hens were collected from eight study sites (each 16-km diameter) and four study sites (each 24-km diameter) in southern Wyoming, USA during 2008–2011.

# CHAPTER 7

# CONCLUSIONS

There has been a large volume of research on the habitat requirements and population demographic rates of greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") throughout its range (see reviews in Connelly et al. 2004, Connelly et al. 2011). However, there has been little research assessing the influence of predator composition on habitat selection, nest success, and hen survival. Increases in avian predator densities are likely to result in higher depredation rates on sage-grouse nests and reduced chick survival (Evans 2004, Cresswell 2008). Predation has been proposed as a potential threat to sage-grouse populations (Braun 1998); however, there are no predators that specialize on sage-grouse during any life history stage (egg, chick, or adult; Connelly et al. 2011). Hagen (2011) suggested that predation is not limiting sage-grouse populations, and management actions designed to alleviate predation, such as predator removal, may only serve to provide a short-term release of predation rates in fragmented habitats and areas with human-subsidized predator populations. Increases in the human footprint have occurred and are likely to continue throughout most of the range of sage-grouse (Leu et al. 2008), which has increased the abundance of generalist predators throughout the western United States (Andrén 1992, Engel and Young 1992, Boarman et al. 1995, Baxter et al. 2007, Sauer et al. 2011).

In Lima's (1998) and Cresswell's (2008) reviews of non-lethal effects of predator-avoidance, they illustrated that presence of a predator had dramatic impacts on

use of habitat by prey species. These effects were found to be as great or greater than the effects of direct predation. Thus, the presence of greater abundances of avian predators may induce changes in sage-grouse behavior associated with habitat usage and affect nest success and hen survival. Sage-grouse reduce time off of their nests when they inhabit areas near high abundances of ravens (Coates and Delehanty 2008); thus, in addition to using indirect mechanisms, sage-grouse may be using avian predator abundance directly to evaluate predation risk while nesting. In Chapter 2, I found that sage-grouse were capable of avoiding areas with relatively higher densities of small, medium, and large avian predators—specifically American kestrels (*Falco sparverius*; hereafter; "kestrels"), black-billed magpies (*Pica hudsonia*; hereafter "magpies"), common ravens (*Corvus corax*; hereafter "ravens"), golden eagles (*Aquila chrysaetos*), *Buteo* hawks, and northern harriers (*Circus cyaneus*; hereafter "harriers")—compared to available sagebrush habitat. My results suggested that sage-grouse avoided avian predators at nest and brood locations on the basis of the size of avian predators rather than individual species identity, equivalence of all species, foraging behavior of predators, or presumed threat to sage-grouse reproductive stage. By selecting habitat with lower densities of avian predators, sage-grouse lower their exposure to avian predation and risk of reproductive failure.

Predation risk trade-offs and non-lethal predator effects, such as avoidance of risky habitats (indirect avoidance) and habitats occupied by greater density of avian predators (direct avoidance; Evans 2004, Verdolin 2006, Cresswell 2008), are mechanisms that explain the differential use of sagebrush habitat (habitat partitioning) by

female sage-grouse. High densities of avian predators and close proximity to anthropogenic and landscape features—specifically oil and gas infrastructure, power lines, major roads, riparian habitat, and rugged topography—are likely to result in reduced adult survival and higher depredation rates on sage-grouse nests (Lima 1998, Evans 2004, Cresswell 2008). I found that sage-grouse hens used direct and indirect mechanisms to lower their exposure to predation and nest depredation particularly from avian predators. Sage-grouse use of habitat was negatively connected to avian predator densities with quality sage-grouse habitat presumably having lower densities of small, medium, and large avian predators. In general, sage-grouse avoided risky habitat by directly avoiding areas with higher densities of small, medium, and large avian predators and indirectly by avoiding areas close to anthropogenic and landscape features (see Chapter 3). Similar to previous research, my analyses confirmed that sage-grouse select locations farther away from anthropogenic and landscape features that could be used as perches or provide subsidized food resources for predators, which included oil and gas structures (Aldridge 2005, Holloran 2005, Walker et al. 2007, Doherty 2008, Holloran et al. 2010, Kirol 2012) and major roads (Holloran 2005, Aldridge and Boyce 2007) at all reproductive stages, power lines (Hanser et al. 2011) at brood locations, and riparian habitat (Doherty et al. 2010, Dzialak et al. 2011) at nest locations. I found that sage-grouse also chose flatter locations at nest-sites similar to the findings of Jensen (2006), Doherty et al. (2010), Dzialak et al. (2011), and Kirol (2012). Thus, human manipulation of habitat that structurally changes habitat and promotes greater density of avian predators may limit sage-grouse populations because habitat that has high-quality cover

and forage may become functionally unavailable to sage-grouse when avian predator densities are at high levels and anthropogenic features are nearby. Habitat partitioning during vulnerable reproductive stages by female sage-grouse relative to predation risk and food availability was a means for sage-grouse hens to lower their risk of predation and nest depredation, while using habitat to meet energetic requirements of hens and chicks.

As sagebrush habitat is developed, raven occupancy and density will increase in areas adjacent to and overlapping with high-quality sage-grouse habitat. The negative effect of ravens on the nest success of grouse has been well documented (Manzer and Hannon 2005, Bui et al. 2010, Coates and Delehanty 2010). For example sharp-tailed grouse (*Tympanuchus phasianellus*) in southern Alberta had 8-times greater nest success in landscapes with <3 corvids/km$^2$ as opposed to landscapes with high densities of corvids (Manzer and Hannon 2005). Around Jackson and Pinedale, Wyoming, Bui et al. (2010) found that higher occupancy rates of ravens were correlated with failed sage-grouse nests. Raven depredation on sage-grouse nests was a common occurrence in northeast Nevada based on infrared video cameras set up at nest sites (Coates et al. 2008), and sage-grouse nest success in northeast Nevada was related to the number of ravens per 10-km transect with nest failure rates increasing 7% with every additional raven/10 km (Coates and Delehanty 2010). My results also indicated that sage-grouse nest success was negatively impacted by the presence of ravens near sage-grouse nests (local scale) and higher raven densities at the study site level (landscape scale; see Chapter 4). This suggests that sage-grouse nesting in areas with subsidized raven populations may have

suppressed nest success, which may contribute to lower sage-grouse population growth rates.

Coates (2007) studied the effect of raven removal on sage-grouse nest success at 4 study areas in Nevada—1 study area with raven removal and 3 study areas without raven removal. Raven abundance was reduced with DRC-1339 treated-egg baits (Coates 2007, Coates et al. 2007). With every 1 km increase in distance away from raven removal routes, Coates (2007) found that sage-grouse nests were 2.1% more likely to fail, and ravens were 13% more likely to be the culprit. This information provided a good indication that reduction of raven abundance by USDA/APHIS/Wildlife Services (WS) may provide a benefit for sage-grouse nesting in areas with subsidized raven populations. My study verified that WS raven management can reduce the abundance of ravens at a relatively large scale (15-km radius or 706.5 $km^2$), and sage-grouse nest success was correlated with reduced densities of ravens on the landscape (see Chapter 4).

The management of ravens may be a potential mitigating strategy for areas of low sage-grouse nest success. In some areas, reductions in raven density at a landscape level may increase the amount of functional habitat for sage-grouse. Coates (2007), Bui et al. (2010), and Hagen (2011) suggested that predator removal may provide a short-term release in predation rates within fragmented habitats and areas with subsidized predator populations. However, Hagen (2011) indicated that predator removal will not mitigate sage-grouse population declines throughout the range of sage-grouse. I agree that the positive effects of raven removal for sage-grouse nest success are likely short-lived gains.

In Chapter 4, I monitored WS raven management as it applied to livestock

depredation; thus, targeted raven management to benefit sage-grouse may produce better results. However, identification of areas where sage-grouse may benefit from raven removal and implementation of a raven removal program targeted at benefitting sage-grouse will not be an easy task. Management of both breeding and transient ravens will be necessary, which will present many challenges. Predator removal may have a place in sage-grouse management when sage-grouse populations are subjected to high densities of ravens as an interim mitigation measure. However, low reproductive rates may persist in many areas due to compensatory predation by other predators (Coates 2007, Bui et al. 2010). Long-term solutions to reduce human-subsidized raven populations are necessary to address the growing raven and sage-grouse conflict. Reducing raven abundance may be possible through non-lethal means, such as reducing availability of supplemental food (road-kill, dead livestock, and garbage) and nesting and perching structures (oil and gas structures, power lines, telephone poles, communication towers, etc.; Jiménez and Conover 2001). More research needs to be focused on understanding raven population dynamics in sagebrush ecosystems, and how to reduce the utility of anthropogenic subsidies (food and nesting structure) for ravens.

In Chapter 5, I tested the hypothesis that the negative effects of corvids would be amplified in areas closer to potential perches and areas with subsidized food resources (anthropogenic and landscape features). I also evaluated interactive effects between corvid densities and microhabitat. Even though I found a negative effect of the abundance of ravens (nest-site or study-site scale), my results did not suggest any amplifying effect of corvid (raven or magpie) abundance with proximity to any anthropogenic or landscape

feature variable. I did not find any evidence that magpies had a negative impact on sage-grouse nest success regardless of the proximity to anthropogenic and landscape features or microhabitat. Similar to Aldridge and Boyce (2007) and Kirol (2012), I did not find any significant correlations between nest success and proximity to anthropogenic development, and there was no evidence of interactive effects between anthropogenic features and corvid densities. Although the landscape features that I assessed represented riskier habitat, I found that nest success was positively correlated with relatively rugged habitat. Rugged terrain, nest-level raven occupancy, and site-level raven density had complex effects on nest success, which has been illustrated as an important factor affecting sage-grouse population growth (Johnson and Braun 1999, Taylor et al. 2012).

Recent research has indicated that sage-grouse hen survival may be the most important demographic parameter driving sage-grouse productivity (Johnson and Braun 1999, Taylor et al. 2012). Effects of anthropogenic and landscape features on survival of sage-grouse hens have not been evaluated in the context of predator communities. In addition, management agencies would benefit from more information on the effects of parental investment and anti-predation strategies on sage-grouse survival, which has not been the focus of sage-grouse research and conservation. Raptors have been identified as significant threats to sage-grouse survival, including golden eagles, *Buteo* hawks, and harriers (Schroeder et al. 1999, Schroeder and Baydack 2001, Danvir 2002). I found that sage-grouse summer survival was negatively correlated with landscape features that represented riskier habitat, especially risk of predation from raptors (see Chapter 6).

Breeding season survival of sage-grouse was negatively impacted by proximity to trees (deciduous and coniferous), more rugged terrain, and golden eagle density when terrain was less rugged. Kirol (2012) also found that terrain roughness was negatively correlated with sage-grouse summer survival in Wyoming. I found lower sage-grouse survival when sage-grouse were exposed to a high density of golden eagles while simultaneously taking topographic ruggedness into account (Chapter 6). I found that the negative effect of topographic ruggedness and golden eagle density was dampened by the combination of greater rugged terrain and high density of golden eagles. Two potential explanations for this finding include 1) rugged topography may provide some refugia from visual predators (e.g., golden eagles), because topographic features such as slight depressions may decrease the effective distance that a raptor can detect a sage-grouse on the ground; and 2) greater density of golden eagles in rugged topography (risky habitat) may competitively exclude other predators. Golden eagles and coyotes are the top predators in sagebrush ecosystems (Mezquida et al. 2006, Hagen 2011), and presence of golden eagles may partially reduce the hunting efficiency of mammalian predators. Thus, landscape features in conjunction with golden eagle density and sage-grouse behavior had dynamic effects on survival. My research also indicated that proximity to anthropogenic features had no effect on sage-grouse survival, and there was no evidence of an interactive effect between anthropogenic features and raptor densities. My sage-grouse survival results also suggest that survival was greater for hens without nests or broods, hens that stayed in intermediate size flocks, and yearling hens.

Many authors have suggested that ground-nesting bird survival, including sage-

grouse, is connected to quantity and quality of habitat, and the presence of adequate sagebrush habitat minimizes predator effects on sage-grouse survival (Connelly et al. 1994, Braun 1998, Aldridge et al. 2008, Connelly et al. 2011). I agree with this, but there needs to be careful consideration of interactive effects of anthropogenic and landscape features and predator community dynamics (risk of predation). The aspects of habitat (anthropogenic and landscape features) that present riskier areas for prey species are confounded by the predator composition that reside in those areas. For this reason, management agencies need to understand how interactions among proximity to anthropogenic and landscape features, microhabitat, and the predator community relate to sage-grouse selection of habitat and demographic rates (e.g., nest success and survival). For instance, I found that areas with higher topographic ruggedness had lower sage-grouse survival, which was dampened by high densities of golden eagles. Sage-grouse hens avoided conventional and natural gas wells (Kirol 2012; see also Chapter 3), which placed them in areas with higher topographic ruggedness (natural gas development is typically in flatter areas). However, the overall sage-grouse survival in areas with higher topographic ruggedness was lower. This indicates that changes in sage-grouse selection of habitat in response to anthropogenic features (fragmentation of habitat) can have dynamic consequences for sage-grouse survival, especially when considering differences in predator compositions. Thus, habitat fragmentation of sagebrush habitats has complex effects on sage-grouse use of the landscape, which in turn can have complex impacts on survival. My results highlight the necessity to assess habitat and predator community dynamics concurrently when designing management plans.

**LITERATURE CITED**

Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation, University of Alberta, Edmonton, Alberta, Canada.

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

Aldridge, C. L., S. E. Nielson, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range wide patterns of greater sage-grouse persistence. Diversity and Distributions 14:983–994.

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794–804.

Baxter, R. J., K. D. Bunnell, J. T. Flinders, and D. L. Mitchell. 2007. Impacts of predation on greater sage-grouse in Strawberry Valley, Utah. Transactions of the North American Wildlife and Natural Resources Conference 72:258–269.

Boarman, W. I., R. J. Camp, M. Hagan, and W. Deal. 1995. Raven abundance at anthropogenic resources in the western Mojave Desert, California. Report to Edwards Air Force Base, California. National Biological Service, Riverside, California, USA.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife

Agencies 78:139–156.

Bui, T. D., J. M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. Condor 112:65−78.

Coates, P. S. 2007. Greater sage-grouse (*Centrocercus urophasianus*) nest predation and incubation behavior. Dissertation, Idaho State University, Pocatello, USA.

Coates, P. S., J. W. Connelly, and D. J. Delehanty. 2008. Predators of greater sage-grouse nests identified by video monitoring. Journal of Field Ornithology 79:421−428.

Coates, P. S., and D. J. Delehanty. 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. Condor 110:627−638.

Coates, P. S., and D. J. Delehanty. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. Journal of Wildlife Management. 74:240–248.

Coates, P. S., J. O. Spencer, Jr., and D. J. Delehanty. 2007. Efficacy of CPTH-treated egg baits for removing ravens. Human-Wildlife Conflicts 1:224–234.

Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53–67 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of

Fish and Wildlife Agencies. Unpublished Report, Cheyenne, Wyoming, USA.

Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage grouse ecology. Idaho Department of Fish and Game Job Completion Report W-160-R-19, Boise, USA.

Cresswell, W. 2008. Non-lethal effects of predation in birds. Ibis 150:3−17.

Danvir, R. E. 2002. Sage grouse ecology and management in northern Utah sagebrush-steppe. Deseret Land and Livestock Wildlife Research Report, Deseret Land and Livestock Ranch and the Utah Foundation for Quality Resource Management, Woodruff, Utah, USA.

Doherty, K. E. 2008. Sage-grouse and energy development integrating science with conservation planning to reduce impacts. Dissertation, University of Montana, Missoula, Montana, USA.

Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, J. P. Mudd, J. B. Winstead, and L. D. Hayden-Wing. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. PloS One 6:1–18.

Engel, K. A., and L. S. Young. 1992. Daily and seasonal activity patterns of common ravens in southwestern Idaho. Wilson Bulletin 104:462–471.

Evans, K. L. 2004. A review of the potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.

Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effects. Pages 95–100 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, University of California Press, Berkeley, USA.

Hanser, S. E., M. Leu, S. T. Knick, and C. L. Aldridge. 2011. Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, Kansas, USA.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, Wyoming, USA.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Jensen, B. M. 2006. Migration, transition range and landscape use by greater sage-grouse (*Centrocercus urophasianus*). Thesis, University of Wyoming, Laramie, USA.

Jiménez, J. E., and M. R. Conover. 2001. Ecological approaches to reduce predation on ground-nesting gamebirds and their nests. Wildlife Society Bulletin 29:62–69.

Johnson, K. H., and C. E. Braun. 1999. Viability and conservation of an exploited sage-grouse population. Conservation Biology 13:77–84.

Kirol, C. P. 2012. Quantifying habitat importance for greater sage-grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. Thesis, University of Wyoming, Laramie, USA.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the West: a large scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. BioScience 48:25–34.

Manzer, D. L., and S. J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. Journal of Wildlife Management 69:110–123.

Mezquida, E. T., S. J. Slater, and C. W. Benkman. 2006. Sage-grouse and indirect interactions: potential implication of coyote control on sage-grouse populations. Condor 108:747–759.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski Jr., and W. A. Link. 2011. The North American breeding bird survey, results and analysis 1966–2010. Version 12.07.2011. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schroeder, M. A., and R. K. Baydack. 2001. Predation and the management of prairie grouse. Wildlife Society Bulletin 29:24–32.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Birds of North America. Philadelphia, Pennsylvania, USA.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife

Management 76:336−347.

Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457–464.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

# MOSQUITO POPULATIONS IN THE POWDER RIVER BASIN, WYOMING: A COMPARISON OF NATURAL, AGRICULTURAL AND EFFLUENT COAL BED NATURAL GAS AQUATIC HABITATS

By

Melissa Kuckler Doherty

A thesis submitted in partial fulfillment
of the requirements of the degree

of

Master of Science

in

Entomology

MONTANA STATE UNIVERSITY
Bozeman, Montana

November 2007

© COPYRIGHT

by

Melissa Kuckler Doherty

2007

All rights reserved

APPROVAL

of a thesis submitted by

Melissa Kuckler Doherty

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style and consistency and is ready for submission to the Division of Graduate Education.

Dr. Greg Johnson

Approved for the Department of Animal and Range Science

Dr. Bret Olson

Approved for the Division of Graduate Education

Dr. Carl Fox

## STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a master's degree at Montana State University, I agree that the Library shall make it available to borrowers under rules of the Library.

If I have indicated my intentions to copyright this thesis by including a copyright notice page, copying is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U. S. Copyright Law. Requests for permission for extended quotation from or reproduction of this thesis in whole or in parts may be granted only by the copyright owner.

Melissa Kuckler Doherty
November 2007

# ACKNOWLEDGEMENTS

I would like to thank the following faculty for their advice, guidance and input throughout the process of this research project. Dr. Greg Johnson and ARS ABADRL for their help, guidance and patience throughout the research process. My committee members, Dr. Kevin O'Neill, Dr. David Weaver, and Dr. Billie Kearns for their input and advice on research designs, analysis and writing. Dr. David Naugle for his experience and input in regards to resource management and wildlife management applications. And finally, the faculty of the Montana State University entomology group for their dedication and hard work put into the class work and seminars of the entomology graduate program.

I would also like to thank all the private landowners of the Powder River basin. Private landowners including Don and Kathy Spellman, the Odegard family, the Lutterman family, the Hepp family and Sparo Zezas made this project possible, not only with their enormous generosity for land-use permission, but their un-paralleled knowledge of the landscape. Without them this project wouldn't have happened (and I would have spent several nights in the truck due to flat tires or unexpected mud puddles).

Finally, I would like to thank my family and friends who faithfully supported me throughout my masters program especially my husband, Kevin Doherty, who always had time to help and listen, even as he pursues his own graduate degree. I would also like to thank my fellow students in the MSU Entomology program as well as the University of Montana Wildlife Department for their support throughout my research program.

TABLE OF CONTENTS

1. REVIEW OF RELAVENT LITERATURE ..... 1

Introduction ..... 1
West Nile Virus ..... 4
Historical Distribution ..... 4
North American Distribution ..... 5
Northeastern Wyoming Distribution ..... 7
Wildlife Susceptibility to West Nile Virus ..... 8
Clinical Symptoms in Wildlife ..... 8
Avian Susceptibility ..... 9
Mammal Susceptibility ..... 11
West Nile Virus Implication for Wildlife ..... 12
West Nile Virus Vector Biology ..... 13
Larval Distribution ..... 15
Adult Dispersal Patterns ..... 17
Species Specific Biology ..... 20
*Culex tarsalis* ..... 19
*Aedes vexans*. ..... 23
*Aedes dorsalis* ..... 24
*Aedes melanimon* ..... 25
Mosquito Control Strategies ..... 26

2. ADULT MOSQUITO ABUNDANCE AND WEST NILE VIRUS INFECTION RATES IN NATURAL, AGRICULTURAL AND COALBED NATURAL GAS PONDS ..... 31

Introduction ..... 31
Materials and Methods ..... 33
Field Methods ..... 33
Experimental Design ..... 33
Study Sites ..... 35
Sagebrush Steppe under CBNG Development ..... 35
Sagebrush Steppe with limited CBNG development: CX Ranch ..... 36
Sagebrush Steppe with limited CBNG Development: Padlock Ranch ..... 37
Irrigated Agricultural Water Sources ..... 37
Mature Coal Bed Natural Gas Ponds ..... 38
New Coal Bed Natural Gas Ponds ..... 38
Laboratory Methods ..... 39
Statistical Methods ..... 40
Results ..... 42
2004 Mosquito Collections ..... 42

TABLE OF CONTENTS-CONTINUED

2005 Mosquito Collections ..... 50
Mosquito Infection Rates ..... 55
Weather Data ..... 58
Discussion ..... 58

3.COMPARITIVE LARVAL MOSQUITO ABUNDANCE IN NATURAL, AGRICULTURAL AND COAL BED NATURAL GAS PONDS ..... 62

Introduction ..... 62
Materials and Methods ..... 64
Study Sites ..... 64
Field Methods ..... 65
Laboratory Methods ..... 66
Statistical Methods ..... 66
Results ..... 68
Mosquito Populations ..... 68
Larval Use of Vegetative Cover Types ..... 74
Weather Data ..... 75
Discussion ..... 75
Management Recommendations ..... 81

REFERENCES CITED ..... 85

# LIST OF TABLES

Table Page

1. 2002 and 2003 West Nile virus infections in Wyoming by County. .....32

2. Mean counts of 4 species of adult mosquitoes by week in the Powder River Basin of Montana and Wyoming 2004. .....48

3. Mean counts of adults of 4 species of mosquitoes by week in the Powder River basin of Montana and Wyoming 2005. .....51

4. Mosquito infection rates for *Culex tarsalis* collected in the Powder River basin, Wyoming in 2004 and 2005. .....56

5. Average monthly temperature and rainfall data for Sheridan, WY, May - August 2004 and 2005.....57

6. Weekly larval mosquito mean counts per dip (SE) by study area for the four most abundant larval species collected, Powder River basin Wyoming, 2005.....73

# LIST OF FIGURES

Figure Page

1. Study site locations for adult mosquito trapping in 2004 and 2005 within the Powder River basin of Wyoming and Montana.....2

2. Percent composition of adult mosquito species collected by CDC black light traps, Powder River Basin, Wyoming 2004 and 2005.....43

3. Average mosquitoes collected per trap night by study area with standard errors, Powder River Basin, Wyoming 2004. .....44

4. Means and standard errors for *Culex tarsalis* per trap night by study site in the Powder River basin, Wyoming, 2004 and 2005.....46

5. Means and standard errors by study area for the four most abundant mosquito species collected in the Powder River basin, Wyoming, 2004. .....47

6. Means and standard errors by study area for the four most abundant mosquito species collect in the Powder River basin, Wyoming, 2005.....52

7. *Culex tarsalis* mean catch counts over time by study area, Powder River basin, Wyoming, 2005. .....53

8. Mosquito larvae collected by taxon in the Powder River basin, Wyoming, 2005.....70

9. Mean larval abundance (SE bars) of *Culex tarsalis* per dip from 5 aquatic habitats types in the Powder River basin, Wyoming, 2005.....71

10. Timing of larval abundance for four species of mosquitoes in the Powder River basin, WY, 13 May – 24 August, 2005. .....72

11. *Culex tarsalis* abundance over time by aquatic habitat in the Powder River basin, Wyoming, 2005. .....76

12. *Culex tarsalis* production by local habitat plant type across the Powder River basin, Wyoming for the week of 4 August 2005 (Julian date 216).....77

13. *Culex tarsalis* abundance by local habitat cover type across the Powder River basin, Wyoming for the week of 4 August 2005. .....78

# ABSTRACT

Coal bed natural gas development in northeastern Wyoming has increased surface water in ranching and agricultural areas over undeveloped land. This increase of water increases larval habitat for mosquitoes, potentially increasing adult populations of West Nile virus vector mosquitoes. I compared adult and larval mosquito populations in four different habitat types in the Powder River basin including agricultural, natural, CBNG and upland sagebrush steppe.

Adult mosquitoes were sampled weekly (2004) or bi-weekly (2005) using CDC miniature black-light traps baited with dry ice. A fixed-effect mixed model indicated that in a normal rainfall year (2005) mature CBNG ponds had the highest adult mosquito populations of all sites sampled, and the highest population of the WNV vector *Culex tarsalis*. In a drought year (2004) where total rainfall from May – August was 59% of the seasonal average, agricultural areas had the highest mosquito abundance, likely due to increased irrigation. Adult *Culex tarsalis* tested positive for WNV across the PRB in 2004 and 2005, with highest minimum infection rates in those areas with large *Culex tarsalis* populations.

Larval mosquitoes were sampled bi-weekly from 13 May - 24 August 2005, using a 350 ml dipper in a 20 point vegetated transect along the pond perimeter. Pond vegetation characteristics were recorded between 3 and 17 August including vegetation density, type and class. Larval *Culex tarsalis* were the most abundant mosquito in the region, representing 47.7% of the total sampled population. A fixed-effects mixed model found *Culex tarsalis* produced at similar rates in natural, new, old and outlet CBNG sources; irrigated agriculture produced significantly less ($P \leq 0.02$) *Culex tarsalis* in 2005. New and old CBNG ponds and outlets also produced *Culex tarsalis* over a longer period of time than natural or irrigated agricultural sites.

This study indicates that CBNG ponds are significantly increasing the overall population of vector mosquitoes in the PRB, as well as adding to the duration of larval habitats that would normally be ephemeral. Thus CBNG ponds and associated habitats enhance mosquito abundance and may serve to increase pathogen transmission in an otherwise arid ecosystem.

# CHAPTER 1

# REVIEW OF RELAVENT LITERATURE

## Introduction

The Powder River basin (PRB) includes the Powder River and its tributaries in northeast Wyoming and southeastern Montana. This area reaches east from Gillette, Wyoming, west to the Bighorn Mountains, and north to Miles City, Montana (Environmental Protection Agency 2006) (Figure 1). The PRB is in a semi-arid habitat dominated by sagebrush grassland primarily used for grazing and wildlife management. The dominant shrubs in this system are Wyoming big sagebrush, *Artemisia tridentata wyomingensis* Beetle and Young, and silver sagebrush, *Artemisia cana* Pursh. Smaller patches of native short grass prairie, conifer forest, greasewoods, riparian woodlands and non-native grasses are common throughout the region (Hemstrom et al. 2002; Walker et al. 2004).

Historically, the major industries in the Powder River basin include cattle ranching and coal mining. The latter has now expanded to include coal bed natural gas (CBNG) production (formerly termed coal bed methane). This process extracts natural gas from sub-surface coal seams. Fifteen surface coal mines are located around Gillette, Wyoming, and several large sub-surface coal seams extend west from Gillette toward the Bighorn Mountains (Vicklund 2000). These coal seams contain large amounts of natural

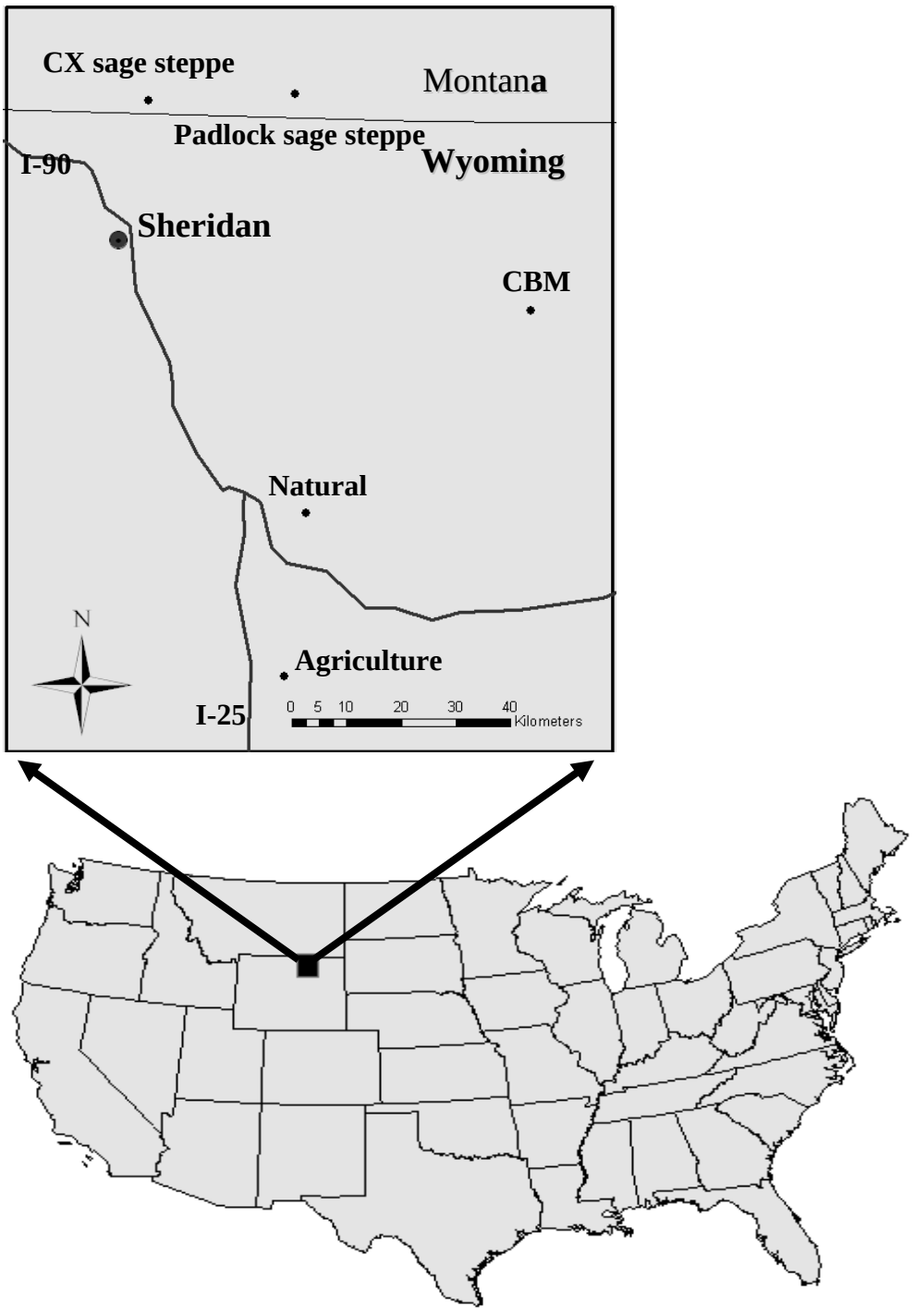



Figure 1. Study site locations for adult mosquito trapping in 2004 and 2005 within the Powder River basin of Wyoming and Montana.

gas (61 Tcf: trillion cubic feet ≈ 1.83 x $10^{12}$ cubic meters), which is currently being extracted for commercial use by the natural gas industry at the rate of ≈ 2.33 x $10^{7}$ $m^{3}$ per day (DOE 2002). Methane extraction includes the removal of groundwater from a coal seam to allow confined natural gas to flow in sub-surface voids. The effluent water is discharged into existing stock ponds, newly constructed ponds, or surface drainages that do not continue in to larger water bodies (Clark et al. 2001). Since 1999, an estimated 19,000 CBNG well heads have been constructed in the PRB, with 20,000 more projected in the next ten years, each of which will produce an estimated 400 barrels of discharge water per pond per day (DOE 2002; USGS 2000). A recent GIS study on mosquito habitat in the PRB indicates that CBNG development has increased potential mosquito larval habitat by 75.2% from 1999 to 2004 (Zou et al. 2006). This corresponds with a recent land-use change study in the same region that indicates a 9-fold increase in surface water in ranching areas, and a 2-fold increase in surface water in agricultural zones (Naugle et al. unpublished data).

Concerns have been expressed by the public as well as local natural resource agencies regarding the environmental impacts of CBNG, including surface disturbances from roads, wells, power lines and ponds; dewatering of local aquifers, and methane discharge water quality (Regele and Stark 2000). While these ponds do provide water to native wildlife and habitat for migratory duck species, CBNG ponds have the potential to produce mosquitoes that could transmit pathogens such as West Nile virus (WNV). An increase in mosquitoes and pathogen transmission in the PRB could pose a health risk to human, livestock and native wildlife in the region. The research project reported here

was initiated to monitor WNV in 2003 after the first sage-grouse was detected with WNV in Northeastern Wyoming. My objectives were to assess adult and larval mosquito population trends as well as the impacts of CBNG development on mosquito populations in areas of sage-grouse use in the PRB.

## West Nile Virus

### Historical Distribution

West Nile virus is an encephalitic virus and a member of the Japanese encephalitis group in the genus *Flavivirus*, family Flaviviridae. WNV is closely related to both eastern equine encephalitis (EEE) and Saint Louis encephalitis (SLE), which are endemic to North America. West Nile virus was first isolated from a febrile woman near the Nile River in Uganda in 1937, and has since caused large human epidemics in Africa, Europe and Asia (Smithburn et al. 1940; Baqar et al. 1993). Human outbreaks of WNV have been documented in southern France in 1962, southern Russia in 1963, Belarus in 1977, the Ukraine in 1985, Romania in 1996, the Czech Republic in 1997 and again in Russia in 1999 (Hubalek and Halouzka 1999). These outbreaks have been geographically associated with wetlands and flooding from heavy rains and are more likely to occur in the summers of warm, wet years.

Eurasian and African outbreaks of WNV have been closely associated with ornithophilic mosquitoes. The virus has been isolated from 43 Old World species of mosquitoes in the genera *Culex* and *Aedes* including the trans-Atlantic species *Culex pipiens* L. and *Aedes aegypti* L. (Hubalek and Halouzka 1999). The primary Old World

vectors of WNV include *Culex univittatus* Theobald in Africa, *Culex modestus* Kamimura and Wada and *Culex pipiens* in Europe, and *Culex quinquefasciatus* Say in Asia (Hayes 2005). Further research has shown that WNV is enzootic in wild birds migrating between Africa and Asia, and these animals are considered the primary vertebrate hosts for this disease in the Old World (Hayes 1989). Mammals, reptiles and amphibians do not play a large role in maintaining transmission cycles in natural populaions in the Old World; although, horses, lemurs and frogs have been shown to obtain transmissible infection rates in the laboratory (Rodhain et al. 1985).

North American Distribution

West Nile virus was first detected in the Western Hemisphere in New York City in the summer of 1999. That year, there were 62 human infections in the New York City area, and 7 deaths. Since its introduction to North America, WNV has spread westward across the United States, as well as into Canada, Mexico and parts of the Caribbean (Rochrig et al. 2002).

It is not known how WNV was introduced into the U.S. in the initial 1999 outbreak of WNV in New York City. Speculations regarding WNV transmission to New York include movement of infected mosquitoes via air transportation, illegal importation of exotic birds, lost migrant birds and possible terrorist acts. Biologists confirmed mortalities due to WNV infections in 18 species of native and non-native birds in 1999 including more than 3,000 American crows (*Corvus brachyrhynchos* Brehn). It had been anticipated that, among birds, corvids would be most vulnerable to the virus, as they were highly susceptible to WNV infection via mosquito bites, and had mortality rates >40%

once infected (Hayes 2005; Steele et al. 2000). Since 1999 WNV has spread at a rate of approximately 67 km per month throughout the spring and summer, and now has been found in 284 species of birds in North American (Rappole and Hubalek 2003; CDC 2006). The rapid spread of WNV and its annual reoccurrence in native biota indicates that it will likely remain an enzootic disease in North America.

As of the October 2007, there had been 24,447 human cases of WNV in the United States, with 920 fatalities (CDC 2007). Of the 4,146 reported human WNV cases in the U.S., 71% were neuroinvasive, 28% were uncomplicated West Nile fever, and 6.8% were fatal (O'Leary et al. 2004). The median age for fatal cases in the U.S. is 77.5 years, with the fatality-to-case ratio increasing significantly with age. The risk of WNV is also significantly higher in males among middle aged (>40 years) and elderly individuals, with the fatality-to-case ratio 1.3 times higher for men > 70 years old (O'Leary et al. 2004).

There are several methods used by monitoring agencies in the United States for detecting WNV in the environment. These methods include 1) pooling collected adult mosquitoes for virus detection, 2) collecting dead birds for virus detection, 3) drawing and testing of sentinel chicken blood for antibodies indicating exposure to WNV, and 4) testing non-human mammal serum for WNV antibodies (primarily equine) (Morris et al. 1994). Data collected in 2002 using these methods indicated that 72% of primary detections were from virus-infected dead birds, 18% were from non-human mammals, 6% were from infected mosquitoes, and 2% were from sentinel birds (O'Leary et al. 2004). While it seems that dead bird surveillance is the most effective monitoring

technique for WNV surveillance, it is more effective in densely populated areas where dead birds are noticed and reported to the proper authorities. In rural areas, methods such as mosquito monitoring and use of sentinel chickens are the most effective methods for disease monitoring. Dead bird surveillance may become a less effective form of virus monitoring in the future if native bird species acquire immunity to WNV through repeated exposures.

Northeastern Wyoming Distribution

West Nile virus was first documented in Wyoming on 18 August 2002 in a horse in Goshen County, three years after WNV was found in New York. This case, along with reports of two infected humans and 95 other horse cases were reported in the fall of 2002 (Wyoming Department of Health 2006). In 2003 a major outbreak of WNV occurred throughout the western United States including Wyoming, Montana and Colorado. In 2003 Wyoming had a total of 393 human and 230 horse cases, with 10 human fatalities (Table 1).

On 24 July 2003 WNV was detected in a radio-collared greater sage-grouse, *Centrocercus urophasianus urophasianus* Aldrich, hen on the Montana/ Wyoming border. That summer 18 sage-grouse died from WNV among radio-marked individuals in four populations in the western US and southern Canada, creating a 25% average decline in survival for this time period (Naugle et al. 2004). Late-summer survival of sage-grouse in the northern PRB was markedly lower at 1 site with confirmed WNV mortalities (20% survival) than at 2 sites without (76% survival) (Walker et al. 2004). Moreover, declines in male and female lek attendance at the WNV site in spring 2004

indicated that outbreaks have threatened local populations with extirpation (Walker et al. 2004). In 2004 WNV spread to sage grouse populations in Colorado and California, and female survival in late summer was 10% lower at 4 sites with confirmed WNV mortalities (86% survival) than at 8 sites without WNV (96%). West Nile virus mortality decreased to 2% during the cool summer of 2005 (mean temperature = 19ºC), increased again in 2006 when hot temperatures (mean temperature = 22ºC) returned in 2006 (D. Naugle, University of Montana, unpublished data).

## Wildlife Susceptibility to West Nile Virus

Historically, the impact of emerging diseases on wildlife populations has not been given much notice by the general public. However, attention has been elevated around WNV outbreaks in wildlife populations because of its potential threat to human health. While we do not know how WNV spread into the Western Hemisphere, we know that wildlife disease emergences historically are amplified by changes in host pathogens or the environment (Daszak et al. 2000). Often these changes introduce pathogens to naïve hosts who have no natural resistance. In the case of WNV, almost all of our North American wildlife fauna was naïve to infection, and it is unknown which species will acquire resistance through immune response (i.e., antibody production); which will become amplifying hosts to the pathogen; and which will remain susceptible.

### Clinical Symptoms in Wildlife

West Nile virus is an encephalitic pathogen that affects the brain and neural tissues, causing bleeding, fever, and cell death in infected animals. In general, birds are

more susceptible to this virus than other groups of animals. Clinical signs of this disease in birds include weight loss, head tremors, blindness, ataxia, weakness in the legs, and seizures. Birds that survive a WNV infection may have neural damage as well as damage to the pancreas, kidney, and heart (Steele et al. 2000). Detection of WNV in avian carcasses can be done through necropsies of natal bird organ tissues or oral and cloacal swabs, followed by vero cell plaque assays and confirmatory RT-PCR assays to detect WNV (Komar et al. 2002). WNV has also been found in ovarian and testicular tissues in birds, suggesting that infected adults may be able to pass an infection to their offspring, or so-called vertical transmission (Komar et al. 2003).

Avian Susceptibility

While many different species of birds have been found to be infected with WNV, only those that have high viremias can be considered amplifying hosts. Certain birds are the only known amplifying hosts for this pathogen in the Western Hemisphere. In order for a feeding mosquito to become infected, a bird must have a viremic titer of at least $10^{7.1}$ plague forming units (PFU/ml) (Komar et al. 2003). Birds that have been challenged with WNV in the laboratory, and have reached sufficient titers to serve as an amplifying host include those of the orders Passeriformes (perching birds), Charadriiformes (wading shore birds), Strigiformes (owls), and Falconiformes (diurnal birds of prey) (Molaei et al. 2006). Birds able to sustain high viremic levels have a high susceptibility to the disease. Mean infectiousness was ranked for reservoir competence by Komar et al. (2003). The blue jay (*Cyanocitta cristata* L.), the common grackle (*Quiscalus quiscula* L.), the house finch (*Carpodacus mexicanus* Muller) and the

American crow were the top four species of 25 tested as competent reservoirs for WNV in southern California. Of these birds, blue jays and American crows transmitted the virus between infected animals and non-exposed cage mates through fecal and salivary secretions with a cage transmission rate of 1.0 (on a 0 – 1 scale) for both species (Komar et al. 2003). This may have contributed to the high infection rate and mortality seen in the field, because both of these species of birds have social or semi-social behaviors. Young, altricial birds may also be more exposed to mosquito feeding due to incomplete feather covering and immobility. Colonial species, such as the American white pelican *Pelecanus erythrorhynchos* L., may occupy habitats near mosquito production areas, which increases exposure to juvenile birds, and may concentrate the mosquito-avian amplification cycle in some areas (Rocke et al. 2005).

Sage-grouse infected with WNV show symptoms similar to other avian groups. Radio-marked grouse rarely move more than a few meters during the two days before death, and have a weak flight when flushed (Walker et al. 2004). Intact sage-grouse that died from WNV were often found facedown in good condition with no external signs of trauma. Infected grouse may also be at elevated risks of predation, potentially contributing to a reduced survival rate in 2004 and 2005. A total of 363 sera samples were taken from wild grouse across Wyoming, Montana and Alberta; in 2004 and none tested positive for WNV antibodies, indicating that these birds had not yet developed an immune response to this pathogen (Naugle et al. 2005).

Mammal Susceptibility

Equines, as well as several other domestic animals have exhibited WNV symptoms. These symptoms include symmetrical or asymmetrical ataxia, staggering, stumbling, toe dragging, leaning, and wide-based stance (McLean et al. 2002). The strain of WNV that occurs in North America is particularly virulent in horses, causing a clinical infection rate of 42% in seropositive animals and a death rate of 36% in those animals with clinical symptoms (Bunning et al. 2002). A vaccine is available to protect equines from WNV, and its use has greatly reduced the WNV morbidity and mortality. Other mammals that have been experimentally tested for WNV infections include dogs, cats, cattle, sheep, chickens, turkeys, domestic geese, pigs, and goats. None of these animals, including horses, has been found to carry a virus titer high enough for them to serve as amplifying hosts for the New York strain of WNV (Bunning et al. 2002; Austgen et al. 2004; McLean et al. 2002). Many of these animals, including house pets such as dogs and cats, have been found to develop antibodies to this disease, and occasionally mild symptoms such as lethargy and a loss of appetite occur. These symptoms are not debilitating and may go unnoticed (Austgen et al. 2004).

Most wild mammals in the New World appear to be resistant to WNV. Some species including several lagomorphs carry high viremias without showing clinical symptoms, indicating they may serve as reservoir hosts within their range. The majority of those mammals that have been challenged with WNV in the laboratory do not get viremias higher than $10^{7.1}$ PFU/ml, which is the level required for acquisition of virus by a feeding mosquito (Bunning et al. 2002; Austgen et al. 2004). An exception to this is the

cottontail rabbit (*Sylvilagus floridanus* L.), which carried WNV titers of $\geq 10^{4.3}$ PFU/ml for approximately 2.2 days (Tiawsirisup et al. 2005). Cottontail rabbits do not show clinical signs of infection and are able to infect *Cx. pipiens* and *Cx. salinarius* with minimum estimated infection rates of 11.5/ 1000 ± 5.5 and 20.5/ 1000 ± 6.4% respectively (Tiawsirisup et al. 2005). While little research has been done on their role in WNV amplification in the field, cottontail rabbits, as well as other lagomorphs, are widespread across the Western Hemisphere south of Canada, and may play a role in virus amplification or virus overwintering in some systems.

West Nile Virus Implication for Wildlife

The effects of WNV on wildlife populations are virtually unknown for any species in the Western Hemisphere. However, research is being conducted to determine which species will experience the greatest consequences from this disease (Marra et al. 2004). The sage-grouse and other birds that are already under stresses due to habitat changes from CBNG, may need additional conservation management in areas affected by WNV to sustain current population levels. There is also some indication that scavenger and predatory species may contract WNV from consuming infected prey, and their populations may be at risk in outbreak years (McLean et al. 2002). Domestic cats presented with up to three infected mice contracted WNV from consuming infected carcasses in the laboratory (Austgen et al. 2004), and there have been several incidental cases of predatory birds such as Cooper's hawks (*Accipiter cooperii* Bonaparte) and great horned owls (*Bubo virginianus* Gmelin) succumbing to WNV after consuming infected prey in the wild (McLean et al. 2002). As more research is done on WNV epidemiology

in natural systems, we will be able to build better models to assess risk factors to wildlife populations, and be more equipped to make informed decisions for wildlife management.

West Nile Virus Vector Biology

Since its appearance in the western United States in 2002, WNV has been one of the most important vector-borne diseases in the region. The competency of the local mosquito vector *Cx. tarsalis*, public and equine health risks, and threat to native wildlife populations has generated many research programs to investigate the biology and ecology of mosquitoes and epidemiology of WNV. We now have a basic knowledge of regional vectors and mosquito infection rates in North America, and are continuing to learn about the regional methods of over-wintering and competent reservoir hosts.

The primary mode of transmission for WNV in North America is by the bite of an infected mosquito. In the United States, WNV has been isolated from 60 mosquito species; however, many of these species are not bridge vectors for this pathogen (Turell et al. 2001, Molaei et al. 2006). Mosquitoes that are bridge vectors must feed on both avian and mammalian hosts forming a link between the amplifying and susceptible hosts (Riesen and Reeves 1990). These are the mosquitoes of greatest concern for human health.

The isolation of WNV from a mosquito does not necessarily mean that a mosquito species is capable of transmission. Primary vectors are insects that are (1) physiologically competent to acquire virus from an infected host and transmit to a susceptible host, (2) are frequently infected with a virus in nature, and (3) naturally occur in areas that are foci for virus transmission (Molaei et al 2006). These insects must feed

on both avian and mammalian hosts, and disseminate virus through the midgut in order to transmit virus through the salivary gland. Vector mosquitoes spread WNV between amplifying hosts, thus amplifying the virus in the ecosystem.

In North America, there are fewer than 10 species of mosquitoes that are considered bridge vectors for WNV (Turell et al. 2001). *Culex pipiens* is considered a moderately efficient vector of WNV, and is the primary vector of WNV in the northeast and midwest along with *Culex restuans* and *Culex salinarius* Coquillett (Nasci et al. 2001, Molaei et al. 2006). *Culex pipiens* has the highest percentage of reported positive pools in the United States, 57% in 2001 and 47% in 2002. Outbreaks of Saint Louis encephalitis have been reported in humans with minimum infection rates of 3 per thousand, indicating that this species of mosquito has the ability to spread encephalitic viruses at low infection rates (Nasci et al. 2001). After 2002, infection rates have dropped yet this species remains in the top three for percentage of total positive pools in the U. S. (Hayes 2005).

In the southeastern United States, the southern house mosquito, *Cx. quinquefasciatus*, is a bridge vector of WNV with 51.4% of total positive mosquito pools from the U.S. in 2004 (Hayes 2005). While this species was considered a low to moderate vector of WNV in a laboratory study, its abundance and preference to feed on both birds and mammals make it a competent vector for WNV in the southern U. S. (Turell 2005). *Culex quinquefasciatus* has also been found to undergo non-viremic transmission between infected and non-infected mosquitoes feeding simultaneously on naïve mice, with infection rates as high as 5.8% (Higgs et al. 2005). No detectable

viremia was found in the host mice after feeding, and transmission was thought to be through high virus titers secreted in mosquito saliva while feeding at high densities. This phenomenon has not been described in the field or in other vector species of mosquitoes in North America. Non-viremic transmission may however explain high WNV infection rates within the *Cx. quinquefasciatus* geographical range, as the mosquito infection rate could increase much faster if mosquitoes are able to obtain WNV infections by feeding adjacent to an infected mosquito rather than having to obtain an infected bloodmeal from a viremic host.

Other species of mosquitoes that may be important vectors of WNV in the United States include *Culex restuans* Theobald, *Culex nigripalpus* Theobald and *Culex salinarius* Coquillett (Turell 2005). These species are all found in the eastern United States, and have been found to be competent WNV vectors under laboratory conditions.

The most common mosquitoes in the PRB of Wyoming and Montana include the floodwater mosquitoes *Aedes vexans* Meigen, *Aedes melanimon* Dyar, and *Aedes dorsalis* Meigan, and *Cx. tarsalis*, a species which colonizes newly-created surface pools. Each of these species has a unique life history as both immature and adults which allow them to survive in this region. I will first discuss basic mosquito biology, and then describe species-specific characteristics.

Larval Distribution

Immature mosquitoes pass through four larval stages in aquatic habitats before pupating and emerging as adult mosquitoes. Each species of mosquito has different habitat requirements for optimal development ranging from flooded grasses to stagnant

wastewater treatment plants. Within a given body of water, microhabitats may exist that support different species of mosquitoes. A study in Iowa found that temporary pools supported *Cx. tarsalis*, *Cx. pipiens* and *Ae. vexans*, while intermittently flooded vegetation areas around the perimeter of their study site included species such as *Anopheles punctipennis* Say, *Culiseta inornata* Williston and *Cx. pipiens* (Mercer et al. 2005). Of the total larval mosquito population within their study areas, 65.7% of mosquitoes were found in temporary pools with intermittently flooded and permanently flooded areas providing habitat for the remaining 34.3%. Open-water habitats contained no mosquito larvae in this study, and generally provide habitat for very few mosquitoes in wetland areas (Thullen et al. 2002). Factors such as vegetation density, dissolved nitrogen content, organic matter, and phosphate availability contribute to the productivity of a wetland for mosquito development, and the availability of these resources in any given microhabitat may be the determining factor on the species that will live in that habitat (Lawler and Dritz 2005; Jiannino and Walton 2004).

Laboratory results show that mortality among larvae at densities greater than 500 per mosquito rearing pan was increased by 60% in *Cx. tarsalis*, *Cx. restuans* and *Cs. inornata* (Buth et al. 1990). A shorter development time due to warmer water temperatures reduced mortality under laboratory conditions, but was not seen in the field, likely due to fluctuating ambient temperatures. *Culex tarsalis* and *Cs. inornata* occurring concurrently under natural conditions can have higher densities than single species populations, indicating that these two species may fill different niches within the same aquatic environment (Fanara and Mulla 1974).

Adult Dispersal Patterns

Distribution of adult mosquitoes after eclosion vary both among species and environmental conditions. Mosquito flights have been classified as migratory, appetential and consummatory, and commence for one of five reasons: (1) resting sites, (2) carbohydrate sources, (3) blood meals, (4) ovipositional sites, or (5) mates (Bidlingmayer 1985, Service 1997). Migratory flights have been observed in *Cx. tarsalis* in southern California in pre-diapausal insects including unidirectional flights of up to 17.7 km (Bailey et al. 1965). This type of dispersal may be common in the Powder River basin where overwintering habitat is sparse. Appetential flights are upwind searching flights for olfactory host clues, mates or carbohydrate sources (Bidlingmayer 1985). Once a food source or mate is detected, consummatory flight begins in which a food source is sought and consumed. In cases where food sources are sparse, adult mosquitoes may fly several kilometers in the appentential flight mode, often moving long distances from their original larval habitat. Cases have been observed where high larval densities have also increased dispersal distances by newly emerged adults spiraling several meters upwards in an attempt to catch wind currents (Bailey et al. 1965). In any case, once a mate and or blood meal is found, appentential flight mode begins again in search of a suitable oviposition site based on a species individual needs.

One of the main reasons that *Cx. tarsalis* is such an efficient vector of WNV in the western United States is that it feeds on both birds and mammals. A study conducted in central California indicates 97.2% of all blood-fed mosquitoes in the spring fed on host birds, whereas between May and October, 58.5% of blood meals were from avian hosts,

and 41.4% were from mammals (Tempelis and Washino 1967). This shift in feeding habits is most likely due to avoidance behavior by avian host species or the relatively high availability of mammalian over avian hosts in late summer when altricial nestling birds have fledged (Kilpatrick et al. 2006). A shift in feeding hosts may contribute to the spread of WNV among mammals (Kilpatrick et al. 2006).

After a female mosquito takes an infected blood meal, a specific amount of time called the extrinsic incubation period (EIP) is required before that insect is capable of transmitting the virus. The EIP is dependent on the species of vector mosquito, virus replication rate and ambient weather temperatures. The movement of adult mosquitoes to cool, shaded resting places during the day, and subsequent host-seeking behaviors at night allows them to maintain themselves in a thermal environment with lower temperature variation than in the surrounding habitat (Meyer et al. 1990). This may reduce the EIP in insects that occupy environments with a wide range of maximum and minimum temperatures. *Culex tarsalis* in southern California had an estimated EIP of 5-7 days at 28ºC, which would allow for virus transmission within 1 – 2 gonotrophic cycles (Riesen et al. 2006). Reisen indicates that virus activities in the western United States were closely linked to above-average temperatures in 2004 and 2005, where EIP's were likely reduced to a point where transmission could occur after two gonotrophic cycles and viremic mosquitoes were more prevalent in the environment.

Information regarding EIP and temperature relationships has been used to create a predictive model for WNV outbreaks based on degree-day accumulations over time. In a hot year (2003), this model predicted the WNV cases in Wyoming with a 91.3% total

accuracy, and was 65.2% accurate in 2004, which was relatively cool and dry (Zou et al. In press). Predictive modeling such as the proceeding degree-day model may be useful in the future to forecast WNV outbreak in high risk areas along with proper surveillance.

Mosquitoes have several different survival strategies for overwintering in cool climates. Some species over-winter as adults in diapause, others lay eggs that remain viable over the winter, and several species survive the winter as larvae (Clements 1992). Mosquitoes that over-winter as adults have a higher rate of survival if they enter diapause directly, rather than taking a blood meal first. Female mosquitoes are stimulated to enter diapause by short day lengths and low water temperatures as early instar larvae (Tauber and Tauber 1976). As these mosquitoes prepare for dormancy the development of the primary ovarian follicles stops and production of trypsin and chymotrypsin-like proteases that are used for digesting bloodmeals are reduced (Tauber and Tauber 1976; Robich and Denlinger 2005). These females switch from blood meals to sugar gluttony shortly before entering diapause as a way to increase hypertrophy of the fat bodies before winter (Robich and Denlinger 2005). The only exception to this is when females take a blood meal and develops fat body rather than eggs, a process called gonotrophic disassociation. This is the only known way that an adult mosquito can over-winter WNV without undergoing vertical transmission of the disease (Turell et al. 2002).

## Species Specific Biology

*Culex tarsalis.* *Culex tarsalis* is a widely distributed mosquito species preferring rural areas west of the Mississippi River from Canada into Mexico. This species is a

highly efficient vector of WNV, and it has remained one of the top four species of mosquitoes in the United States for total positive pools since WNV spread west of the Mississippi River in 2002 (Hayes 2005, Turell 2005). This species of mosquito has been widely studied throughout its range because of its ability to transmit pathogens such as WNV, St. Louis encephalitis, and western equine encephalitis between birds and mammals. *Culex tarsalis* was the only species of mosquito collected in abundance in the PRB that regularly takes both avian and mammalian blood meals, and thus it has the most veterinary and medical importance.

*Culex tarsalis* populations have been reported to have high numbers of host-seeking females in August and September in northern climates, as their populations build though the summer from over-wintered females (Knight et al. 2003). *Culex tarsalis* emerges from diapause during the spring, seeks a bloodmeal and completes a gonotrophic cycle. Adults mate in large swarms at dusk, with males copulating each evening, and most females mating 1-2 days post emergence (Riesen et al. 2002). Females lay eggs on the surface of freshwater pools in rafts of 100 eggs or more, seeking out suitable ovipositional habitats by using non-volatile chemical cues (Isoe et al. 1995). Some of the ovipositional cues that female *Cx. tarsalis* use include flooded and decomposing grasses, cattle manure and aquatic bacterial composition. *Culex tarsalis* larvae have been observed at highest densities in vegetation cover dominated by cattails (*Typhia* spp.) root masses and high stem density (Walton et al. 1990). The eggs that are laid are not drought resistant and will hatch several days after being deposited depending on environmental conditions. (Clements 1992)

Larvae of *Cx. tarsalis* are found in newly flooded habitats, and are often the first species of mosquito to colonize a water source (Fanara and Mulla 1974). Flooded areas with high percentages of plant cover, like saltgrass, have the highest larval populations of *Cx. tarsalis* in California, and this affinity for colonizing freshly flooded grasslands probably is true for this species throughout its range (De Szalay and Resh 2000). The two factors that were found to be most significant in predicting larval abundance of this mosquito in California include maximum water temperature and pond age with newly flooded habitats as the most productive. In this system, duck ponds are flooded annually to provide waterfowl with winter habitat, and gravid *Cx. tarsalis* females are the first mosquito species to utilize this resource. This behavior may be initiated to avoid predators who take 3-4 weeks to reach abundance levels that have a significant effect on larval mosquito populations (Walton et al. 1990). The range of temperatures that are optimal for larval *Cx. tarsalis* development in the laboratory is between 10°C and 37°C, with a mean of 32°C (Fanara and Mulla 1974). The development time for *Cx. tarsalis* larvae under natural conditions ranges from 19.8 to 25.3 days in Southern Manitoba, and may be shorter in warmer climates (Buth et al. 1990).

Adult females are opportunistic feeders, taking bloodmeals from either birds or mammals (Gunstream et al. 1971). *Culex tarsalis* are crepuscular/ night feeders, and spend most of their days resting under vegetation (Turell et al. 2005). The highest activity levels of host seeking females occurs between 10 PM and 1 AM (Bast 1961; Knight et al. 2003; Riesen et al. 1997). In the spring and early summer, females preferentially seek avian blood meals, many of which are from nestlings (Blackmore and

Dow 1958). Catches of host-seeking *Cx. tarsalis* are found at highest densities in traps surrounded by elevated vegetation, and lowest over tree snags, open water, sandbars and in urban areas. In areas of southern California surrounding the Salton sea, proportions of blood meals taken from avian hosts were directly related to the density of host seeking females. Abundances of host seeking females may preferentially feed on young altricial birds in the nest, which have few defensive behaviors. These birds however quickly mature and develop defensive behaviors to reduce insect feeding (Lothrop and Riesen 2001; Bast 1961). This leads to a change in feeding behavior by *Cx. tarsalis* from birds to mammals in the late summer and fall (Gunstream et al. 1971). Those insects that have been infected with WNV in the early summer may transmit the virus to humans and horses by this shift in feeding.

Laboratory studies indicate that 74-100 of *Cx. tarsalis* become infected with WNV after taking blood meals with $10^{7.1}$ PFU/ml, which is a common virus titer in many North American birds (Goddard et al. 2002). These infected mosquitoes have an estimated WNV transmission rate of 81 and 91% after ingesting blood-meals containing $10^{6.5}$ and $10^{7.3}$ PFU/ml respectively (Turell et al. 2002b). A female *Cx. tarsalis* requires 35-40 days between egg cycles, and in northern climates they average 2.6-2.9 generations per season (Buth et al. 1990). This requires female mosquitoes to acquire an infected blood meal in her first gonotrophic cycle, survive at least 35 days, and then probe a susceptible host such as a human, horse or sage-grouse to transmit virus.

*Culex tarsalis* must either be re-infected with WNV each spring while taking a bloodmeal, undergo diapause as an infected adult or vertically transmit virus from gravid

female to egg. Laboratory studies have shown vertical transmission from infected females to $F_1$ progeny with a minimum mosquito infection rate of 6.9 per thousand; however, this mechanism was not seen in all *Cx. tarsalis* samples tested, and may change between local populations (Goddard et al. 2003). This overwintering mechanism is most likely coupled with others such as reservoir hosts and infectious migratory birds, with variations in composition between regions.

*Culex tarsalis* is the primary vector for several encephalitic diseases including western equine encephalitis, Saint Louis encephalitis in the western United States, and West Nile virus (Knight et al. 2003). These pathogens are amplified in the enzootic cycle between birds and mosquitoes, most likely among passeriform birds. Encephalitic diseases can affect humans and domestic mammals; however, they are dead end hosts to the pathogen, not developing high enough viremias to infect subsequent feeding mosquitoes.

*Aedes vexans*. *Aedes vexans* is a floodwater mosquito commonly found around flood irrigation systems and spring snowmelt locations across North America (Knight et al. 2003). This species of mosquito is a crepuscular/ night feeder that prefers to take blood meals on large mammals such as cattle and white-tailed deer, and is rarely collected with evidence of an avian blood meal (Gunstream et al. 1971; Turell 2005). Females of this species lay individual eggs in moist soils subject to flooding. Floodwater mosquitoes, such as *Ae. vexans*, have desiccation-proof egg shells that allow an embryo to survive long periods in a dry environment. Eggs with this adaptation can remain viable for several years and will be stimulated to hatch when the right environmental and

physical conditions such as flooding and snowmelt occur (Clements 1992). These eggs must undergo a period of desiccation prior to inundation in a low oxygen environment as well as exposure to cold to stimulate hatching (Bates 1970).

Laboratory and field-testing indicate the *Ae. vexans* is not a primary vector of WNV in North America although studies indicate that they do transmit the pathogen at low rates (Turell et al, 2001). *Aedes vexans* is not an ornithophagic mosquito, and thus is unlikely to obtain WNV from a viremic bird. Laboratory testing has shown that even after being orally challenged with an infected blood meal, these insects were refractory to infection with dissemination rates of 8%. Of those insects where virus passes through the midgut, 100% were able to transmit virus to a new host, and would be a potential vector in the field (Turell et al. 2001). *Aedes vexans* can transmit western equine encephalitis virus in the western United States. These cases are also incidental as WEE is amplified by avian hosts in the same manner as WNV except when secondary amplification cycles occur involving small mammals such as hares (*Lepus americanus* Erxleben*),* and ground squirrels (*Spermophilus richardsoni* Elegans*)* (Knight et al. 2003).

*Aedes dorsalis.* *Aedes dorsalis* is a floodwater mosquito that is often attracted to ephemeral areas with high salt contents for oviposition (Knight et al. 2003). This species of mosquito is found as adults throughout the summer in the western and northeastern United States and southern Canada (Darcie and Ward 1981). *Aedes dorsalis* requires habitat that is relatively wet, and is common in areas flooded by snowmelt and irrigation events in dryer climates. Host-seeking females are considered opportunistic blood feeders, and take a majority of their blood meals from large mammals. They prefer to

feed at night, but they will feed during the day if a suitable host enters their resting area (Turell et al. 2005).

*Aedes dorsalis* is not considered a primary vector of WNV in North America but is involved in WEE transmission in some parts of their range (Gunstream et al. 1971; Turell et al. 2005). Research in California indicates that *Ae. dorsalis* as well as *Ae. melanimon* and *Ae. campestris* can perpetuate a secondary transmission cycle of WEE among mammals, especially lagomorphs (Riesen et al. 1998). Larvae of *Aedes dorsalis* have tested positive for WEE in the lab at low rates, indicating vertical transmission which would allow for virus overwintering.

*Aedes melanimon*. *Aedes melanimon* is a floodwater mosquito found across the western United States and southwestern Canada (Darsie and Ward 1981). This species lays eggs in areas of flooded vegetation with gonotrophic cycle, varying from 4 to 5 days (Jensen and Washino 1991). Female *Ae. melanimon* feed on mammals including cattle and humans, seeking hosts at dusk. This species of mosquito has high adult survivorship and abundance across the summer, along with a short gonotrophic cycle length all of which contribute to the increased probability of obtaining and disseminating a pathogen by an individual vector (Goddard et al. 2002).

The CDC considered *Ae. melanimon* a competent vector for WNV in the United States although it is not considered a primary vector (CDC 2006; Goddard et al. 2002). *Aedes melanimon* has been implicated as a secondary vector of WEE in parts of California because of its contribution to the amplification and transmission of a secondary virus cycle in cottontail rabbits (*Sylvilagus floridanus*) in WEE outbreak years

(Jensen and Washino 1991). The primary vector for WEE in the western U. S. is *Culex tarsalis*, with wild bird populations serving as the basic viral reservoir (CDC 2006). *Culex tarsalis* may also feed on mammalian hosts and transmit WEE, providing an opportunity for *Ae. melanimon* to acquire the WEE pathogen. *Ae. melanimon* that obtain a bloodmeal on WEE infected mammalian hosts can quickly transmit the WEE pathogen through the susceptible host population including horses and humans, thus creating a secondary transmission cycle absent of primary vectors and hosts.

## Mosquito Control Strategies

Tactics used for mosquito control in the United States include chemical, biological and physical control mechanisms. Each of these tactics has positive and negative attributes that should be assessed on a case by case basis before being implemented. These attributes are cost, environmental effects, duration of control, and ease of use.

Biological control includes the introduction and conservation of natural mosquito predators to maintain mosquito populations at a reduced level. This incorperates the introduction of invertebrate and vertebrate predators such as Coleoptera adults and larvae, Odonata adults and larvae as well as several predatory fish species. Invertebrate predators such as naiad Odonata and Notonectidea can significantly reduce larval mosquito populations in habitats that are greater than 1 month old, and become increasingly effective at controlling mosquito populations in mature ponds (Riesen et al. 1989; Walton et al. 1990). *Mesocyclops longisetus* Thiebaud and *Macrocyclops albidus* Jurine have been introduced in Louisiana rice fields, marshes and ditches to effectively control

*Anopheles* spp. and *Culex quinquefasciatus* (Marten et al. 1994). Although these invertebrates may not eliminate mosquito populations, they may be used to suppress populations in small aquatic habitats.

Vegetation management in larval mosquito habitats is also a viable mosquito control strategy in some situations, especially in man-made or intensively managed aquatic habitats. Methods used in vegetation management include burning aboveground plant material, intermittently thinning, deepening of shallow areas to reduce emergent vegetation and turning soils of ephemeral habitats during dry seasons. In general, opening densely vegetated areas reduces mosquito habitat while increasing the habitats of mosquito predators and wildlife species (De Szalay and Resh 2000; Batzer and Resh 1992; Jiannino and Walton 2004). Specifically, if densely vegetated areas are modified to contain small hummocks of emergent vegetation dispersed within deepened open water, mosquito refuge is decreased while predator habitat is increased. This results in adult mosquito emergence 100- and ten-fold lower in hummock and thinned treatments than in densely vegetated control treatments (Thullen et al. 2000). This practice allows for mosquito management while maintaining wildlife habitat without the use of pesticides or labor-intensive annual treatments.

Fish have been used extensively across the United States for mosquito larval control purposes for more than 50 years with varying effects (Walton 2007). The most commonly stocked fish is the mosquitofish (*Gambusia affinis* Baird and Girard and *Gambusia halbrooki* Girard), but there has been some interest in the use of native fishes for mosquito control purposes (Knight et al. 2003). Mosquitofish are effective predators

in man-made environments, however they do not over-winter well in cool climates making them difficult to maintain in some areas (Cech and Linden 1987). Where mosquitofish are stocked they are efficient predators of mosquito larvae in habitats that contain little or no vegetation, however both fry and adults have a higher survival rate in areas with vegetation to act as shelter from predators (Walton 2007). Dense floating vegetation, as well as decaying emergent vegetation provides cover for mosquito larvae, and reduces the efficacy of the mosquitofishes biocontrol abilities (Berkelhamer and Bradley 1989). Other fishes that have been tested for larvivorous activity include the Sacramento blackfish (*Orthodon microlepidotus* Ayres), Pacific blue-eye (*Pseudomugil signifier* Knar), and the killifish (*Rivulus marmoratus* Poey) with varied results (Taylor et al. 1992; Willems et al. 2005). Many of these fishes are effective predators at the juvenile stage, and then move on to larger prey as they grow. These species may be valuable in an integrated pest management program where the juveniles are allowed to control mosquito populations at a given period of their development, and then other control measures are used for the subsequent portion of the mosquito season.

Pesticide use, including adulticides and larvicides, is common in urban areas with high mosquito populations, and has been used as a preventative measure in parts of the PRB. Larvicides are more effective at controlling mosquito populations because larvae are in a confined area compared to widely dispersed like adults. Products such as *Bacillus thuringiensis* var. *israelensis* (Bti) are microbial larvicides that disrupt the insect's digestive system, and provide a 90-100% reduction in *Ae. vexans* and *Culex* spp.(Berry et al. 1987, Russel et al. 2003). Larviciding oils are also used as a larviciding

material, controlling mosquito larvae and pupae by creating a thin film on the water surface that disrupts the insect's ability to obtain atmospheric oxygen through its siphon. Larviciding oils are most effective in habitats with little emergent vegetation and little wind (Lampman et al. 2000). Products such as Golden bear have a $LD_{50}$ activity of 3.6 µl/ 54 $cm^2$ and have an activity time of more than 16 hours in the field (Lampman et al. 2000).

Mosquito adulticides are often distributed as a mist or aerosol, using aerial application, truck foggers, or backpack foggers in areas of high adult mosquito density (CDC 2006). Some products that are commonly used by the mosquito control industry are pyrethrins and 5% malathion (AMCA 2006). These products can be very effective, but require specific environmental conditions for proper use including wind speed, temperature and humidity and do not have long term treatment effects. These conditions often make adulticides less effective than larval treatments, and many mosquito abatement districts choose to use these products as a back-up to larval treatments.

Ponds from coal bed natural gas development in the Powder River basin vary in shape, size, vegetation cover and maturity. Regardless of their individual mosquito production, as a whole they greatly increase the potential for mosquito abundance in this region. Recent research comparing the mosquito abundance of various pond types in Delaware indicate that shallow sided, highly vegetated habitats produce the largest number of mosquito larvae overall (Gingrich et al. 2006). Mosquito abundance in the PRB will most likely be highest in those habitats that remain wet throughout the season, and have a high density of vegetation around the shorelines. Those CBNG ponds that fit

this description may be very productive, while newer ponds may take time to develop these mosquito production characteristics. Finding ways to reduce mosquito production in existing ponds, and modify the design of future ponds to reduce their utility as larval mosquito habitat may greatly decrease the overall mosquito production of the PRB, and reduce the risk of WNV transmission among humans, livestock and wildlife in this region.

# CHAPTER 2

# ADULT MOSQUITO ABUNDANCE AND WEST NILE VIRUS INFECTION RATES IN NATURAL, AGRICULTURAL AND COALBED NATURAL GAS PONDS

## Introduction

West Nile virus was first detected in Wyoming on 18 August 2002, resulting in 96 equine, 2 human and 17 avian cases across the state by the end of the year. An epidemic occurred in 2003, with 393 human cases and 9 fatalities, 230 positive horses, and 182 confirmed bird deaths (Table 1) (Wyoming Department of Health 2006). Of those cases, 23.4% of the human and 19.5% of the equine reports in Wyoming were from Sheridan, Johnson and Campbell counties, all within the geographic boundaries of the Powder River Basin (PRB). The PRB has been under development for coal bed natural gas (CBNG) extraction for the past 16 years, with the majority of development taking place after 1996. This development includes the creation of effluent CBNG ponds. Prior to 2003 no quantitative or qualitative data regarding mosquito production had been collected from these ponds. However there is concern over the potential they may produce putative vectors of WNV and have a negative impact on human, equine, and wildlife health.

The 2003 WNV outbreak included the first reported case of WNV in a greater sage-grouse (*Centrocercus urophasianus*; "sage-grouse") near Spotted Horse,

Table 1. 2002 and 2003 West Nile Virus infections in Wyoming by County. The counties of the Powder River Basin (*italics*) account for 30% of the human WNV cases in Wyoming in 2002, and 70% in 2003 (Wyoming Department of Health 2006).

| County | Human Infections | | Human Deaths | | Horse Infections | | Avian Infections | | Total Infections | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 2002 | 2003 | 2002 | 2003 | 2002 | 2003 | 2002 | 2003 | 2002 | 2003 |
| Albany | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 19 | 0 | 29 |
| Big Horn | 0 | 4 | 0 | 0 | 8 | 22 | 0 | 1 | 8 | 27 |
| ***Campbell*** | ***0*** | ***71*** | ***0*** | ***1*** | ***9*** | ***15*** | ***1*** | ***16*** | ***10*** | ***102*** |
| Carbon | 0 | 1 | 0 | 0 | 2 | 3 | 0 | 2 | 2 | 6 |
| Converse | 0 | 19 | 0 | 0 | 0 | 16 | 0 | 2 | 0 | 37 |
| Crook | 0 | 9 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 11 |
| Fremont | 0 | 24 | 0 | 1 | 4 | 54 | 0 | 7 | 4 | 85 |
| Goshen | 2 | 89 | 0 | 3 | 41 | 3 | 13 | 64 | 56 | 156 |
| Hot Springs | 0 | 4 | 0 | 0 | 0 | 4 | 0 | 1 | 0 | 9 |
| ***Johnson*** | ***0*** | ***8*** | ***0*** | ***0*** | ***1*** | ***13*** | ***2*** | ***2*** | ***3*** | ***23*** |
| Laramie | 0 | 31 | 0 | 1 | 11 | 15 | 0 | 26 | 11 | 72 |
| Lincoln | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Natrona | 0 | 28 | 0 | 0 | 4 | 11 | 0 | 24 | 4 | 63 |
| Niobrara | 0 | 4 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 6 |
| Park | 0 | 6 | 0 | 0 | 4 | 27 | 0 | 6 | 4 | 39 |
| Platte | 0 | 62 | 0 | 2 | 4 | 7 | 1 | 10 | 5 | 79 |
| ***Sheridan*** | ***0*** | ***13*** | ***0*** | ***0*** | ***4*** | ***17*** | ***0*** | ***5*** | ***4*** | ***35*** |
| Sublette | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 3 |
| Sweetwater | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 3 | 0 | 5 |
| Teton | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Uinta | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Washakie | 0 | 2 | 0 | 0 | 0 | 4 | 0 | 1 | 0 | 7 |
| Weston | 0 | 12 | 0 | 1 | 1 | 6 | 0 | 0 | 1 | 18 |
| Total | 2 | 393 | 0 | 9 | 96 | 230 | 17 | 189 | 115 | 812 |

Wyoming, causing a 75% decline in the local radio collared population (Naugle et al. 2004). These mortalities were closely associated with sage-grouse habitats undergoing development for CBNG extraction, including the development of holding ponds for effluent water extracted in the drilling process. This research project was developed to

quantify the differences in mosquito populations when aquatic habitats (e.g., CBNG ponds) are increased on the landscape, and the infection rates of WNV vectors in this region. I hypothesized that the presence of CBNG impoundments in the PRB will be associated with a greater abundance of larval and adult mosquitoes, specifically *Culex tarsalis*.

My primary objective in 2004 was to quantify the adult mosquito populations in five different types of aquatic habitats that were suspected of producing mosquitoes in the PRB, Wyoming. In 2005, I continued to sample adult mosquito populations in four of the 2004 study sites. I also compared larval mosquito production and vegetation habitat characteristics in each of these study sites to test for differences in larval mosquito production in the available aquatic habitats in the PRB (Chapter 3).

## Materials and Methods

### Field Methods

Experimental Design. In 2004 and 2005 adult mosquitoes were collected using battery operated $CO_2$-baited CDC miniature black light traps (John W. Hock Company, Gainsville, FL). Lights were removed from the traps to exclude non-mosquito fauna. Traps with approximately 1 kg dry ice were set out in the evening and programmed to turn on at dusk and operate until collection the next morning. Upon retrieval, adult mosquito samples were transported on wet ice until they could be euthanized with tri-ethylamine and stored at -10°C for later processing (identification and virus assay).

Individual trap sites were randomly selected from aquatic habitats identified using hardcopy USGS EROS data center landsat telocomposit 7,4,3 band combinations (red, green, blue) for each study area. These color bands highlight riparian habitats when viewing satellite imagery maps (Randy McKinley USGS, personal communications). Forty- five trap sites were selected in 2004 between five different study areas in Campbell and Johnson counties, Wyoming. These sites included natural (7 sites), and irrigated agriculture water sources (8 sites), sagebrush steppe (2 study areas, 20 sites) and a combination of mature and new coal bed natural gas ponds (10 traps). Adult mosquitoes were sampled twice weekly from 11 July – 9 September (Julian dates 193 – 253). Some missing samples were due to weather and landowner restrictions.

Adult mosquitoes were sampled from 20 trap locations in 2005 in Campbell and Johnson Counties, Wyoming. The total number of trap sites was reduced in 2005 because sagebrush steppe study areas were omitted to allow time for larval sampling, and adult collections in 2004 were very low. These trap locations were in four different study areas including natural water sources, irrigated agriculture, mature CBNG ponds, and new CBNG ponds. Each site was randomly selected from those sampled in 2004 for a total of 5 ponds per study site. Light traps were placed in habitats between emergent aquatic vegetation and flooded grasses whenever possible based on the vegetation characteristics at each individual pond. When these habitats were not available, light traps were placed within 2 m of the shoreline near shallow water. Light traps were set bi-weekly in each study area from 15 May - 23 August (Julian dates 134 – 246). Larval samples were taken the day adult traps were set.

Study Sites

The research area was split into five blocks in 2004, each representing a unique aquatic habitat in the PRB. These sites included; 1) developed CBNG, 2) irrigated agriculture, 3) undeveloped sagebrush steppe, 4 and 5) (Figure 1). In 2005, I modified the design and selected 1) mature CBNG ponds, 2) new CBNG ponds, 3) irrigated agriculture and 4) sagebrush steppe under CBNG development. These study areas were chosen for their current land use, proximity to radio-collared sage-grouse habitats, landowner cooperation and aquatic habitat resources. A detailed description of each site follows:

Sagebrush Steppe under CBNG Development. Sagebrush steppe under CBNG development (natural water sources) was sampled in 2004 and 2005 and included springs, drying river beds, oxbow lakes, and stock ponds. Qualifying stock ponds were not artificially filled from anthropogenic sources (e.g., CBNG water). These natural ponds were part of the PRB landscape prior to CBNG development in northeastern Wyoming. The ponds used in this block were in a study area located 24 km south of Buffalo, Wyoming off Interstate 90 ( 13T 0390639, 4917115, elevation 1220 m) in land grazed by cattle during the course of the study. Water sources in this area are ephemeral. They are filled with runoff from snowmelt and rain water early in the season and then become dry in mid to late summer. Several small rainstorms occurred throughout the summer, allowing these aquatic habitats to stay wet into August in 2005, but precipitation was insufficient either field season to fill natural depressions to early spring levels.

Aquatic vegetation was sparse around natural water sources in northeastern WY due to the ephemeral nature of natural springs in this dry environment. Average vegetation cover around the natural water sources sampled was 63% (n=5), which included bluebunch wheatgrass (*Pseudoroegneria spicata* Pursh), western wheatgrass (*Agropyron smithii* Rydb), prairie junegrass (*Koeleria macrantha* Ledeb), blue grama (*Bouteloua gracilis* Vasey), Japanese brome (*Bromus japonicus* Thunb.), cheatgrass (*Bromus tectorum* L.), crested wheatgrass (*Agropyron cristatum* L.), sage brush (*Artemisia* spp.) and cattail (*Typha* spp.).

Sagebrush Steppe with Limited CBNG Development: CX Ranch. This site was north of Sheridan, Wyoming on the Montana/ Wyoming border (13T 0348842, 4990002, elevation 1120 m). Upland sagebrush-steppe habitat in the PRB was dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis* Beetle) and intermixed native and non-native grasses such as bluebunch wheatgrass (*Pseudoroegneria spicata* Pursh), western wheatgrass (*Agropyron smithii* Rydb), prairie junegrass (*Koeleria macrantha* Ledeb), blue grama (*Bouteloua gracilis* Vasey), Japanese brome (*Bromus japonicus* Thunb), cheatgrass (*Bromus tectorum* L.) and crested wheatgrass (*A. cristatum* L.). Plains silver sagebrush (*Artemisia cana cana* Pursh) was also present in drainages but at much lower abundance. This sagebrush-steppe habitat has limited CBNG development. The few CBNG ponds that are present are approximately 1 acre in size, shallow, and subject to heavy cattle use. Light traps were set in 2004 near naturally occurring water sources (5 traps), and in upland sage areas (3 traps) where sage-grouse

were radio-tracked in high densities in 2003 and 2004. This area was not sampled in 2005.

Sagebrush Steppe with Limited CBNG Development: Padlock Ranch. This study area is north of Sheridan Wyoming on the Montana/ Wyoming border and east of the CX ranch (13T 0380795, 4984181, elevation 1160 m). No CBNG ponds are currently filled in this area. Naturally occurring water sources include man-made stock ponds, overflowing stock tanks and one naturally occurring ephemeral pool. The sites of proposed CBNG ponds are known in this study area, and several of our 2004 light traps were placed where CBNG ponds will be located once gas extraction starts. This area was not sampled in 2005.

Irrigated Agricultural Water Sources. Agricultural water sources included small ponds and ditches from flood irrigated agricultural such as hay and alfalfa. Study locations were (1) 32 km south of Buffalo, Wyoming on interstate 25 (13T 0361201, 4897075, elevation 1550 m), (2004 and 2005) and (2) 8 km east of Buffalo, Wyoming on Wyoming highway 16 (2005 only). Water sources for flood irrigation included Upper Crazy Woman Creek, and Clear Creek in privately managed fields. In 2004, two flood irrigation events occurred the weeks of May 27$^{th}$ and June 25$^{th}$ (Julian dates 147, 176). In 2005, one flooding event occurred from June 8$^{th}$ – June 10$^{th}$, based on the regular irrigation practices of the landowner (Julian date 159 – 161). After each irrigation event, water persisted in 3 of 5 impoundments throughout the season, while the remaining 2 evaporated within two weeks (personal observational). Aquatic vegetation in agricultural

water sources (n=5) were predominately cattails (*Typha* spp.) with various rushes (*Juncaceae* spp.).

Mature Coal Bed Natural Gas Ponds. Mature coal bed natural gas ponds were located around Spotted Horse Wyoming, on Wyoming highway 16 (13T 0436498, 4948103, elevation 1.23 km). Mature CBNG ponds received effluent CBNG water for ≥ 5 years and vegetation covered more than 50% of the shoreline. Many of these ponds were previously used as livestock watering ponds by private landowners and were excavated and enlarged to accommodate larger water influxes from CBNG development. Effluent water from CBNG development was added to these ponds at various rates, maintaining relatively stable water levels throughout the field season. Vegetation cover ranged from 45.6% to 89% between ponds, including sedges, rushes, forbs and flooded upland grasses, with an average vegetation cover of 54.5%.

New Coal Bed Natural Gas Ponds. New CBNG ponds were also located near Spotted Horse Wyoming, on Wyoming highway 16 (13T 0433045, 4949482, elevation 1.2 km). These ponds received effluent CBNG water for ≤ 5 years and vegetation covered less than 50% of the shoreline. Several of these ponds were also former stock ponds, and were recently excavated for effluent CBNG water storage. Other ponds were constructed specifically for CBNG water use and were occasionally used for livestock watering. Many of these ponds are continuously filled with water from CBNG wells and maintained relatively constant water levels with the exception of one pond (Smith pond) where water level fluctuated several feet over the course of the summer. Average

vegetation cover per sampling point was 21%, and was predominately flooded upland grasses, algae and forbs.

The CX upland sagebrush-steppe and padlock upland sagebrush-steppe study sites were combined to represent one upland sagebrush habitat block in the final statistical analysis after preliminary statistical tests indicated no significant differences between these study sites for variables tested.

Laboratory Methods

Mosquito samples were stored at -10°C and sorted on a laboratory chill table (BioQuip 1431) using a 63–500x stereomicroscope. All mosquito specimens collected in 2004 were identified to genus using the key of Darcie and Ward (1981), with putative WNV vectors in the *Culex* or *Aedes* genera identified to species for Padlock and CX Ranch upland sagebrush-steppe areas by members of USDA ARS Arthropod-Borne Animal Disease Research Laboratory (ABADRL) in Laramie, Wyoming. *Aedes* and *Culex* mosquitoes captured from other study areas in 2004 and all study areas in 2005 were sorted to species.

RNA extractions for WNV were conducted on pools of female mosquitoes in 2004 and 2005 by USDA ARS ABADRL. A maximum of 50 and minimum of 20 specimens were tested per pool with a total of 923 pools in 2004 and 244 in 2005. Those light trap collections that contained < 20 mosquitoes of the same species were pooled with other samples for the same trapping location in a given month. If 20 insects were not collected from a trap site in a month, the pool was run with < 20 specimens, and is later noted as such.

RNA extraction was conducted with the RNeasy 96 kit (Qiagen, Valencia, CA). Samples were ground in liquid nitrogen, mixed with 1 mL buffer RLT and centrifuged at 8000 x *g* for 10 minutes. Half of the supernatant was stored at -80 °C, and the remaining was used in the extraction according to manufacturer's specifications. Approximately 50 µL of eluate was recovered per sample and stored at -20 °C until used in the TaqMan assay. RT-PCR was run (Lanciotti et al. 2000) on the ABI Prism 7000 sequence detection system with TaqMan one step RT-PCR master mix reagents (Applied Biosystems, Foster City, CA, USA). Primer and probe combinations (DNA Technologies Inc., Coralville, IA, USA) were then synthesized (Lanciotti et al. 2000; Lanciotti and Kerst 2001). Positive samples from the WNENV primer/ probe were tested with the WN3'NC primer/ probe set. Pools were considered positive when CT values were <37, and the normalized fluorescent signal (Rn) was 2x greater than the average of eight non-template controls for both primer/ probe sets.

Statistical Methods

Data from the 2004 and 2005 field seasons were analyzed separately due to differences in study designs and data collection protocols. Differences in adult mosquito abundance between habitat types were analyzed in SAS PROC MIXED by species with a generalized mixed effect linear model. In 2004, the sagebrush-steppe study areas were combined to represent one upland sagebrush steppe habitat after an initial PROC MIXED model was run and no significant differences in mosquito populations were found between sampling sites. Because sequential mosquito counts can be serially-correlated and mosquito counts estimated for the same habitat closer in time are more likely to be

correlated than measures more distant in time, I modeled the appropriate covariance structure that best represented the data in SAS PROC MIXED (Littell et al. 1996, 1998). The covariance structure is derived from variances at individual times and correlations between measures at different times on the same habitat (Littell et al. 1998). I used a compound symmetry (CS) error structure where all measures at all times have the same variance and all pairs of measures on the habitat have the same correlation (Littell et al. 1996). SAS PROC MIXED is a generalization of a standard linear model and data are permitted to exhibit correlation and nonconstant variability (SAS 8.2 online doc.). I used the REPEATED statement in PROC MIXED to model the covariation within habitats, which accounts for the violation of independence of the observations on the same pond at different times (Littell et al. 1998). The RANDOM statement was used to model the variation between habitats, which accounts for heterogeneity of variances from individual ponds (Littell et al. 1998). The random effects factor was the sub-sample of ponds within treatment group that were randomly chosen from all available ponds in the study area. In this manner, my results are able be to extrapolated to all ponds in the study area. All other factors in the model were fixed effects. Maximum likelihood methods were then used to fit a mixed-effects (both random and fixed effects) general linear model in SAS PROC MIXED.

Minimum infection rates of mosquito pools were calculated using the Pooled Infection Rate add-in for Microsoft Excel® (Biggerstaff 2006). Infection rates were first calculated for each species, and then re-grouped and analyzed by study area and study site for those species found to have positive pools in a given year.

Weather data were obtained from the United States National Weather Service archival climatological data for Sheridan, Wyoming (National Weather Service 2006). Average monthly temperatures from May-August were recorded, including the departure from normal. Precipitation data were recorded as monthly totals including the departure from normal, as well as the number of days with 0.02, 0.3, 1.3, and 2.5 centimeters or more of rainfall.

## Results

### 2004 Mosquito Collections

A total of 38,543 adult mosquitoes representing 10 taxonomic groups were sorted from 554 trap nights in 2004. *Culex tarsalis* accounted for 37% of the total catches, followed by *Ae. dorsalis* (31.4%), *Ae. vexans* (16.7%), *Ae. melanimon* (10.9%), *Psorophora* spp. (1.6%) and *Ochleratatus* spp, (1.9%). *Cu. inornata*, *Cx. pipiens*, *Culiseta* spp., *Anopheles* spp. each comprised ≤ 1% of the catches (Figure 2).

Total mosquito collections in 2004 varied by site (DF = 3, 587, F = 3.00, $P$ = 0.03), and weeks ($P$ = 0.0001), with highest weekly collections in the months of May and June. Overall, more mosquitoes were collected from irrigated agriculture sites in 2004 than any other study area with an average of 171.6 (SE = 27.0) specimens collected per trap night. CBNG and natural areas averaged 109.0 (SE = 24.4) and 163.1 (SE = 27.2)

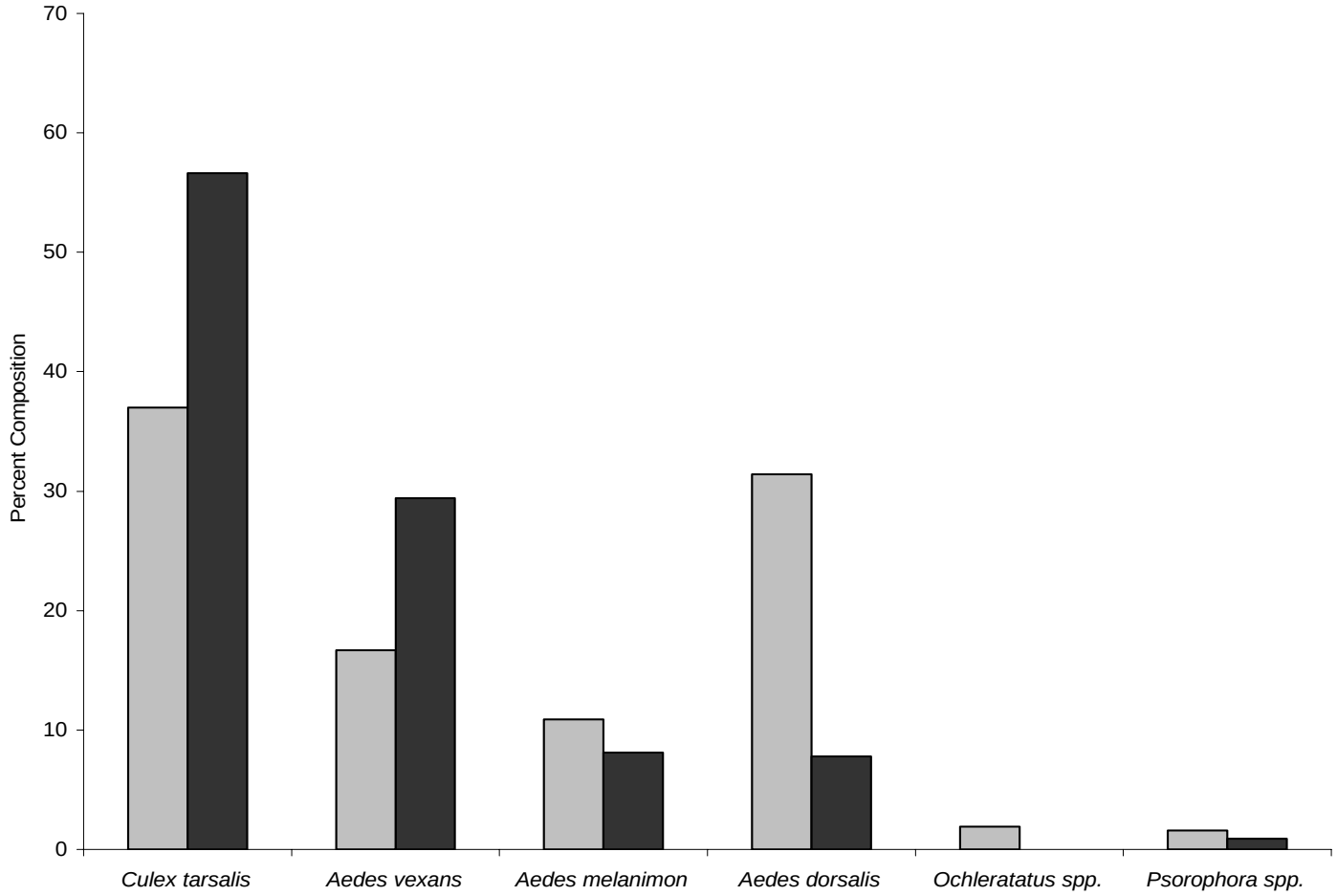





Figure 2. Percent composition of adult mosquito species collected by CDC black light traps, Powder River Basin, Wyoming 2004 and 2005.

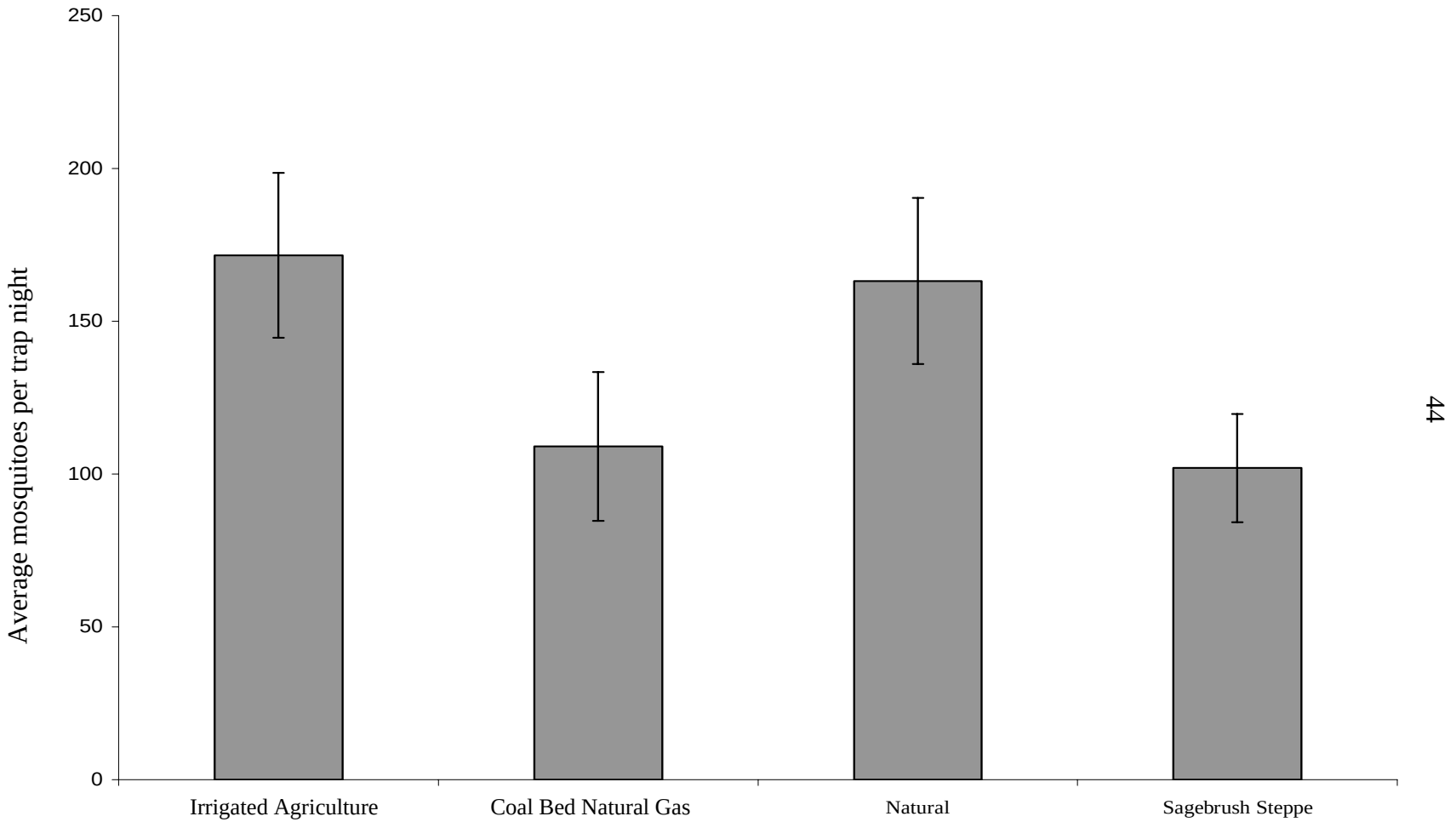





Figure 3. Average mosquitoes collected per trap night by study area with standard errors, Powder River Basin, Wyoming 2004.

mosquitoes per trap night, respectively (Figure 3). Sagebrush-steppe study sites had the lowest average mosquito counts of all study sites, with a mean of 102.0 (SE = 17.7) and were significantly lower than mosquito populations from natural ($P = 0.013$) and irrigated agricultural sites ($P = 0.03$).

*Culex tarsalis* collections in 2004 differed (3, 587 df, F = 10.3, $P < 0.0001$) between the five study areas sampled. They were significantly higher in irrigated agricultural sites than natural or sage-steppe study areas (mean ± SE 44.3 ± 6.9, $P \leq 0.007$) (Figure 4, Figure 5). *Culex tarsalis* populations were the lowest in sagebrush steppe sites (10.1 ± 4.9). Sagebrush steppe populations were significantly lower than all other populations sampled ($P \leq 0.05$), though the presence of adult mosquitoes in this area is perhaps unusual considering that these traps were not near aquatic habitats.

*Culex tarsalis* collections in 2004 varied by week (DF = 8, F = 4.8, $P < 0.0001$). The highest mean estimates for the entire PRB were found at week 7 (Julian date 176) (48.2 ± 6.6, $P = 0.0001$), and the lowest estimate were found at week 12 (Julian date 246) (2.5 ± 8.5, $P = 0.77$). Differences in least square means indicate a significant difference between weeks 4 and 7 ($P = 0.001$), 6 and 7 ($P = 0.006$), and 8 - 12 and 7 ($P \leq 0.01$) (Table 2). No differences were found between other weeks sampled.

*Aedes vexans* was most abundant in irrigated agriculture areas (3, 586 df, F = 10.13, $P < 0.0001$) with significantly higher collections than any other sampled habitat (Figure 5). Mean collection sizes in agricultural areas were 58.1 mosquitoes per trap night (SE = 10.1). There were no significant differences by week found for this species

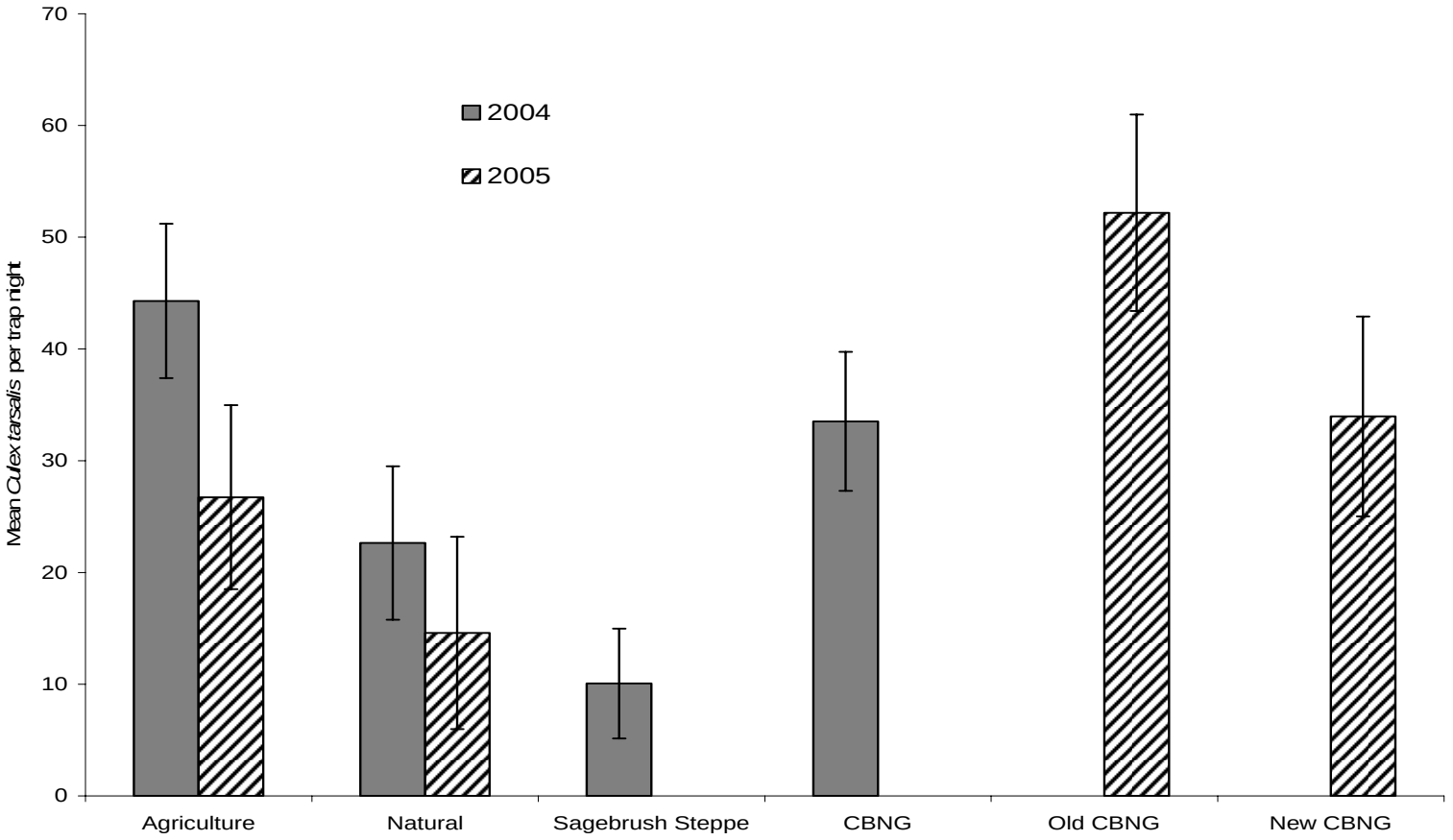



Figure 4. Means and standard errors for *Culex tarsalis* per trap night by study site in the Powder River basin, Wyoming, 2004 and 2005.

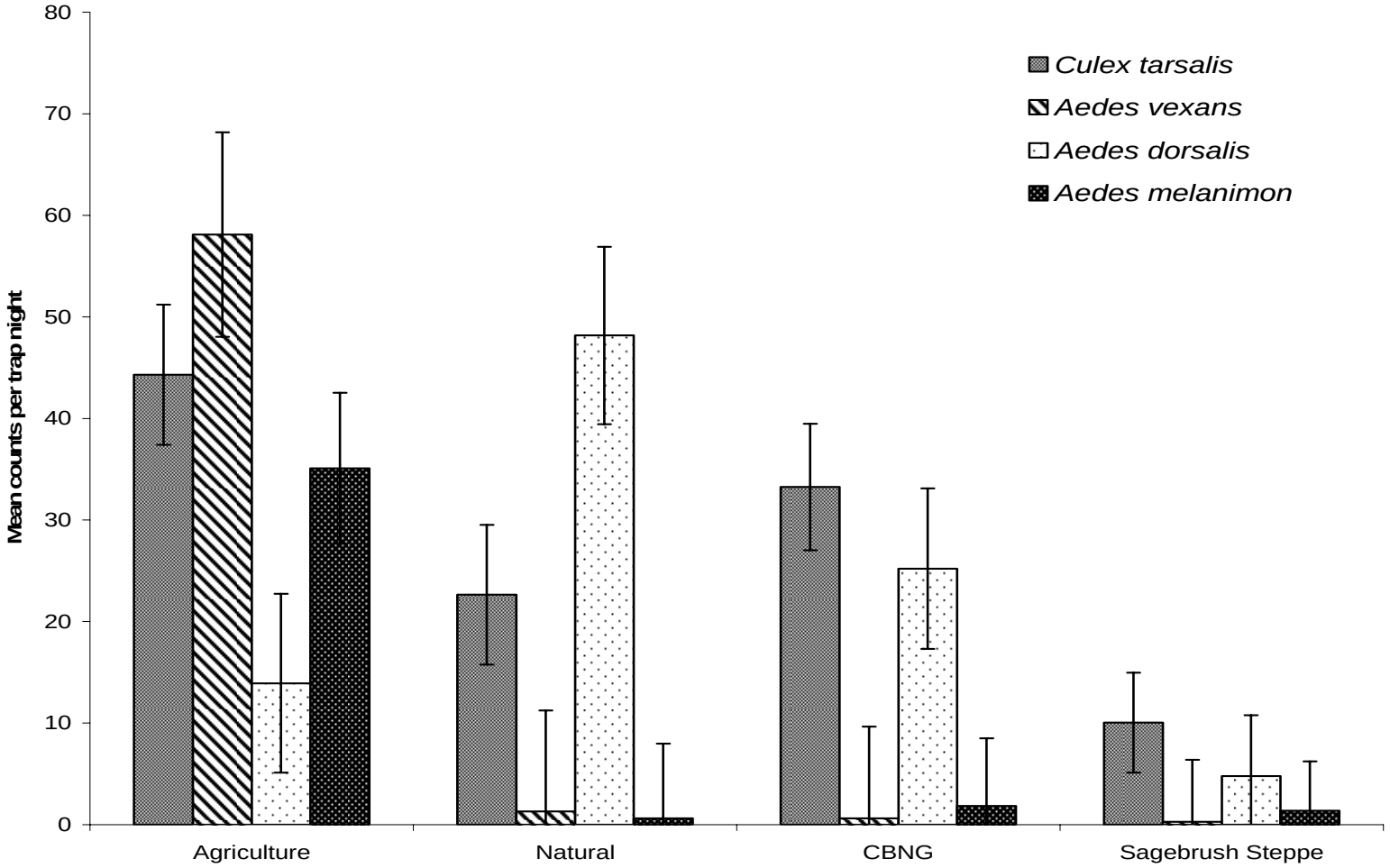



Figure 5. Means and standard errors by study area for the four most abundant mosquito species collected in the Powder River basin, Wyoming, 2004.

Table 2. Mean counts of 4 species of adult mosquitoes by week in the Powder River Basin of Montana and Wyoming 2004.

| | Julian date and week of sampling | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species and habitat type | 134 Week 4 | 148 Week 5 | 162 Week 6 | 176 Week 7 | 190 Week 8 | 204 Week 9 | 218 Week 10 | 232 Week 11 | 246 Week 12 |
| *Culex tarsalis* | | | | | | | | | |
| CBNG | N/A | 5.50 | N/A | 66.50 | 30.30 | 22.38 | 37.81 | 56.25 | 101.69 |
| Agriculture | 0.67 | 1.37 | 13.67 | 35.70 | 54.12 | N/A | 77.90 | 7.70 | 12.10 |
| Natural | 0.75 | 0.50 | 3.50 | 9.00 | 17.07 | 20.86 | 75.21 | 9.71 | 17.50 |
| Sagebrush | 0.00 | 0.34 | 13.25 | 4.11 | 14.22 | 4.68 | 25.25 | 6.99 | 10.35 |
| *Aedes melanimon* | | | | | | | | | |
| CBNG | N/A | 0.00 | N/A | 56.00 | 40.90 | 19.88 | 104.44 | 32.88 | 12.25 |
| Agriculture | 1.22 | 0.00 | 0.00 | 2.10 | 4.06 | N/A | 0.75 | 0.80 | 0.10 |
| Natural | 1.25 | 1.14 | 0.07 | 0.00 | 1.43 | 0.14 | 5.57 | 1.86 | 0.43 |
| Sagebrush | 1.13 | 0.44 | 0.25 | 1.11 | 0.55 | 0.08 | 0.35 | 0.20 | 2.88 |
| *Aedes vexans* | | | | | | | | | |
| CBNG | N/A | 0.00 | N/A | 485.50 | 41.50 | 77.88 | 79.44 | 24.50 | 39.88 |
| Agriculture | 0.00 | 0.00 | 0.00 | 1.50 | 5.35 | N/A | 0.45 | 0.10 | 0.30 |
| Natural | 0.00 | 0.00 | 0.29 | 0.29 | 0.21 | 0.00 | 1.86 | 3.86 | 5.93 |
| Sagebrush | 0.00 | 0.00 | 0.00 | 0.23 | 0.30 | 0.03 | 0.20 | 0.15 | 0.30 |
| *Aedes dorsalis* | | | | | | | | | |
| CBNG | N/A | 0.25 | N/A | 13.25 | 1.10 | 4.88 | 4.25 | 16.88 | 36.19 |
| Agriculture | 1.11 | 10.42 | 37.83 | 47.80 | 92.88 | N/A | 25.15 | 5.45 | 2.15 |
| Natural | 1.25 | 0.14 | 18.64 | 5.71 | 10.29 | 3.29 | 183.86 | 28.14 | 92.29 |
| Sagebrush | 39.50 | 1.10 | 0.25 | 4.40 | 4.58 | 0.50 | 0.90 | 1.90 | 15.40 |

of mosquito across the PRB ($P = 0.48$), likely due to low *Ae. vexans* collections in CBNG, sagebrush steppe and natural areas (Table 2).

Abundance of *Ae. dorsalis* was significantly higher in natural aquatic habitats ($48.2 \pm 8.7$, $P \leq 0.04$) than any other study area (Figure 5). *Aedes dorsalis* collections indicated no difference between irrigated agriculture and CBNG (3, 587 df, F = 8.59, $P = 0.32$). Sagebrush steppe areas supported the lowest catches of *Ae. dorsalis* ($4.8 \pm 6.0$) which was significantly lower than natural or CBNG sites ($P = 0.03$, $P < 0.0001$) (Table 2). Weekly collections of *Ae. dorsalis* across the PRB were highest in mid-summer ($P = 0.043$) (Julian date 213), with abundances decreasing in late August and September likely due to ephemeral larval habitats in natural areas, decreased photoperiod and cool summer temperatures.

The majority of the *Ae. melanimon* collected in 2004 was found in the agricultural sites, with an average of 33.6 specimens per trap night (SE = 5.79, 3, 587 df, F = 7.08, $P = 0.0001$). All other study sites averaged less than 1.2 specimens per trap night and were not found to be a significant source for this species. No weekly significant differences were found for *Ae. melanimon* in the 2004 field season (Table 2).

*Culex pipiens* was rarely caught in 2004, with no significant difference between study areas, and a maximum average collection of 0.04 in the agricultural study site (SE = 0.02). Other species of mosquitoes captured representing <1% of the total population included *Ae. campestris* Dyar, *Ae. implicatus* Vockeroth, *Ae. trivittatus* Coquillet, *Ae. nigromaculus* Ludlow, *Ae. c. canadensis* Theobald, *Ae. provocans* Walker, *Ae.*

*cataphylla* Dyar, *Ae. idahoensis* Theobald, *Ae. hendersoni* Cockerell, *Cu. inornata* Williston *Culiseta* spp,. and *Anopheles* spp.

2005 Mosquito Collections

Overall, 6,469 adult mosquitoes representing 16 taxonomic groups were sorted and pooled for WNV testing in 2005 from 160 trap nights. From these samples *Cx. tarsalis* was the most abundant mosquito collected, representing 56.6% of the total mosquito population. Other species that were identified include *Ae. vexans* (29.4%), *Ae. melanimon* (8.1%) and *Ae. dorsalis* (7.8%). *Ae. campestris*, *Ae. implicates*, *Anopheles* spp., *Psorophera* spp., *Ae. trivittatus*, *Ae. nigromaculus*, *Ae. c. canadensis*, *Cx. pipiens*, *Ae. provocans*, *Ae. cataphylla*, *Ae. idahoensis*, and *Ae. hendersoni* all comprised ≤ 1% of the total collection in 2005.

Total mosquito populations were significantly different from one another at the $P = 0.10$ level in 2005 (3, 129 df, F = 2.68, $P = 0.049$), with irrigated agriculture areas producing the highest total mosquito counts over the field season (107.6 ± 23.3). These irrigated sites were significantly different from natural ($P = 0.05$) and old CBNG ($P = 0.02$) sites, with most of the specimens in this area identified as *Ae. vexans* followed by *Cx. tarsalis*, *Ae. melanimon* and *Ae. dorsalis* (Figure 6). Significant differences were found between weekly total mosquito production (8, 129 df, F = 3.03, $P = 0.004$), with week 5–7 having higher total mosquito counts than any other week sampled (Julian date 162–178) (Figure 7).

Table 3. Mean counts of adults of 4 species of mosquitoes by week in the Powder River Basin of Montana and Wyoming 2005.

| | Julian date and week of sampling | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species and habitat type | 134 Week 1 | 148 Week 2 | 162 Week 3 | 176 Week 4 | 190 Week 5 | 204 Week 6 | 218 Week 7 | 232 Week 8 | 246 Week 9 |
| *Culex tarsalis* | | | | | | | | | |
| Old CBM | N/A | 0.00 | 0.00 | 5.40 | 66.60 | 103.00 | 121.50 | 55.20 | 54.50 |
| New CBM | N/A | 0.00 | 0.00 | 3.60 | 75.60 | 66.00 | 52.40 | 41.80 | 24.00 |
| Natural | 0.00 | 0.00 | 0.00 | 2.20 | 11.00 | 31.40 | 64.60 | 5.75 | N/A |
| Agriculture | 0.00 | 0.20 | 0.00 | 22.00 | 20.60 | 145.40 | 34.00 | 2.67 | 0.00 |
| *Aedes melanimon* | | | | | | | | | |
| Old CBM | N/A | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| New CBM | N/A | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Natural | 0.00 | 0.00 | 0.00 | 0.60 | 0.20 | 0.00 | 0.00 | 0.25 | N/A |
| Agriculture | 0.00 | 0.00 | 0.00 | 7.00 | 21.00 | 108.60 | 4.00 | 0.00 | 0.00 |
| *Aedes vexans* | | | | | | | | | |
| Old CBM | N/A | 0.00 | 0.00 | 0.00 | 0.80 | 2.40 | 0.67 | 0.60 | 18.00 |
| New CBM | N/A | 0.00 | 0.00 | 3.60 | 75.60 | 66.00 | 52.40 | 41.80 | 24.00 |
| Natural | 0.00 | 0.00 | 0.00 | 2.20 | 11.00 | 31.40 | 64.60 | 5.75 | N/A |
| Agriculture | 0.00 | 0.20 | 0.00 | 22.00 | 20.60 | 145.40 | 34.00 | 2.67 | 0.00 |
| *Aedes dorsalis* | | | | | | | | | |
| Old CBM | N/A | 0.00 | 0.00 | 0.40 | 5.80 | 3.20 | 2.67 | 3.20 | 4.50 |
| New CBM | N/A | 0.00 | 0.00 | 4.60 | 12.20 | 8.60 | 1.20 | 7.60 | 0.00 |
| Natural | 0.00 | 0.40 | 0.00 | 48.00 | 2.60 | 5.80 | 3.20 | 12.00 | N/A |
| Agriculture | 0.00 | 2.20 | 0.00 | 8.00 | 2.40 | 0.00 | 0.40 | 0.50 | 1.00 |

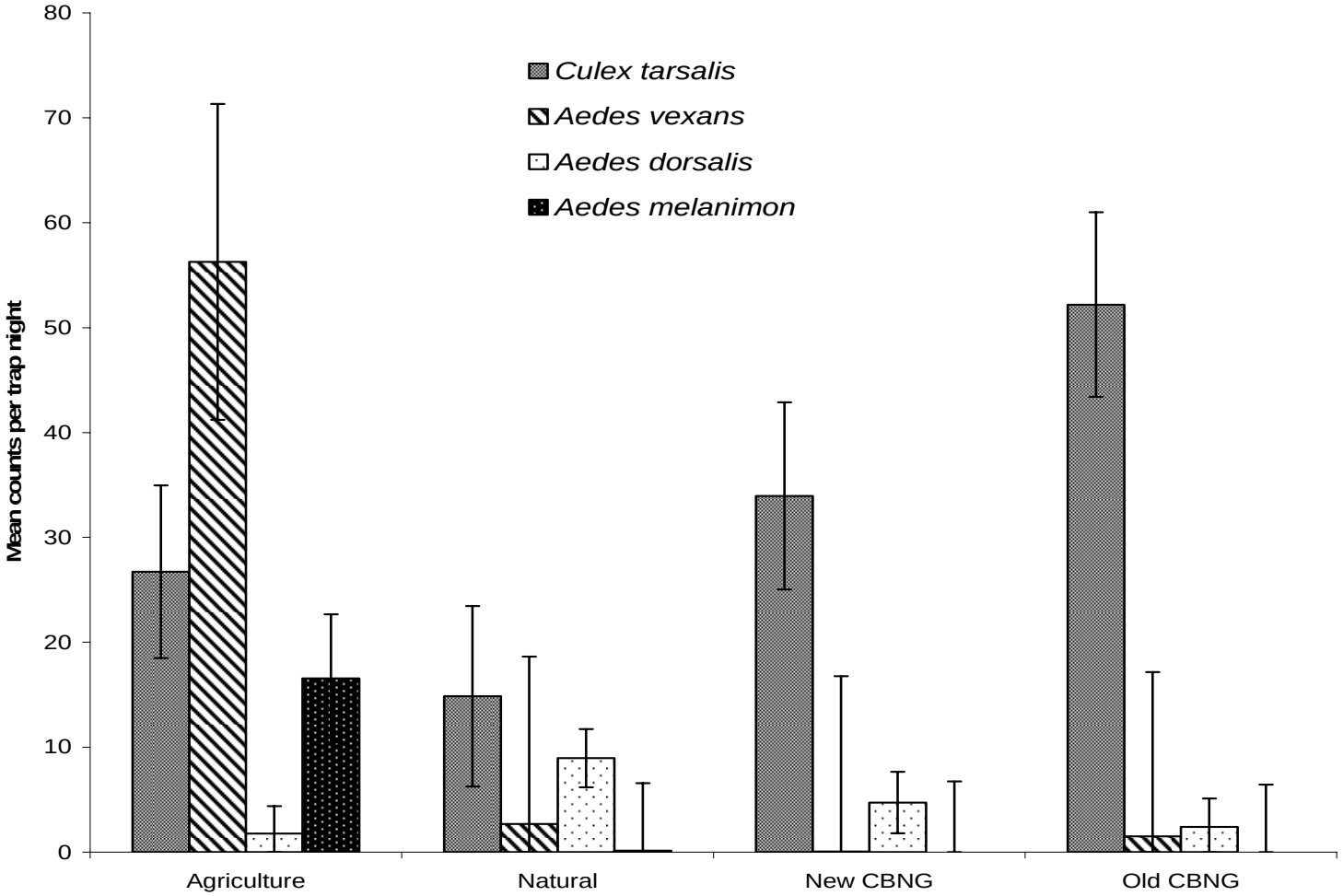



Figure 6. Means and standard errors by study area for the four most abundant mosquito species collect in the Powder River Basin, Wyoming, 2005.

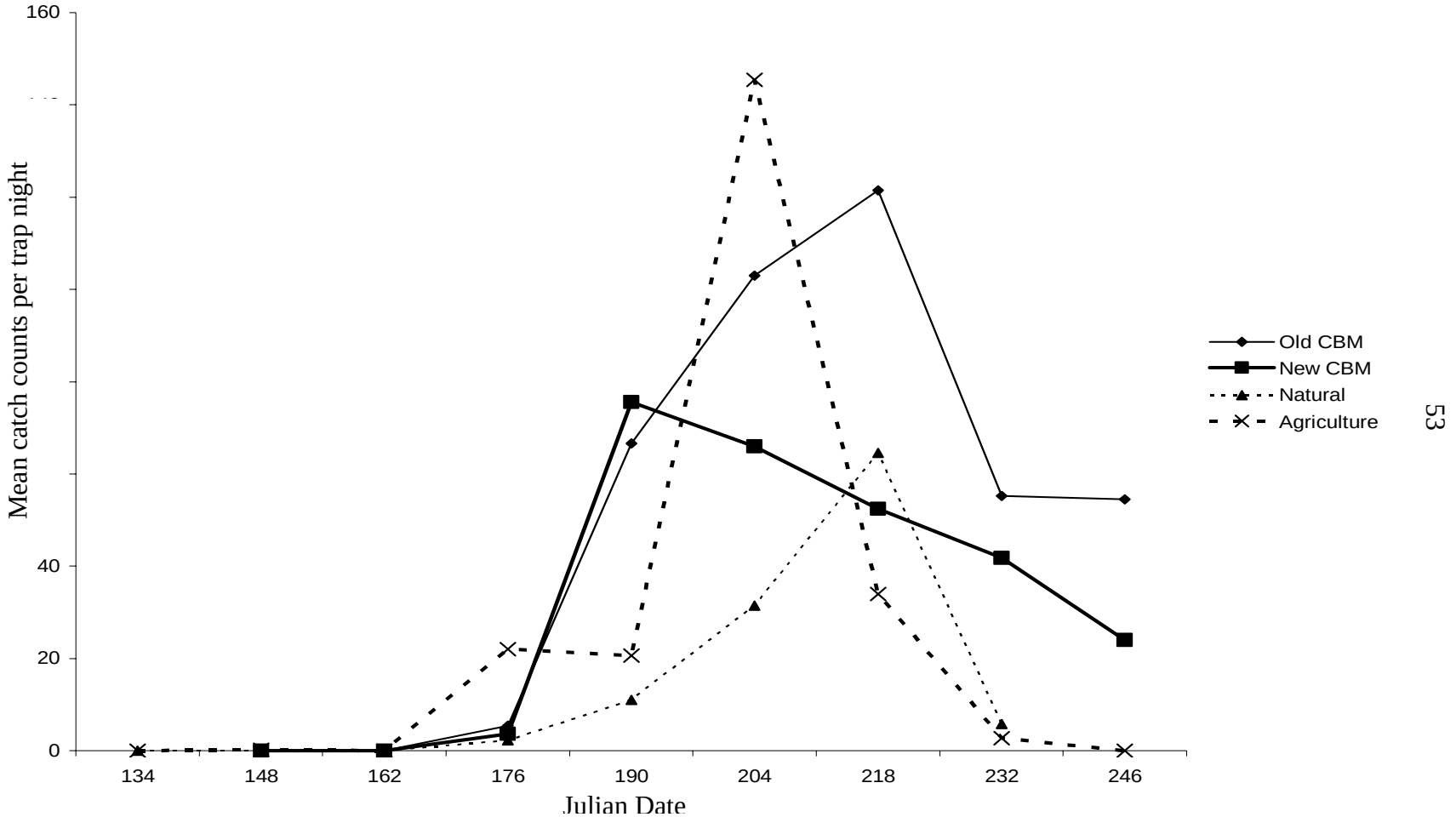



Figure 7. *Culex tarsalis* mean catch counts over time by study area, Powder River basin, Wyoming, 2005.

*Culex tarsalis* was the most abundant mosquito collected during 2005 (Figure 2), with old CBNG sites producing significantly more mosquitoes than irrigated agriculture or natural water sources (33.9 ± 8.9, 3, 129 df, F = 2.41, $P \leq 0.03$) (Figure 6). Weekly population counts were significant for *Cx. tarsalis* in 2005, with weeks 5–8 (Julian date 162–188) producing more mosquitoes than all other weeks sampled (8, 129 df, F = 11.3, $P \leq 0.008$) (Figure 7, Table 3). Week six had the largest average catch of all weeks sampled, with mean counts of 86.3 *Cx. tarsalis* per trap night (SE = 9.5).

*Aedes vexans* were most abundant in irrigated agricultural areas in 2005, similar to 2004 sampling (3,129 df, F = 3.43, $P = 0.019$). Mean counts of *Ae. vexans* in agricultural areas were 56.3 mosquitoes per trap night, which was significantly higher than all other study sites sampled (Figure 6) ($P \leq 0.015$). While irrigated agricultural areas were significantly more productive for *Ae. vexans* than other study site there was no significant weekly population trend seen in 2005 (8, 129 df, F = 1.04, $P = 0.41$) (Table 3). Abundances of *Ae. dorsalis* in 2005 were much lower than 2004 samples, with no significant differences between study areas (Figure 6) (3, 129 df, F = 1.54, $P = 0.20$). The highest abundances were around natural water sources, as in 2004, however mean catches were much lower (8.9 ± 2.8), with no significant differences from other study areas. No significant weekly trends were seen in *Ae. dorsalis* populations in 2005 (8, 129, F = 1.28, $P = 0.26$) (Table 3).

*Aedes melanimon* population trends were similar in 2005 to the previous year samples, with abundances higher in irrigated agriculture than other sampled water sources (Figure 6). In 2005 these differences were not significant (3, 129 df, F = 1.9, $P =$

0.13). There were no significant weekly trends for *Ae. melanimon* in 2005 (8, 128 df, F = 0.96, *P* = 0.47) (Table 3), likely due to the reduced irrigation practices in 2005 from that seen in 2004.

Mosquito Infection Rates

A total of 923 and 244 pools of insects were tested for WNV using PCR assays in 2004 and 2005 respectively, with WNV isolation from 16 pools between both years. Species that were tested for WNV included *Cx. tarsalis* (241, 125 mosquitoes tested in 2004 and 2005 respectively), *Ae. vexans* (52, 22), *Ae. provocans* (1- 2005), *Ae. nigromaculus* (2, 1), *Ae. melanimon* (38, 8), *Psorophera* spp. (10- 2004), *Ochleratatus* spp. (21- 2004), *Culiseta* spp. (8- 2004), *Ae. implicates* (1- 2005), *Ae. dorsalis* (124, 11), *Ae. campestris* (1- 2005) and the biting midge *C. sonorensis* (428, 75). All the positive pools detected were from *Cx. tarsalis* samples, with minimum infection rate of 1.22 per thousand from 2004, and 0.84 per thousand from 2005 (Table 4).

Infected pools of mosquitoes were collected in different study areas in 2004 and 2005. Of the 12 infected pools found in 2004, 8 were from agricultural areas, 2 were from CBNG and 2 were from CX sagebrush steppe with minimum infection rates of 2.90, 0.60 and 1.48 per thousand respectively. In 2005, all the positive pools detected were from CBNG areas. Two infected pools were found at old CBNG ponds with an infection rate of 0.99, and 2 infected pools were detected in new CBNG areas with an infection rate of 1.96.

Table 4. Mosquito infection rates for *Culex tarsalis* collected in the Powder River basin, Wyoming in 2004 and 2005.

| Year | Species | Infection Rate | Lower Limit | Upper Limit | Number Pools | Number Positive Pools | Number Individuals |
|---|---|---|---|---|---|---|---|
| 2004 | *Cx. tarsalis* | 1.22 | 0.66 | 2.07 | 239 | 12 | 10,120 |
| 2005 | *Cx. tarsalis* | 0.84 | 0.27 | 2.03 | 123 | 4 | 4,804 |

*Culex tarsalis* infection rates

| | Group | Infection rate | Lower Limit | Upper Limit | Number Pools | Number Positive Pools | Number Individuals |
|---|---|---|---|---|---|---|---|
| 2004 | Agriculture | 2.90 | 1.36 | 5.52 | 63 | 8 | 2,936 |
| | Natural | 0.00 | 0.00 | 2.23 | 38 | 0 | 1,637 |
| | CBNG | 0.60 | 0.11 | 1.98 | 79 | 2 | 3,338 |
| | CX Sagebrush steppe | 1.48 | 0.27 | 4.87 | 36 | 2 | 1,372 |
| | Padlock Sagebrush steppe | 0.00 | 0.00 | 4.21 | 23 | 0 | 837 |
| 2005 | Agriculture | 0.00 | 0.00 | 3.35 | 29 | 0 | 1,065 |
| | Natural | 0.00 | 0.00 | 5.17 | 18 | 0 | 663 |
| | Old CBNG | 1.96 | 0.36 | 6.43 | 29 | 2 | 1,030 |
| | New CBNG | 0.99 | 0.18 | 3.26 | 47 | 2 | 2,043 |

Table 5. Average monthly temperature and rainfall data for Sheridan, WY, May - August 2004 and 2005 (National Weather Service 2006).

| Month | Year | Average Monthly Temperature (°C) | Departure from Normal (°C) | Total Monthly Precipitation (centimeters) | Departure from Normal (centimeters) | Days with total rainfall ≥ (inches) | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | 0.01 | 0.10 | 0.50 | 1.00 |
| May | 2004 | 11.6 | 0.4 | 1.8 | -4.3 | 11 | 2 | 0 | 0 |
| | 2005 | 10.6 | -1.1 | 15.7 | 9.6 | 12 | 6 | 3 | 3 |
| June | 2004 | 15.9 | -0.9 | 2.9 | -2.2 | 9 | 3 | 1 | 0 |
| | 2005 | 16.8 | 0.6 | 7.5 | 2.3 | 10 | 4 | 3 | 0 |
| July | 2004 | 20.4 | -0.1 | 4.4 | 1.5 | 11 | 6 | 1 | 0 |
| | 2005 | 22.2 | 3.0 | 2.6 | -0.3 | 4 | 2 | 1 | 0 |
| August | 2004 | 18.7 | -2.2 | 1.4 | -0.6 | 7 | 1 | 0 | 0 |
| | 2005 | 18.8 | -2.2 | 3.0 | 1.0 | 11 | 5 | 0 | 0 |

Weather Data

Average monthly temperature and rainfall data for Sheridan, WY, May-August 2004 and 2005 indicate normal to below average temperatures in 2004 and 2005 (National Weather Service 2006). 2004 average temperatures ranged from 11 - 20 °C in 2004, and 11 - 22 °C in 2005 (Table 5). Departures from normal temperatures were -3 °C in 2004 and -0.1 °C in 2005. Average monthly rainfall in 2004 ranged from 1.4 – 4.4 centimeters in 2004 and 2.6 – 15.7 centimeters in 2005. Departures from normal rainfall was -5.5 centimeters in 2004 and +12.7 centimeters in 2005, indicating major changes in total rainfall between 2004 and 2005 field seasons. A total of 52 days accumulated > 0.25 centimeters of total rainfall between May and August 2004, with zero days accumulating >2.54 centimeters total rainfall. The 2005 field season included 64 days with > 0.25 centimeters total rainfall, with three days accumulating >2.54 centimeters total rainfall in May 2005.

## Discussion

The Powder River Basin of Wyoming is currently undergoing both local and landscape scale changes in land use and development due to the production of coal bed natural gas. Satellite imagery shows that CBNG development has had a 2-fold increase in road, 2-3x increase in powerlines, 5x increase in number of total ponds in ranching areas with a 9x increase in total area of water, and a 2x increase in area of ponds and water in agricultural areas (Naugle et al. in press). Further imagery indicates that these ponds have contributed to a 75% increase in potential *Cx. tarsalis* habitat area across this region

(Zou et al. 2006). *Culex tarsalis*, the vector responsible for transmitting WNV in northeastern Wyoming, is a species of mosquito native to the PRB (Hayes 2005, Turell et al. 2005); however, their population levels have increased in some areas due to human development in both agriculture and CBNG fields. This in combination with my research data allows me to reject my hypothesis that CBNG development has not increased mosquito production in the PRB including the WNV vector *Cx. tarsalis*.

In 2004 *Cx. tarsalis* was the most abundant mosquito collected across the PRB and was second in abundance to *Ae. vexans* in 2005. *Culex tarsalis* populations were highest in irrigated agriculture and CBNG sites, both of which are artificially supplemented with water throughout the summer. These sites were vegetated by sedges, rushes, forbs and flooded upland grasses. Many of these ponds also included inlets and outlets, which were significant production areas for *Cx. tarsalis* larvae in 2005 (Chapter 3). *Culex tarsalis* populations have been observed in southern California with high densities around irrigated agriculture (Riesen et al. 1992), and are known to be one of the first mosquito species to colonize wastewater ponds in the southwestern United States (Walton et al. 1990; Fanara and Mulla 1974). Our *Cx. tarsalis* collections show similar patterns to those observed in anthropogenic water sources in California, with the highest catch counts in Wyoming observed around irrigated and CBNG habitats.

In 2004 high populations of *Cx. tarsalis* were observed in agricultural sites, followed by sites under CBNG development. That summer had below average precipitation in northeastern Wyoming (-41.7% average, National Weather Service 2006) and subsequently our study sites had a 2-fold increase in irrigation of hay fields (Sparo

Zezas, personal communications). In contrast, rainfall in 2005 was 12.7 centimeters above the seasonal average, with normal seasonal temperatures and irrigation practices. This was reflected in adult mosquito populations with total mosquito production in irrigated agricultural areas increasing by 27% above average under drought conditions, and *Cx. tarsalis* production increasing by 39%. In comparison, natural sites saw a 10% decrease in *Cx. tarsalis* production from 2005 to 2004. These mosquitoes have been observed under drought conditions in California, and have demonstrated similar trends, with increased populations in irrigated agriculture during a dry year (1990) (Riesen et al. 1992). Overall, drought conditions may facilitate increased mosquito production in agricultural areas by increasing flood irrigation habitats when naturally occurring habitats are drying down due to lower precipitation.

Seasonal trends in mosquito populations for both the 2004 and 2005 field season were strongest in *Cx. tarsalis* populations across the PRB. These populations increased over the course of the spring and summer, with peak population the week of 22 July (x = 86.3 per trap). Similar population trends have been observed in California with peak *Cx. tarsalis* populations the first week of July (Isoe and Millar 1995, Knight et al. 2003). No other strong weekly trends were seen in other species of mosquitoes collected in the PRB. *Aedes vexans* were slightly more abundant in the early spring, with no significant differences found between sampling weeks in 2004 or 2005.

West Nile virus mosquito infection rates varied between study years and study sites across the Powder River basin. In 2003, female *Cx. tarsalis* caught in CDC light traps tested positive for WNV with an infection rate of 7.16 per thousand, and *Culicoides*

*sonorensis* were found with a WNV infection rate of 2.31 per thousand (Naugle et al. 2004). In 2004 and 2005, study areas with the highest adult *Cx. tarsalis* population also had the highest mosquito infection rates, with agricultural sites having infection rates of 2.90 in 2004, and old CBNG sites had infection rates of 1.96 in 2005. *Culex tarsalis* average 2.6- 2.9 generations per season in northern climates, with infected females needing to survive a minimum of 2 gonotrophic cycles in warm years to infect a susceptible host and continue amplifying WNV in the environment (Riesen et al. 2006). Because this is a relatively long time for adult mosquito survival, population levels may need to be above a given threshold to maintain WNV primary infection cycles within an ecosystem. Threshold modeling of local mosquito populations including regional temperature data may be a potential predictive tool for WNV monitoring in the future.

Landscape changes due to CBNG development and irrigated agriculture in the PRB have created habitats with significantly higher mosquito populations than natural landscapes of northeastern Wyoming. CBNG ponds placed in upland sagebrush steppe habitat have created areas with significantly more mosquitoes than the original landscape, including the WNV vector *Cx. tarsalis*. These mosquitoes have been detected with WNV in 2003, 2004 and 2005 and WNV has been documented in greater sage grouse in CBNG fields. Modifications to current water usage practices will likely be required to mitigate the potential threat of WNV to human health and wildlife.

# CHAPTER 3

## COMPARITIVE LARVAL MOSQUITO ABUNDANCE IN NATURAL, AGRICULTURAL AND COAL BED NATURAL GAS PONDS

### Introduction

The effects of energy development on the economy, environment, and wildlife populations of western North America is an issue of concern as new energy resources are explored across the west. The PRB coal seam boundary which spatially defines where CBNG development occurs is ~ 2.4 million ha; roughly the size of New Hampshire. Within this area the Bureau of Land Management (BLM) has already authorized plans to drill 51,000 CBNG wells on federal mineral holdings in the PRB of Wyoming and the potential exists for another 15,000 in Montana (BLM 2003 a, b). Coal bed natural gas is currently being extracted for commercial use in the Powder River basin by the natural gas industry at the rate of 23 million $m^3$ per day (Department of Energy 2002). Methane extraction includes the removal of groundwater to allow confined gases to flow to well heads. This groundwater is discharged into existing cattle ponds, newly constructed ponds, or surface drainages (Clark et al. 2001). Coal bed natural gas development and associated infrastructure in the PRB has caused rapid, large-scale changes to sagebrush habitats of Montana and Wyoming. The potential impacts that could result from the high density of wells, power lines, roads, increased vehicle traffic, pipelines, compressor stations, and water storage ponds within a gas field this size is of concern to wildlife managers tasked with conservation of sensitive species. Since 1999, an estimated 19,000

CBNG well heads have been constructed in the PRB, with 20,000 more projected in the future, each of which will produce discharge water that must be held in CBNG ponds, re-injected into the aquifer, or otherwise dispersed (Department of Energy 2002).

Coal bed natural gas ponds vary in shape, age and structure creating varied types of aquatic habitats in a region that has previously been considered semi-arid (Hemstrom et al. 2002; Walker et al. 2004). These ponds are potential habitats for mosquito production, including the mosquito *Culex tarsalis*, the main vector for West Nile virus (WNV) in the western United States (Hayes 2005; Turell et al. 2005; Zou et al. 2006).

Coal bed natural gas development has affected several species of wildlife native to the PRB (Daszak et al. 2000; Marra et al. 2004), including the greater sage-grouse (*Centrocercus urophasianus*) (Naugle et al. 2004, 2005; Walker et al. 2004). The new networks of roads, power lines, pipelines, compressor stations and wellheads from energy development result in cumulative impacts that are detrimental to sage-grouse survival (Holloran 2005; Aldridge and Boyce In Press). Along with these habitat changes, the introduction of new pathogens to the sage-grouses native range may cause population declines that, when compounded, are beyond the scope of recovery for this species. The introduction of WNV to the PRB reduced late summer survival of female sage grouse by 75% in some areas in 2003. Additional vectors of WNV in the PRB from CBNG ponds may increase WNV sage grouse mortality in this region.

Populations of adult *Cx. tarsalis* mosquitoes have been found throughout the PRB including in natural, agricultural and CBNG habitats. This species was positive for WNV in select areas of the PRB and is the likely vector of this pathogen to human, equine, and

wildlife species (Hayes 2005, Turell 2005). Migratory flights of host-seeking or ovipositional-site-seeking female *Cx. tarsalis* have been found to travel up to 17.7 km in California (Bailey et al. 1965), indicating that females caught in a $CO_2$ baited light trap may have emerged in a different aquatic habitat than where they were collected as adults. To identify where mosquitoes are being produced in the PRB and the specific habitats preferred for larval mosquitoes, I sampled four different types of aquatic habitats including CBNG, natural and irrigated agriculture. I hypothesized that the type of habitat created by CBNG development would have larger populations of mosquitoes than are present in natural and agricultural water sources in the same region.

## Materials and Methods

### Study Sites

Aquatic habitats sampled for adult mosquitoes were also sampled for mosquito larvae production. A complete description of these study sites is found in Chapter 2. Five habitats were sampled; these included sagebrush steppe under CBNG development (natural water sources), irrigated agricultural water, new CBNG ponds, mature CBNG ponds and CBNG pond outlets.

Coal bed natural gas outlets were also sampled for larval production separately from the CBNG ponds. These areas were not sampled for adult mosquitoes because they are contiguous with the ponds. These outlets are a result of water seeping under the earthen dam created to hold CBNG water. Neither age nor vegetation type of the contributing CBNG pond was included in the classification of CBNG outlets. Outlets

were treated as a separate block in the analysis, as they had different vegetation and shoreline characteristics, and they produced mosquitoes independently of their contributing CBNG pond. These outlets were small areas, generally less than 50 m in length and 3 m in width and no more than 46 cm in depth. Water levels were relatively stable throughout the 2005 field season, although outlet lengths were often reduced during hot, dry weather. Average vegetation cover was 40% in late August, predominately covered by rushes, sedges, flooded upland grasses and emergent wetland grasses.

Field Methods

Mosquito larvae were collected bi-weekly from 13 May–24 August (Julian date 114-226), 2005 in each of the five habitat blocks. Each block contained five randomly selected aquatic habitats which were sampled at 20 points along a transect at 5 m intervals. Each point was sampled four times using a 350 ml standard dipper. A sample was taken at 0.5 m intervals in each of the cardinal directions while I stood in the water and faced the body of the pond to be sampled with the shoreline behind me. All larvae collected from a sampling points were pooled and concentrated into 20 ml vials and preserved in 95% alcohol for processing.

I characterized pond vegetation on 3-17 August 2005 when vegetation had matured enough to be accurately identified to major groups (e.g., rushes, sedges, flooded upland grasses and forbs). I used a standard 46 x 46 cm Daubenmire (1959) frames to sample each larval sampling point for vegetation variables including plant cover (%), cover type and plant type. Cover variables included emergent, submergent, open water,

and flooded upland vegetation. Plant type variables included algae, forbs, grasses, rushes, sedges woody plants, and open water. I converted categorical estimates of plant cover to percentages using methods developed by Daubenmire (1959) (1 = 2.5%, 2 = 15%, 3 = 37.5%, 4 = 62.5%, 5 = 85%, 6 = 97.5%) for each larval sampling point, and averaged these values for each pond, and for each study site.

Weather data obtained from the United States National Weather Service archival climatological data for Sheridan, Wyoming (National Weather Service 2006). Average monthly temperatures from May - August were recorded, including the departure from normal. Precipitation data were recorded as monthly totals including the departure from normal, as well as the number of days with 0.02, 0.25, 1.27 and 2.54 centimeters or more of rainfall.

Laboratory Methods

Second, third and fourth stage larvae were counted and identified to genus and/ or species (Darsie and Ward 1981). *Aedes* and *Culex* larvae were identified to species; *Culiseta* and *Anopheles* were identified to genus. First instar and pupae were recorded but were not identified due to lack of appropriate morphological characteristics for species keys in this region. All specimens were stored in 70% ethanol for future reference.

Statistical Methods

For data analysis comparing mosquito abundance among aquatic habitats, mean values were calculated for each mosquito species from the 20 points sampled per pond to avoid pseudoreplication (Hulbert 1984). Data analysis conducted to assess the impact of

different aquatic vegetation characteristics among pond types used each larval sampling point individually, as vegetation characteristics could vary from point to point within a pond.

Larval abundance of mosquitoes between pond types was analyzed in SAS PROC MIXED with a generalized mixed effect linear model (Littell et al. 1996). Number of mosquito larvae per time period was transformed as ln ($x + 1$) to meet the assumption of normality. Because sequential larval counts can be serially-correlated and larval counts estimated for the same pond closer in time are more likely to be correlated than measures more distant in time, I modeled the appropriate covariance structure that best represented the data in SAS PROC MIXED (Littell et al. 1996, 1998). The covariance structure is derived from variances at individual times and correlations between measures at different times on the same pond (Littell et al. 1998). I used a compound symmetry (CS) error structure where all measures at all times have the same variance and all pairs of measures on the pond have the same correlation (Littell et al. 1996). SAS PROC MIXED is a generalization of a standard linear model and data are permitted to exhibit correlation and non-constant variability (SAS 8.2 online doc.). I used the REPEATED statement in PROC MIXED to model the covariation within ponds, which accounts for the violation of independence of the observations on the same pond at different times (Littell et al. 1998). The RANDOM statement was used to model the variation among ponds, which accounts for heterogeneity of variances from individual ponds (Littell et al. 1998). The random effects factor was the sub-sample of ponds within treatment group that were randomly chosen from all available ponds in the study area. All other factors in the

model were treated as fixed effects. Maximum likelihood methods were then used to fit a mixed-effects (both random and fixed effects) general linear model in SAS PROC MIXED.

Timing of larval production between aquatic habitats for each of the four most abundant species was assessed using a 1-way ANOVA blocked by week. I used a 1-way ANOVA to assess differences in larval populations on a week-by-week basis because these were only within week comparisons, and ponds were not repeatedly sampled within weeks.

I also used a 1-way ANOVA to assess whether the production of *Cx. tarsalis* was related to vegetation characteristics in the four habitat types that were sampled. I used *Cx. tarsalis* because it is the most abundant mosquito species in the PRB and is known to vector WNV in the western U.S. Only larval counts taken the week that vegetation characteristics were measured were used in analyses.

## Results

### Mosquito Populations

A total of 6,483 mosquito larvae was captured and identified from 12,636 individual dips. The dominant species identified across all study sites was *Cx. tarsalis*, which accounted for 47.8% of the individual larvae collected (Figure 7). *Culiseta* spp. represented 20.8% of the collections, followed by *Ae. vexans* (4.2%), *Ae. dorsalis* (3.1%), *Ae. melanimon* (2.3%) and *Ae. campestris* (0.1%). Unidentified 1$^{st}$ instar larvae and pupae accounted for 20.9% and 0.08% of the total collection, respectively.

*Culex tarsalis* abundance was significantly different at the 90% level (df = 4, $P$ = 0.09) between the five sampled aquatic habitats. Post-hoc tests showed that *Cx. tarsalis* abundance was similar across all types of CBNG and natural sites ($P \geq 0.41$, Figure 8). *Culex tarsalis* abundance was lowest in agricultural sites, with a mean count of 0.47 larvae per sampling point (post hoc $P = 0.03$) (Table 6). *Culex tarsalis* showed strong seasonal differences ($P < 0.0001$) with a peak in larval populations the week of 18 July (Julian date 184) (Figure 9). *Culex tarsalis* abundance increased precipitously from mid-June to mid-July, (Julian date 142–184) and sustained high production through mid-August (Figure 9). The habitat type that contributed most to this peak was CBNG outlet ponds (141.6 ± 1.7, $P = 0.03$; Figure 10). *Culex tarsalis* abundance in new CBNG, old CBNG and natural sites also increased the week of 18 July, but with no significant differences between group means ($P \geq 0.95$), and to a lesser extent when compared to CBNG outlet ponds ($P = 0.03$).

Abundance of *Culiseta* differed ($P = 0.05$) between the five sampled aquatic habitats. *Culiseta* abundance was similar in agricultural, natural and CBNG outlets ($P \geq 0.001$), and was lowest in new and old CBNG sites ($P = 0.196$ and $P = 0.053$, Table 6). Unlike other species, *Culiseta* did not show strong seasonal differences in 2005, but timing of abundance peaks was variable between aquatic habitats ($P = 0.09$). *Culiseta* populations in CBNG outlets and natural sites peaked in mid-summer (Julian date 142-184; Figure 8).

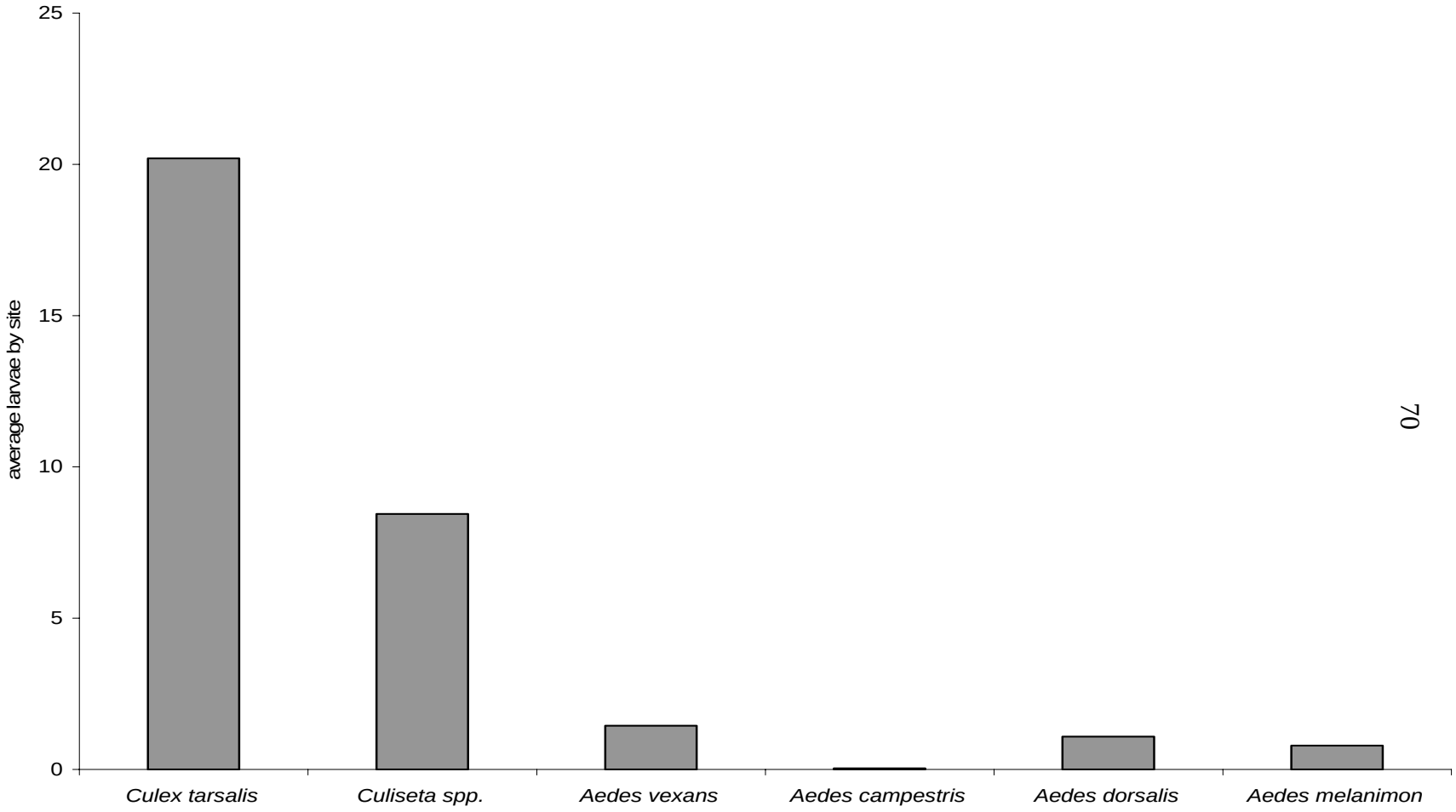



Figure 8. Mosquito larvae collected by taxon in the Powder River Basin, Wyoming, 2005.

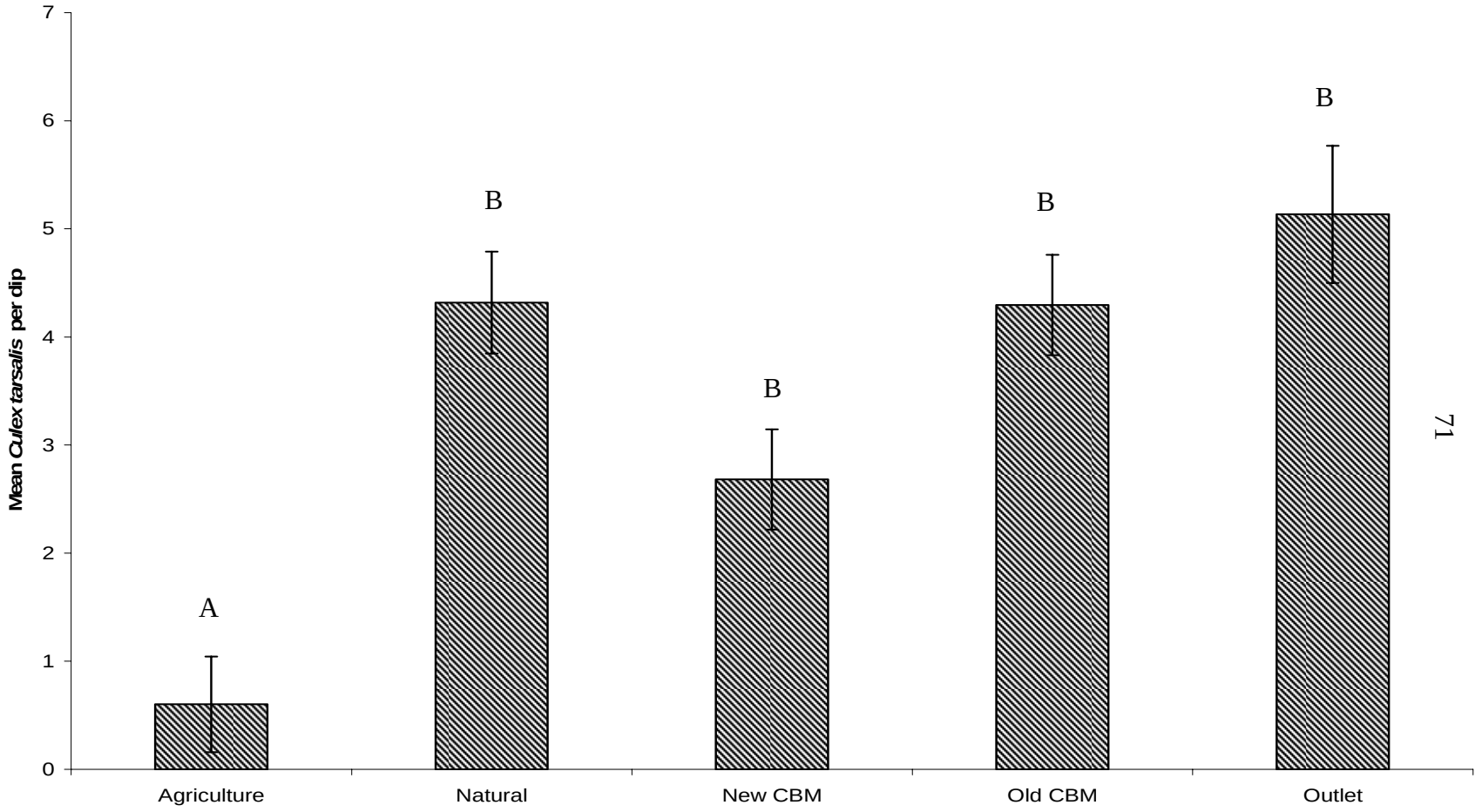





Figure 9. Mean larval production (SE bars) of *Culex tarsalis* per dip from 5 aquatic habitats types in the Powder River Basin, Wyoming, 2005. (Statistical differences > 0.05 denoted by letters).

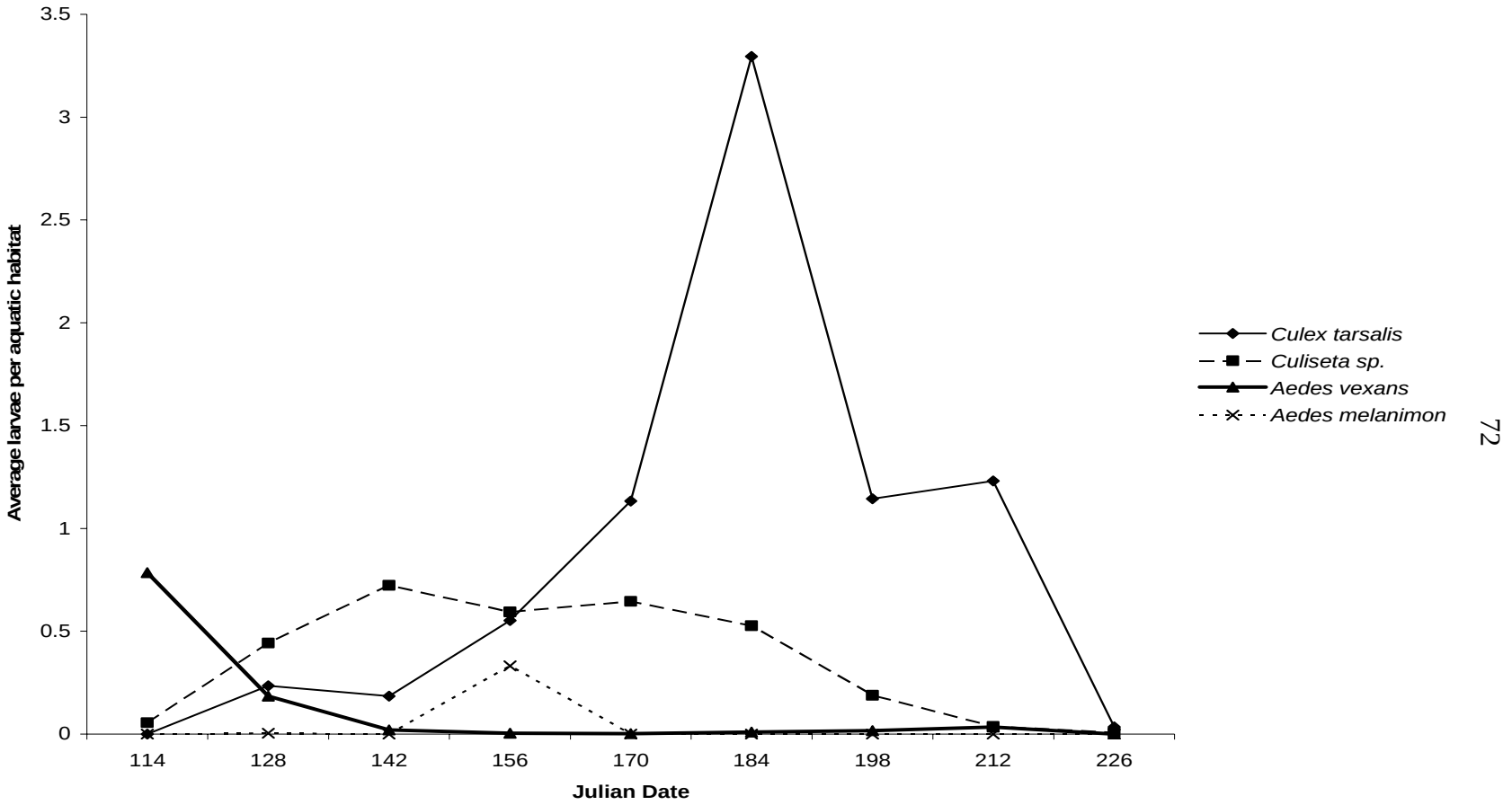



Figure 10. Timing of larval production for four species of mosquitoes in the Powder River Basin, WY, 13 May – 24 August, 2005.

Table 6. Weekly larval mosquito mean counts per dip (SE) by study area for the four most abundant larval species collected, Powder River basin Wyoming, 2005.

| Julian date and week of sampling | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species and habitat type | 128 Week 1 | 142 Week 2 | 156 Week 3 | 170 Week 4 | 184 Week 5 | 198 Week 6 | 212 Week 7 | 226 Week 8 | Season Total |
| *Culex tarsalis* | | | | | | | | | |
| Agriculture | 0.00(0) | 0.38(.71) | 0.25(.67) | 0.38(1.01) | 1.13(1.32) | 1.07(1.16) | 1.43(1.21) | 0.37(.85) | .47(.33) |
| Natural | 0.00(0) | 2.84(.71) | 1.06(.67) | 5.07(1.01) | 7.32(1.57) | 32.55(1.37) | 29.45(1.43) | 1.45(2.17) | 4.28(.43) |
| New CBNG | N/A | 0.64(.71) | 0.32(.67) | 0.78(1.01) | 5.48(1.32) | 13.97(1.16) | 7.01(1.21) | 2.06(1.07) | 2.97(.43) |
| Old CBNG | N/A | 2.93(.71) | 2.33(.67) | 2.76(1.01) | 1.96(1.32) | 23.85(1.16) | 1.30(1.21) | 13.01(1.07) | 4.12(.43) |
| CBNG Outlet | N/A | 0.00(1.00) | 0(.94) | 1.72(1.47) | 10.87(1.97) | 141.59(1.71) | 3.85(1.78) | 13.67(1.57) | 5.18(.51) |
| *Aedes vexans* | | | | | | | | | |
| Agriculture | 0.80(1.25) | 0.64(.60) | 0.00(.25) | 0.00(.10) | 0.15(.07) | 0.43(.14) | 0.43(.21) | 0.53(.21) | .36(.12) |
| Natural | 1.69(1.25) | 4.44(.60) | 0.48(.25) | 0.25(10) | 0(.07) | 0.15(.15) | 0.19(.24) | 0.00(.43) | .70(.12) |
| New CBNG | N/A | 0.38(.60) | 0.15(.25) | 0(.10) | 0(.07) | 0(.14) | 0.15(.21) | 0(.25) | .09(.12) |
| Old CBNG | N/A | 1.65(.60) | 0.25(.25) | 0(.10) | 0(.07) | 0(.14) | 0(.21) | 0(.25) | .20(.12) |
| CBNG Outlet | N/A | 0(.84) | 0(.32) | 0(.14) | 0(.07) | 0(.18) | 0(.29) | 0(.34) | 0(0) |
| *Aedes melanimon* | | | | | | | | | |
| Agriculture | 0(0) | 0(0) | 0(0) | 1.54(.59) | 0(0) | 0(0) | 0(0) | 0(0) | .20(.07) |
| Natural | 0(0) | 0.22(.10) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | .03(.07) |
| New CBNG | N/A | 0(.10) | 0(0) | 0(.59) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) |
| Old CBNG | N/A | 0(.10) | 0(0) | 0(.59) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) |
| CBNG Outlet | N/A | 0(.10) | 0(0) | 0(.83) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) |
| *Culiseta* spp. | | | | | | | | | |
| Agriculture | 0.59(.43) | 1.90(1.02) | 4.99(1.18) | 2.96(.97) | 3.23(.90) | 0.78(.87) | 5.61(.51) | 0.63(.22) | 2.02(.32) |
| Natural | 0.25(.43) | 2.23(1.02) | 0.97(1.18) | 2.10(.97) | 6.46(1.06) | 6.55(1.01) | 0.57(.59) | 0(.45) | 1.67(.36) |
| New CBNG | N/A | 1.31(1.02) | 1.56(1.18) | 0.15(.97) | 0(.90) | 0.15(.87) | 0(.51) | 0(.26) | .38(.32) |
| Old CBNG | N/A | 2.80(1.02) | 2.61(1.18) | 0(.97) | 0(.90) | 0.59(.87) | 0(.51) | 0(.26) | .54(.32) |
| CBNG Outlet | N/A | 0(1.48) | 0(1.74) | 3.60(1.41) | 10.20(1.30) | 6.63(1.24) | 0(.71) | 0.82(.35) | 1.56(.39) |

Agricultural sites produced two population peaks, one in early summer and another later in the year; both peaks coincided with the release of irrigation water on fields. The second peak produced more larvae of *Culiseta* in agricultural sites ($P = 0.02$) than in any other habitat type at that time of the year (Table 6).

Abundance of *Aedes vexans* differed ($P = 0.030$) between the five sampled aquatic habitats, being highest in natural habitats ($P = 0.030$), intermediate in agricultural and new and old CBNG sites, and absent from CNBG outlets (Table 6). Timing of production varied seasonally ($P = 0.0005$) and was highest across all habitat types in late May (Table 6). Natural water sources produced the highest mean *Ae. vexans* counts per dip on 22 May, 2005 (Julian date 142), likely due to flooding from snowmelt and spring rain events.

Abundance of *Aedes melanimon* was similar in agricultural and natural sites ($P = 0.27$); no larvae were captured in CBNG habitats of any type (Figure 6). Abundance of *Ae. melanimon* varied seasonally ($P = 0.085$) with a peak in early summer (26 June, Julian date 177) (Table 6).

Larval Use of Vegetative Cover Types

Abundance of *Cx. tarsalis* differed ($P = 0.056$) between the four vegetative cover types (Figure 12). Abundance was greater in flooded upland vegetation than in open water, emergent, or submergent cover types ($P < 0.00001$); very few larvae were collected from open water habitats that lacked vegetative cover ($0.0 \pm 0.1$) (Figure 12).

Abundace of *Cx. tarsalis* also differed ($P = 0.01$) between plant types encountered during larval sampling (Figure 11). *Culex tarsalis* abundance was highest in forbs ($1.0 \pm$

0.1) followed by flooded upland grasses (0.9 ± 0.1). Open shoreline with no vegetation, non-vegetated sampling points and those with woody plant cover harbored almost no larvae over the 2005 sampling season, and were not good predictors for *Cx. tarsalis* larval habitats.

Weather Data

Average monthly temperature and rainfall data for Sheridan, WY, May - August 2005 indicate normal to below average temperatures (National Weather Service 2006). 2005 average temperatures ranged from 11 - 22 °C (Table 3). Departures from normal temperatures were -0.1 °C in 2005, and average monthly rainfall 2.6 – 15.7 centimeters. Departures from normal rainfall in 2005 was +12.7 centimeters. The 2005 field season included 64 days with > 0.02 inch total rainfall, with three days accumulating >2.54 inch total rainfall in May 2005.

## Discussion

New and mature CBNG ponds are producing *Cx. tarsalis* larvae similar to or above levels occurring in natural water sources in northeastern Wyoming. These sites also produce *Cx. tarsalis* over longer intervals than natural sites with peak larval production the week of 18 July (Julian date 198). This is comparable to *Cx. tarsalis* production in Nebraska, where the first larvae were found on 25 May, with peak production the week of 11 July (Julian date 191) (Edmunds 1955). The most productive areas for *Cx. tarsalis* larvae were CBNG pond outlets, which have been observed to fluctuate in water level in 2005 (personal observation).

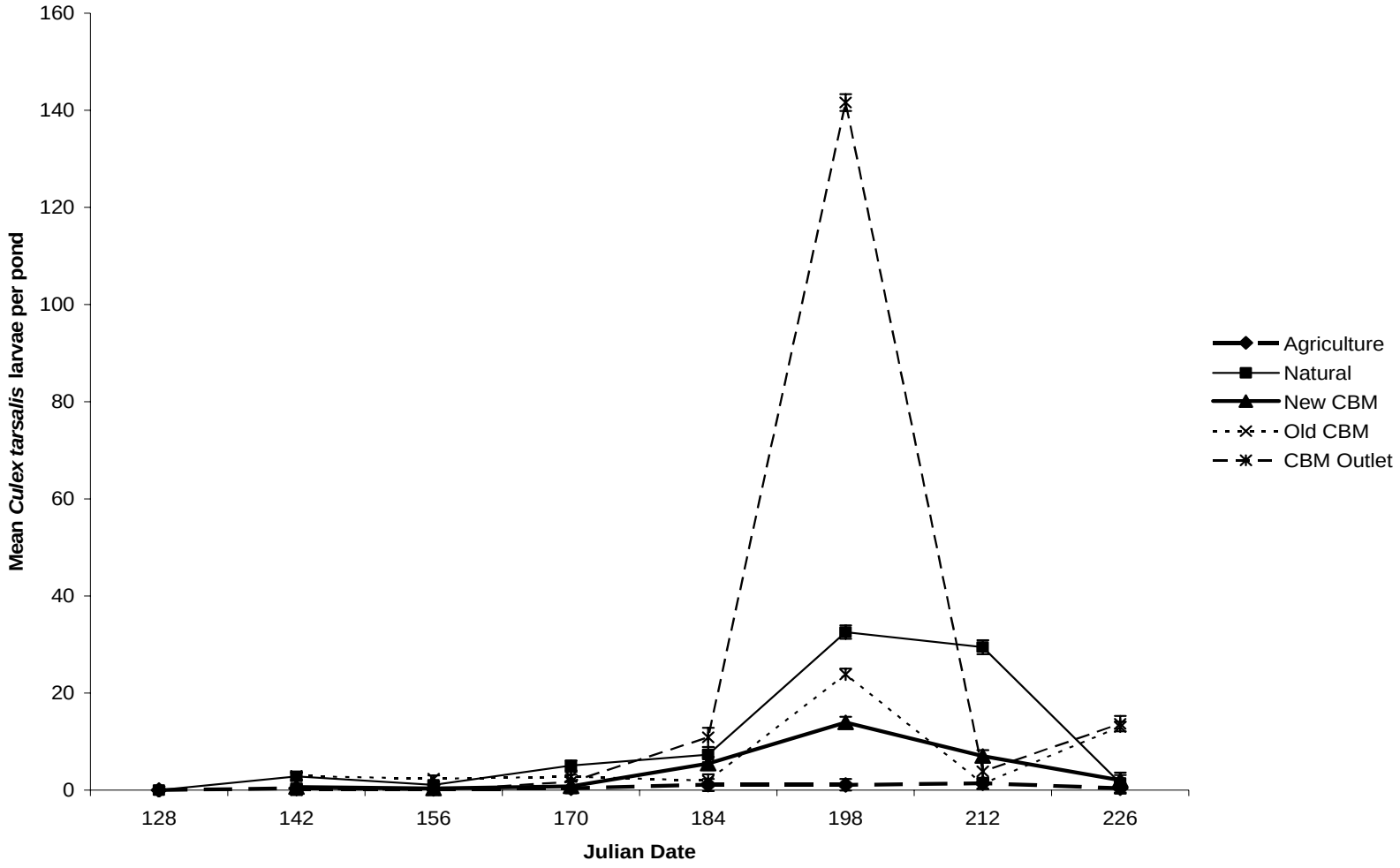



Figure 11. *Culex tarsalis* production over time by aquatic habitat in the Powder River basin, Wyoming, 2005.

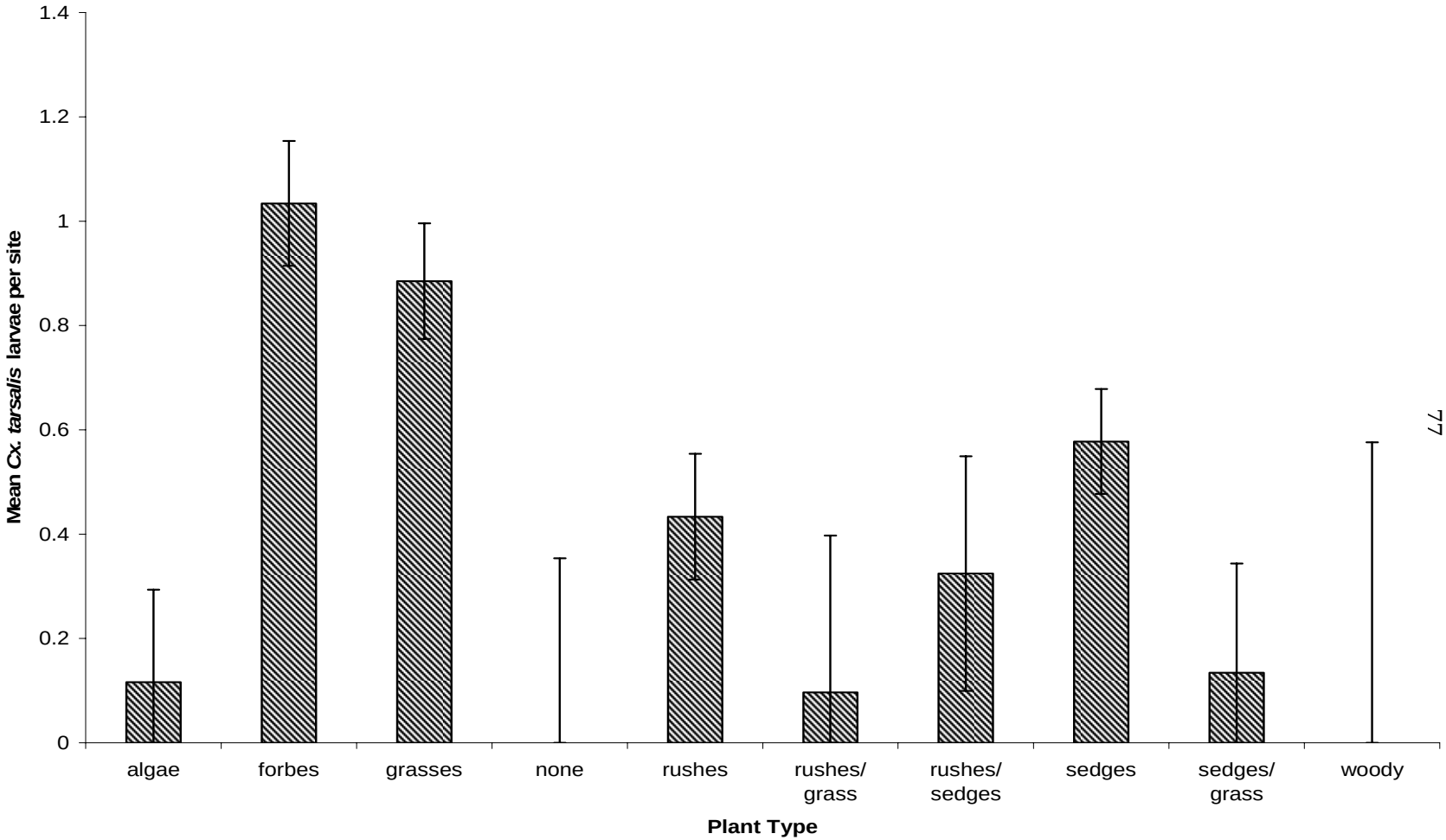



Figure 12. *Culex tarsalis* production by local habitat plant type across the Powder River basin, Wyoming for the week of 4 August 2005 (Julian date 216).

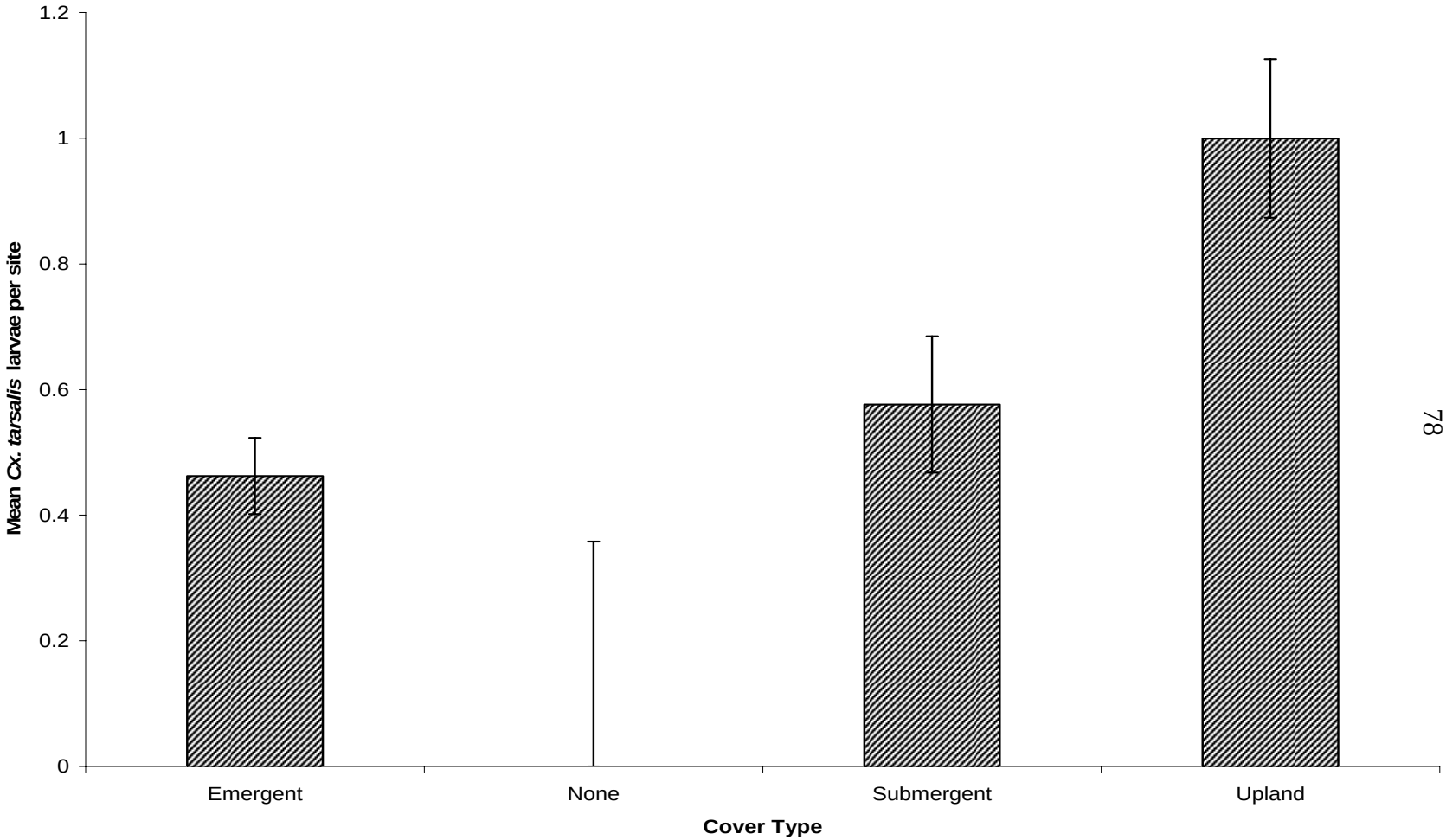





Figure 13. *Culex tarsalis* production by local habitat cover type across the Powder River basin, Wyoming for the week of 4 August 2005.

In other areas *Cx. tarsalis* have been found in high abundances in freshly flooded ponds in Southern California, with peak populations several days after flooding (x = 7) (Beehler and Mulla 1995). Fluctuating water levels of CBNG ponds and pond outlets are similar to the flooded habitats studied in California, and provide more oviposition sites for *Cx. tarsalis* than other aquatic habitats in this region.

High larval production of *Cx. tarsalis* in CBNG sites is consistent with high capture rates of adult *Cx. tarsalis* in light traps in 2005, showing that increased larval populations equate to an increased abundance of host-seeking vectors that can potentially spread WNV. Study areas with the highest adult *Cx. tarsalis* population also had the highest mosquito infection rates in 2004 and 2005, with mature CBNG sites having infection rates of 1.96 infected mosquitoes per 1000 in our 2005 study. In 2003, the U. S. Geological Survey indicated that 70% of WNV cases in humans in Wyoming were from the PRB, which accounts for approximately 11% of the counties in the state (3 counties). That same year, survival of sage-grouse in natural gas fields in the Spotted Horse area of the PRB showed a 75% decline due to WNV infection, and demonstrated little ability to develop antibodies to this pathogen (Naugle et al. 2004, 2005; Walker et al. 2004).

Coal bed natural gas ponds do not currently produce many *Ae. vexans,* which are known vectors for Rift Valley Fever (RVF) in Eurasia and Africa (Ba et al. 2005). They also do not produce significant *Ae. melanimon*, which vector Western Equine Encephalitis (WEE) and Saint Louis Encephalitis (SLE) in the western hemisphere (Jensen and Washino 1991). Larvae of *Ae. vexans* or *Ae. melanimon* were most abundant in natural and irrigated agricultural sites, likely because these sites are ephemeral,

providing muddy substrate for oviposition. I recommend that these habitats be closely monitored if the risk of RVF, WEE, or SLE increases regionally.

Field studies in southern California indicated that *Cx. tarsalis* prefer aquatic habitats surrounded by grasses and annual vegetation with large populations of protozoans, and bacteria, as well as decay of elevated vegetation (Beehler and Mulla 1995; Fanara and Mulla 1974). Vegetation and high primary productivity provide food and cover for larval mosquitoes, making them an important component for oviposition sites. My vegetation assessment indicates that both new and mature CBNG ponds as well as natural water sources are fulfilling these requirements for *Cx. tarsalis* habitats. Recent research using Landsat satellite imagery from the PRB found that CBNG development has resulted in a 75% increase of potential larval habitat for *Cx. tarsalis* (Zou et al. 2006). My larval sampling indicates that CBNG sites are good larval habitats for *Cx. tarsalis*, especially those with flooded grasses and vegetation. As such CBNG ponds are producing mosquitoes at a rate at or above natural water sources in this region.

*Culex tarsalis* do not prefer open water habitats as oviposition sites throughout their range (Jiannino and Walton 2004). In the PRB, I found no *Cx. tarsalis* larvae in open water habitats throughout the 2005 field season. Modifying existing CBNG ponds by reducing aquatic vegetation and making shorelines steeper may reduce *Cx. tarsalis* production in this region without providing habitats for other disease vectors such as *C. sonorensis*. Habitat modifications for *Cx. tarsalis* production have been used with some success in wastewater treatment ponds in southern California (Batzer and Resh 1992; DeSzalay and Resh 2000; Thullen et al. 2002). Coal bed natural gas ponds provide us an

opportunity to experiment with habitat manipulation practices as vegetation can be completely removed from these areas without reducing the efficiency of the site as in a wastewater treatment facility.

## Management Recommendations

Based on available information that I obtained in this study, I recommend a multi-dimensional approach (AMCA 2006) to reduce mosquito production from CBNG ponds across the PRB. A three-pronged approach for mosquito control of *Cx. tarsalis* at CBNG sites would include 1) modifying new CBNG ponds for primary source reduction, 2) site modifications to new CBNG sites and retro-fitting existing ponds to reduce larval production, and 3) initiating mandatory use of larval control methods at existing CBNG sites.

The most effective way to reduce future mosquito production is to limit construction of additional CBNG ponds. One way to limit the number of newly created CBNG ponds is to re-inject water produced during the extraction process into sub-surface voids after gas is removed (USGS 2000; Department of Energy 2002). A new technology for water re-injection is currently being tested in the PRB where no treatment chemicals are needed, and approximately 75% of CBNG production water is capable of being received by the aquifer (Society of Petrolium Engineers 2007). This technology, called the Aquifer Recharge Injection Device (ARID), is currently being tested by Marathon Oil in eleven wells in the PRB with permits for more to come. If new CBNG

ponds are not eliminated, then modifications such as the ones listed below to new and existing ponds would likely reduce mosquito production from these habitats.

The following are seven distinct site modifications that if adhered to, would minimize exploitation of CBNG ponds by *Cx. tarsalis:*

1. Increase the size of ponds to accommodate a greater volume of water than is discharged. This will result in un-vegetated and muddy shorelines that breeding *Cx. tarsalis* avoid (De Szalay and Resh 2000). This modification may reduce *Cx. tarsalis* habitat but could create larval habitat for *Culicoides sonorensis*, a vector of blue tongue disease, and should be used sparingly (Schmidtmann et al. 2000). Steep shorelines should be used in combination with this technique whenever possible (Knight et al. 2003).
2. Build steep shorelines to reduce shallow water (>60 cm) and aquatic vegetation around the perimeter of impoundments (Knight et al. 2003). Construction of steep shorelines also will create more permanent ponds that are a deterrent to colonizing mosquito species like *Cx. tarsalis* which prefer newly flooded sites with high primary productivity (Knight et al. 2003).
3. Maintain the water level below that of rooted vegetation for a muddy shoreline that is unfavorable habitat for mosquito larvae. Rooted vegetation includes both aquatic and upland vegetative types. Avoid flooding terrestrial vegetation in flat terrain or low lying areas. Aquatic habitats with a vegetated inflow and outflow separated by open water produce 5-10 fold fewer *Culex* mosquitoes than completely vegetated wetlands (Walton and Workman 1998). Wetlands with

open water also had significantly fewer stage III and IV instars which may be attributed to increased predator abundances in open water habitats (Walton and Workman 1998).

4. Construct dams or impoundments that restrict down slope seepage or overflow by digging ponds in flat areas rather than damming natural draws for effluent water storage, or lining constructed ponds in areas where seepage is anticipated (Knight et al. 2003).
5. Line the channel where discharge water flows into the pond with crushed rock, or use a horizontal pipe to discharge inflow directly into existing open water, thus precluding shallow surface inflow and accumulation of sediment that promotes aquatic vegetation.
6. Line the overflow spillway with crushed rock, and construct the spillway with steep sides to preclude the accumulation of shallow water and vegetation.
7. Fence pond site to restrict access by livestock and other wild ungulates that trample and disturb shorelines, enrich sediments with manure and create hoof print pockets of water that are attractive to breeding mosquitoes.

The third and final part of my suggested three-pronged approach is to initiate the use of larval control methods at CBNG ponds that have been sampled and are positive for mosquito larvae. Treating CBNG ponds with larvicides such as *Bacillus thuringiensis* var. *israelensis* (Bti) have been shown to provide a 90-100% reduction in *Ae. vexans* and *Culex* spp. larvae in California, and these materials could be used in CBNG ponds to control larvae during weeks of peak densities (Berry et al. 1987; Russel et al. 2003).

Larvicide treatments of CBNG ponds should be conducted by certified pesticide applicators that have been trained to identify mosquito breeding habitats in the field, and can efficiently distribute larviciding materials according to product guidelines. The key to managing mosquito production with larvicide materials is to place the product in areas of high larval densities (Berry et al. 1987). Trained field personnel will need to visit potential mosquito production areas on a weekly or bi-weekly basis during the growing season to check for mosquito production. Treatment will then need to be administered when 1) appropriate larval densities are found (e.g., 5 larvae per dip) and 2) when larvae sampled are in a target genus (e.g., *Culex* spp.). When larvicides are applied they should be used in concentrations according to product guidelines, and only in aquatic areas that are known larval mosquito habitats including flooded upland grasses and emergent aquatic vegetation.

Lastly, additional research is being conducted to assess the efficacy of using native larvivorous fishes to control mosquito population CBNG ponds. It is possible that a combination of water re-injection, CBNG pond modification and larvivorous fishes could be used to reduce the overall mosquito production without the need for a long-term labor-intensive mosquito management programs surrounding CBNG development. Until this is known, this three-pronged approach to managing mosquito production is prudent to reducing the risk of disease to humans and wildlife in the PRB.

# REFERENCES CITED

Aldridge, C. L. and M. S. Boyce. In Press. Linking occurrences and fitness to persistence: a habitat based approach for endangered sage-grouse. Ecological Applications.

[AMCA] American Mosquito Control Association. "Adult [mosquito] Controls". 2006. www.mosquito.org/mosquito-information/control.aspx.

Austgen, L. E., R. A. Bowen, M. L. Bunning, B. S. Davis, C. J. Mitchell and G. J. Chang. 2004. Experimental infection of cats and dogs with West Nile virus. Emerging Infectious Diseases. 10: 82-86.

Ba, Yamar, D. Diallo, C. Mouhamed, F Kebe, I. Dia and M. Diallo. 2005. Aspects of bioecology of two Rift Valley fever virus vectors in Senegal (West Africa): *Aedes vexans* and *Culex poicilipes* (Diptera: Culicidae). Journal of Medical Entomology. 42: 739-750.

Bailey, S. F., D. A. Eliason and B. L. Hoffman. 1965. Flight and dispersal patterns of the mosquito *Culex tarsalis* Coquillett in the Sacramento Valley of California. Hilgardia. 37: 73-113.

Baqar, S. 1993. Vertical transmission of West Nile virus by *Culex* and *Aedes* mosquitoes. American Journal of Tropical Medicine and Hygiene. 48: 757-762.

Bast, T. F. 1961. A note of flight periodicity of mosquitoes. N. J. Mosquito Extermination Association Proceedings from the 48th Annual Meeting: 203-211.

Bates, M. 1970. The natural history of mosquitoes. Peter Smith, Gloucester, Mass. 378 pp.

Batzer, D. P., V. H. Resh. 1992. Macroinvertebrates of a California seasonal wetland and responses to experimental manipulation. Wetlands. 12: 1-7.

Beehler, J. W., M. S. Mulla. 1995. Effects of organic enrichment on temporal distribution and abundance of culicine egg rafts. Journal of the American Mosquito Control Association. 11: 167-171.

Berkelhamer, R. C., T. J. Bradley. 1989. Mosquito larvae development in container habitats: The role of rotting *Scirpus californicus*. Journal of the American Mosquito Control Association. 5: 258-260.

Berry, W. J., M. G. Novak, S. Khounlo, W. A. Rowley and G. L. Melchior. 1987. Efficacy of *Bacillus sphaericus* and *Bacillus thuringiensis* var. *israelensis* for control of *Culex pipiens* and floodwater *Aedes* larvae in Iowa. Journal of the American Mosquito Control Association. 3: 579-582.

Bidlingmayer, W. L. 1985. The measurement of mosquito population changes- some considerations. Journal of the American Mosquito Control Association. 1: 328-348.

Biggerstaff, B. J. 2006. PooledInfRate, Version 3.0: A Microsoft Excel Add-In to compute prevalence estimates from pooled samples. Centers for Disease Control and Prevention, Fort Collins, CO.

Blackmore, J. P. and R. P. Dow. 1958. Differential feeding of *Culex tarsalis* on nestling and adult birds. Mosquito News. 18: 15-17.

BLM 2003a. Final Environmental Impact Statement and Proposed Plan Amendment for the Powder River Basin Oil and Gas Project. http://www.wy.blm.gov/nepa/prb-feis/index.htm.

BLM 2003b. Montana Statewide Final Oil and Gas EIS and Amendment of the Powder River and Billings Resource Management Plans. http://www.mt.blm.gov/mcfo/CBNG/eis/index.html.

Bunning, M. L., R. A. Bowen, C. B. Cropp, K. G. Sullivan, B. S. Davis, N. Komar, M. S. Godsey, D. Baker, D. L. Hettier, D. A. Holmes, B. J. Biggerstaff and C. J. Mitchell. 2002. Experimental infection of horses with West Nile virus. Emerging Infectious Diseases. 8: 380-386.

Buth, J. L., R. A. Brust and R. A. Ellis. 1990. Development time, ovoposition activity and onset of diapause in *Culex tarsalis*, *Culex restuans* and *Culiseta inornata* in Southern Manitoba. Journal of the American Mosquito Control Association. 6: 55-63.

[CDC] Centers for Disease Control. "West Nile Virus". 2006. Division of Vector-Borne Infectious Diseases. www.cdc.gov/ncidod/dvbid/westnile/index.htm.

Cech, J. J. and A. L. Linden. 1987. Comparative larvivorous performance of mosquitofish, *Gambusia affinis*, and juvenile Sacramento blackfish, *Orthodon microlepidotus*, in experimental paddies. Journal of the American Mosquito Control Association. 3: 35-41.

Clark, M. L., K.A. Miller and M. H. Brooks. 2001. U.S. geological survey monitoring of Powder River basin stream-water quantity and quality. Water -Resources Investigations Report 01-4279. Cheyenne, Wyo.

Clements, A. N. 1992. The Biology of Mosquitoes, Volume 1. CABI publishing, New York, NY.

Crans, W. J. 2004. A classification system for mosquito life cycles: life cycle types for mosquitoes of the northeastern United States. Journal of Vector Ecology. 29: 1-10.

Darsie, R. F. and R. A. Ward. 1981. Identification and Geographical distribution of the Mosquitoes of North America, North of Mexico. American Mosquito Control Association, Eatontown, NJ.

Daszak, P., A. A. Cunningham and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife- threats to biodiversity and human health. Science. 287: 443-449.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetational analysis. Northwest Science. 33:43-64.

De Szalay, F. A. and V. H. Resh. 2000. Factors influencing macroinvertebrate colonization of seasonal wetlands: responses to emergent plant cover. Freshwater Biology. 45: 295-308.

[DOE] U. S. Department of Energy. 2002. Powder River Basin coal bed methane development and produced water management study. U. S. Department of Energy. Office of Fossil Energy and National Energy Technology Laboratory Strategic Center for Natural Gas: 1-3.

Dohm, D.J., M.L. O'Guinn and M. J. Turell. 2002. Effect of environmental temperature on the availability of *Culex pipiens* (Diptera: Culicidae) to transmit West Nile virus. Journal of Medical Entomology. 39: 221-225.

Edmunds, L. R. 1955. Notes on the biology and seasonal abundances of the larval stages of *Culex tarsalis* coq. in irrigated areas of Scotts Bluff, Nebraska. Mosquito News. 15:157-160.

Fanara, D. M. and M. S. Mulla. 1974. Population dynamics of larvae of *Culex tarsalis* Coquillett and *Culiseta inornata* (Williston) as related to flooding and temperature of ponds. Mosquito News. 34: 98-104.

Gingrich, J. B., R. D. Anderson, G. M. Williams, L. O'connor and K. Harkins. 2006. Stormwater ponds, constructed wetlands, and other best management practices as

potential breeding sites for West Nile virus vectors in Delaware During 2004. Journal of the American Mosquito Control Association. 22: 282-291.

Goddard, L. B., A. B. Roth, W. K. Reisen and T. W. Scott. 2002. Vector competence of California mosquitoes for West Nile virus. Emerging Infectious Diseases. 9: 311-322.

Goddard, L. B., A. B. Roth, W. K. Reisen and T. W. Scott. 2003. Vertical transmission of West Nile virus by three California *Culex* (Diptera: Culicidae) Species. Journal of Medical Entomology. 40: 743-747.

Gunstream, S. E., R. M. Chew, D. W. Hagstrum and C. H. Templelis. 1971. Feeding patterns of six species of mosquitoes in arid southeastern California. Mosquito News. 31: 99-101.

Hayes, C. 1989. West Nile Fever. Arboviruses: Epidemiology and Ecology. 5: 59-88. CRC, Boca Raton, FL.

Hayes, E. B. 2005. Epidemiology and transmission dynamics of West Nile virus disease. Emerging Infectious Diseases. 11: 1167-1173.

Hemstrom, M. A., M. J. Wisdom, W. J. Hann, M. M. Rowland, B. C. Wales and R. A. Gravenmier. 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the interior Columbia Basin, U. S. A. Conservation Biology. 16: 1243-1255.

Higgs, S., B. S. Schneider, D. L. Vanlandingham, K. A. Klingler and E. A. Gould. 2005. Nonviremic transmission of West Nile virus. Proceedings of the National Academy of Sciences. 102: 8871-8874.

Holloran, M. J. Greater sage-grouse (*Centercercus urophasianus*) population response to natural gas field development in western Wyoming. PhD dissertation, University of Wyoming, December, 2005.

Horsfall, W. R. and A. P. Morris. 1952. Surface conditions limiting larval sites of certain marsh mosquitoes. Annals Entomological Society of America. 45: 492-498.

Hubalek, Z. and J. Halouzka. 1999. West Nile fever - a reemerging mosquito-borne viral disease in Europe. Emerging Infectious Diseases. 5: 643-650.

Hulbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs. 54: 187–211.

Isoe, J. and J. G. Millar. 1995. Characterization of factors mediating oviposition site choice by *Culex tarsalis*. Journal of the American Mosquito Control Association. 11: 21-28.

Jensen, T., R. K. Washino. 1991. An assessment of the biological capacity of a Sacramento valley population of *Aedes melanimon* to vector arboviruses. The American Journal of Tropical Medicine and Hygine. 44: 355-363.

Jiannino, J. A. and W. E. Walton. 2004. Evaluation of vegetation management strategies for controlling mosquitoes in a southern California constructed wetland. Journal of the American Mosquito Control Association. 20: 18-26.

Kilpatrick, A. M., L. D. Kramer, M. J. Jones, P. P. Marra and P. Daszek. 2006. West Nile virus epidemics in North America are driven by shifts in mosquito feeding behavior. Plos Biology. 4: 1-5.

Knight, R. L., W. E. Walton, G. F. Meara, W. K. Riesen and R. Wass. 2003. Strategies for effective mosquito control in constructed treatment wetlands. Ecological Engineering. 21: 211-232.

Komar, N. R. Lanciotti, R. Bowen, S. Langevin and M. Bunning. 2002. Detection of West Nile virus in oral and cloacal swabs collected from bird carcasses. Emerging Infectious Diseases. 8: 741-742.

Komar, N., S. Langevin, S. Hinten, N. Nemeth, E. Edwards, D. Hettler, B. Davis, R. Bowen and M. Bunning. 2003. Experimental infection of North American birds with the New York 1999 strain of West Nile virus. Emerging Infectious Diseases. 9: 311-322.

Lampkin, R., U. Eckenbach, D. Seigler and R. Novak. 2000. Laboratory evaluations of methylated soy oil and monoterpenes as mosquito larvicides. Journal of the American Mosquito Control Association. 16: 153-157.

Lawler, S. P. and D. A. Dritz. 2005. Straw and winter flooding benefit mosquitoes and other insects in a rice agroecosystem. Ecological Applications. 15: 2052-2059.

Linden, A. L., J. J. Cech. 1990. Prey selection by mosquitofish (*Gambusia affinis*) in California rice fields: effect of vegetation and prey species. Journal of the American Mosquito Control Association. 6: 115-120.

Littell, R. C., G. A. Milliken, W. W. Stroup and R. D. Wolfinger. 1996. SAS System for Mixed Models. SAS Institute, Cary, North Carolina, USA.

Litell, R. C., P. R. Henry and C. B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. Journal of Animal Science. 76: 1216-1231.

Lothrop, H. D. and W. K. Riesen. 2001. Landscape affects of the host-seeking patterns of *Culex tarsalis* ( Diptera: Culicidae) in the Coachella valley of California. Journal of Medical Entomology. 38: 325-332.

Marra, P.P., S. Griffing, C. Caffrey, A. M. Kilpatrick, R. McLean and C. Brand. 2004. West Nile Virus and Wildlife. BioScience. 54: 393-402.

Marten, G. G., E. S. Bordes, M. Nguyen. 1994. The use of cyclopoid copepods for mosquito control. Hydrobiologica. 292-293: 491-496.

McKinley, Randy. Personal communication. May, 2004.

McLean, R. G., S. R. Ubico, D. Bourne and N. Komar. 2002. West Nile virus in livestock and wildlife. In: Japanese Encephalitis and West Nile viruses. Springer Publishing, 271-308.

Mercer, D. R., S. L. Sheeley and E. J. Brown. 2005. Mosquito (Dipetera: Culicidae) development within microhabitats of an Iowa wetland. Journal of Medical Entomology. 42: 685-693.

Meyer, R. P., J. L. Hardy and W. K. Reisen. 1990. Diel changes in adult mosquito microhabitat temperatures and their relationship to the extrinsic incubation of arboviruses in mosquitoes in Kern County, California. Journal of Medical Entomology. 27: 607-614.

Milby, M. M. and R. P. Meyer. 1986. The influence of constant versus fluctuating water temperatures on the preimaginal development of *Culex tarsalis*. Journal of the American Mosquito Control Association. 2: 7-10.

Molaei, G., T. G. Andreadis, P. M. Armstrong, J. F. Anderson and C. R. Vossbrinck. 2006. Host feeding patterns of Culex mosquitoes and West Nile virus transmission, Northeastern United States. Emerging Infectious Disease. 12: 468-474.

Morris, C. D., W. G. Baker, L. Stark, J. Burgess and A. L. Lewis. 1994. Comparison of chickens and pheasants as sentinels for Eastern Equine encephalitis and St. Louis encephalitis viruses in Florida. Journal of the American Mosquito Control Association. 10: 545-548.

Nasci, R. J., D. S. White, H. Stirling, J. Oliver, T. J. Daniels, R. C. Falco, S. Campbell, W. J. Crans, H. M. Savage, R. S. Lanciotti, C. G. Moore, M. S. Godsey, K. L. Gottfried and C. J. Mitchell. 2001. West Nile virus isolates from mosquitoes in New York and New Jersey, 1999. Emerging Infectious Diseases. 7: 626-630.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes and M. S. Boyce. 2004. West Nile virus: pending crisis for greater sage-grouse. Ecology Letters. 7: 704-713.

Naugle, D. E., C. L. Aldridge, B. L. Walker, K. E. Doherty, M. R. Matchett, J. McIntosh, T. E. Cornish and M. S. Boyce. 2005. West Nile virus and sage-grouse: what more have we learned? Wildlife Society Bulletin. 33: 1-8.

Naugle, D. R., K. E. Doherty and B. L. Walker. Land use change due to coal bed natural gas development in northwestern Wyoming (in review).

National Weather Service (NOAA). 2006. "Preliminiary Local Climatological Data [Sheridan, Wyoming]". http://www.weather.gov/climate/index.php?wfo=byz.

O'Leary, D. R., A. A. Marfkin, S. P. Montgomery, A. M. Kipp, J. A. Lehman, B. J. Biggerstaff, V. L. Elko, P. D. Collins, J. E. Jones and G. L. Campbell. 2004. The epidemic of West Nile virus in the United States, 2002. Vector-borne and Zoonotic Diseases. 4: 61-70.

Porphyre, T., D. J. Bicout. and P. Sabatier. 2005. Modelling the abundance of mosquito vectors versus flooding dynamics. Ecological Modelling. 183: 173-181.

Rappole, J. H. and Z. Hubalek. 2003. Migratory birds and West Nile virus. Journal of Applied Microbiology. 94: 47S-58S.

Regele, S. and J. Stark. 2000. Coal-bed methane gas development in Montana, some biological issues. Proceedings from the 2000 Coal-bed Methane Workshop. Helena, MT.

Riesen, W. K., M. M. Milby and M. E. Bock. 1984. The effects of immature stress on selected events in the life history of *Culex tarsalis*. Mosquito News. 44: 385-395.

Riesen, W. K. and W. C. Reeves. 1990. Bionomics and ecology of *Culex tarsalis* and other potential mosquito vector species. Epidemiology and control of mosquito-borne arboviruses in California, 1943-1987: California Mosquito Vector Control Association, Sacramento, CA. 254-329.

Riesen, W. K., H. D. Lothrop. 1995. Population ecology and dispersal of *Culex tarsalis* (Diptera: Culicidae) in the Coachella Valley of California. Journal of Medical Entomology. 32: 490- 502.

Riesen, W. K., H. D. Lothrop and R. P. Meyer. 1997. Time of host-seeking by *Culex tarsalis* (Diptera: Culicidae) in California. Journal of Medical Entomology. 34: 430-437.

Riesen, W. K., H. D. Lothrop and R. E. Chilies. 1998. Ecology of *Aedes dorsalis* (Diptera: Culicidae) in relation to Western Equine Encephalomyelitis virus in the Coachella valley of California. Journal of Medical Entomology. 35: 561-566.

Riesen, W. K. 2002. "*Culex tarsalis*: history, biology, ecology, public health and control". National West Nile virus conference. Atlanta, Georgia. July 10, 2002.

Riesen, W. K., H. D. Lothrop and B. Lothrop. 2003. Factors influencing the outcome of mark-release-recapture studies with *Culex tarsalis* (Dipetera: Culicidae). Journal of Medical Entomology. 40: 820-829.

Riesen, W. K., Y. Fang and V. M. Martinez. 2006. Effects of temperature on the transmission of West Nile virus by *Culex tarsalis* (Dipetera: Culicidae). Journal of Medical Entomology. 43: 309-317.

Rios, J., C. S. Hacker, C. A. Hailey and R. A. Parsons. 2006. Demographic and spatial analysis of West Nile virus and Saint Louis Encephalitis in Houston, TX. Journal of the American Mosquito Control Association. 2: 254-263.

Robich, R. M., D. L. Denlinger. 2005. Diapause in the mosquito Culex pipiens evokes a metabolic swich from blood feeding to sugar gluttony. Proceedings of the National Academy of Sciences. 102: 15912 – 15917.

Rocke, T., K. Converse, C. Meteyer and B. McLean. 2005. The impact of disease in the American White Pelican of North America. Waterbirds. 28 (Special Publication 1): 87-94.

Rodhain, F, J. J. Petter, R. Albiqnac, P. Coulanges, C, Hannoun. 1985. Arboviruses and lemurs in Madagascar: experimental infection of *Lemur fulvus* with yellow fever and West Nile viruses. American Journal of Tropical Medicine and Hygiene. 34: 816-822.

Rochrig, J. T., M. Layton, P. Smith, G. L. Campbell, R. Nasci and R. S. Lanciotti. 2002. The emergence of West Nile virus in North America: Ecology, Epidemology and

Surveillance. In: Japanese Encephalitis and West Nile viruses. Springer Publishing, 223-240.

Russell, T. L., M. D. Brown, D. M. Purdie, P. A. Ryan and B. H. Kay. 2003. Efficacy of VectoBac (*Bacillus thuringiensis* variety *israelensis*) formulations for mosquito control in Australia. Journal of Economic Entomology. 96: 1786-1791.

Schmidtmann, E. T., R. J. Bobian, R. P. Beldin. 2000. Soil Chemistries Define Aquatic Habitats with Immature Populations of the *Culicoides variipenni*s Complex (Diptera: Ceratopogonidae). Journal of Medical Entomology. 37: 38-64.

Service, M. W. 1997. Mosquito (Diptera: Culicidae) dispersal- the long and short of it. Journal of Medical Entomology. 34: 579-588.

Smithburn, K. C. 1940. A neurotropic virus isolated from the blood of a native of Uganda. American Journal of Tropical Medicine and Hygiene. 20: 471-492.

Society of Petroleum Engineers. 2007. New water-injection technology for coalbed methane gets trial run. http://updates.spe.org/index.php/2007/10/10/new-water-injectection-technology-gets-trial-run/.

Steele, K. E., M. J. Linn, R. J. Schoepp, N. Komar, T. W. Geisbert, R. M. Manduca, P.P. Calle, B. L. Raphael, T. L. Clippinger, T. Larsen, J. Smith, R. S. Lanciotti, N.A. Panella and T. S. McNamara. 2000. Pathology of fatal West Nile virus infections in native and exotic birds during the 1999 outbreak in New York City. Veterinary Pathology. 30: 208-224.

Systat Software Inc. 2004. Systat 11 users guide. Point Richmond, CA: Systat Software Inc.

Tauber, M. J., C. A. Tauber. 1976. Insect seasonality: Diapause maintenance, termination and post-diapause development. Annual Review of Entomology. 21: 81–107.

Taylor, D. S., S. A. Ritchie and E. Johnson. 1992. The killifish *Rivulus marmoratus*: a potential biocontrol agent for *Aedes taeniorhynchus* and brackish water *Culex*. Journal of the American Mosquito Control Association. 8: 80-83.

Tempelis, C. H. and R. K. Washino. 1967. Host-feeding patterns of *Culex tarsalis* in the Sacramento Valley, CA with notes on other species. Journal of Medical Entomology. 4: 315-318.

Thullen, J.S., J. J. Sartoris and W. E. Walton. 2002. Effects of vegetation management in constructed wetland treatment cells on water quality and mosquito production. Ecological Engineering. 18: 441-457.

Tiawsirisup, S, K. B. Platt, B. J. Tucker and W. A. Rowley. 2005. Eastern cottontail rabbits (*Sylvilagus floridanus*) develop West Nile virus viremias sufficient for infecting select mosquito species. Vector Borne and Zoonotic Diseases. 5: 342-350.

Turell, M. J., M. L. O'Guinn, D. J. Dohm and J. W. Jones. 2001. Vector competence of North American Mosquitoes (Diptera: Culicidae) for West Nile virus. Journal of Medical Entomology. 38: 130-134.

Turell, M. J., M. R. Sardelis, M. L. O'Guinn and D. J. Dohm. 2002. Potential vectors of West Nile virus in North America. In: Japanese Encephalitis and West Nile viruses. Springer Publishing, 241-252.

Turell, M. J., M. L. O'Guinn, D. J. Dohm, J. P. Webb Jr., M. R. Sardelis. 2002. Vector competence of Culex tarsalis from Orange County, California, for West Nile Virus. Vector-Borne and Zoonotic Diseases. 2: 193-196.

Turell, M. J., D. J. Dohm, M. R. Sardelis, M. L. Oquinn, T. G. Andreadis, J. A. Blow. 2005. An update on the potential of North American mosquitoes (Diptera: Culicidae) to transmit West Nile virus. Journal of Medical Entomology. 42: 57-62.

U.S. Environmental Protection Agency. 2006. Watersheds. Revised 4/11/06. http://cfpub.epa.gov/surf/locate/map2.cfm.

U. S. Geological Survey. 2004. West Nile maps. http://westnilemaps.usgs.gov/.

U. S. Geological Survey. 2000. Water Production with Coal-Bed Methane. USGS fact sheet FS-156-00.

Vicklund, L. E. 2000. Historical sagebrush establishment practices in the Powder River basin. Proceedings of the 2000 Billings Land Reclamation Symposium. Billings, MT.

Walker, B. L., D. E. Naugle, K. E. Doherty and T. E. Cornish. 2004. From the field: outbreak of West Nile virus in greater sage-grouse and guidelines for monitoring, handling, and submitting dead birds. Wildlife Society Bulletin. 32: 1000-1006.

Walton, W. E., N. S. Tietze and M. S. Mulla. 1990. Ecology of *Culex tarsalis* (Diptera: Culicidae): factors influencing larval abundance in mesocosms in Southern California. Journal of Medical Entomology. 27: 57-67.

Walton, W. E., P. D. Workman. 1998. Effect of marsh design on the abundance of mosquitoes in experimental constructed wetlands in southern California. Journal of the American Mosquito Control Association. 14: 95-107.

Walton, W. E. 2007. Larvivorous Fish Including *Gambusia*. Biorational Control of Mosquitoes. The American Mosquito Control Association. 7: 184-220.

Willems, K. J., C. E. Webb and R. C. Russell. 2005. A comparison of mosquito predation by the fish *Pseudomulgil signifier* Kner and *Gambusia holbrooki* (Girard) in laboratory trials. Journal of Vector Ecology. 30: 87-90.

Woodrow, R. J., J. J. Howard, D. J. White. 1995. Field trials with methoprene, temephos and *Bacillus thuringiensis serovar israelensis* for the control of larval Culiseta melanura. Journal of the American Mosquito Control Association. 11: 424-427.

Wyoming Department of Health. "West Nile virus detection by county." 2006. Wyoming Department of Health, August 21, 2006, badskeeter@state.wy.us.

Zou, L., S. N. Miller and E. T. Schmidtmann. 2006. Mosquito larval habitat mapping using remote sensing and GIS: Implications of Coalbed Methane development and West Nile Virus. Journal of Medical Entomology. 43: 1034-1041.

Zou, L., S. N. Miller and E. T. Schmidtmann. A GIS tool to estimate West Nile virus risk based on a degree-day model. Environmental Modeling Assessment: In Press.

**Wildlife Biology 20: 320–325, 2014**
doi: 10.2981/wlb.00004
© 2014 The Authors. This is an Open Access article
Subject Editor: Hans Pedersen. Accepted 15 July 2014

# Linking conservation actions to demography: grass height explains variation in greater sage-grouse nest survival

**Kevin E. Doherty, David E. Naugle, Jason D. Tack, Brett L. Walker, Jon M. Graham and Jeffrey L. Beck**

*K. E. Doherty (kevin_doherty@fws.gov), US Fish and Wildlife Service, Lakewood, CO 80228, USA. – D. E. Naugle and B. L. Walker, Wildlife Biology Program, Univ. of Montana, Missoula, MT 59812, USA. DEN also at: USDA Sage Grouse Initiative, Missoula, MT 59812, USA. – J. D. Tack, Fish, Wildlife and Conservation Biology, Colorado State Univ., Fort Collins, CO 80523, USA. – J. M. Graham,Mathematical Sciences, Univ. of Montana, Missoula, MT 59812, USA. – J. L. Beck, Dept of Ecosystem Science and Management, Univ. of Wyoming, Laramie, WY 82071, USA*

Conservation success often hinges on our ability to link demography with implementable management actions to influence population growth ($\lambda$). Nest success is demonstrated to be important to $\lambda$ in greater sage-grouse *Centrocercus urophasianus*, an imperiled species in the North American sagebrush-steppe. Enhancing this vital rate through management represents an opportunity to increase bird numbers inside population strongholds. We identified management for grass height as an action that can improve nest success in an analysis of sage-grouse nests (n = 529) from a long-term study (2003–2007) in the Powder River Basin, southeast Montana and northeast Wyoming, USA. Average grass height by study area and year varied (11.4–29.2 cm) but its positive effects on nest survival were consistent among study years and study areas that differed in absolute rates of nest success. We tested the predictive ability of models by grouping output from log-link analyses (2004–2006) into two bins with nest success probabilities $< 0.45$ and $> 0.55$, and validated the relationship with additional data from 2003 and 2007. Nests with probabilities $> 0.55$ were 1.64 (2004–2006) to 3.11 (2007) times more likely to hatch than those $< 0.45$, except in 2003 when an early wet spring resulted in universally high grass height at nest sites (29.2 cm) and high predicted nest success (64%). The high predictive power of grass height illustrates its utility as a management tool to increase nest success within priority landscapes. Relationships suggest that managing grass height during drought may benefit sage-grouse populations.

Achieving desired conservation outcomes requires planning at scales that match the biological needs of wide-ranging focal species (Nicholson et al. 2013). Inherent in conservation success is our ability to link demography to implementable management actions that influence population growth ($\lambda$; Mills 2012). Implementing locally beneficial conservation practices inside intact ecosystems maximally benefits species for which landscape context matters (Wilson et al. 2007, Schultz 2010). Advances in spatial ecology make landscape prioritization more feasible (Millspaugh and Thompson 2009), but identifying intact targets is only a first step (Knight et al. 2008). Still missing in most plans is a demographic link between a conservation action and its ability to influence demographic traits influencing $\lambda$ (Wisdom et al. 2000, Caswell 2001).

Greater sage-grouse *Centrocercus urophasianus* (hereafter sage-grouse) are native only to western arid and semiarid sagebrush *Artemisia* spp. landscapes (Schroeder et al. 1999), and extirpated from half their range (Schroeder et al. 2004), the species is a candidate for listing under the federal Endangered Species Act (US Fish and Wildlife Service 2010). Major fragmenting threats include energy development (Naugle 2012), wildfire (Bukowski and Baker 2013, Murphy et al. 2013), cultivation for row crop production (Foley et al. 2011) and others (Knick et al. 2013). The current sage-grouse distribution encompasses 76 million hectares, yet population densities are highly clumped across their range (Doherty et al. 2010a). In efforts to focus conservation actions, the US Fish and Wildlife Service identified "Priority Areas for Conservation" (PACs; US Fish and Wildlife Service 2013) by consulting US states to incorporate the best available population and habitat data into site delineation. Research has focused on reducing threats to populations within PACs (Baruch-Mordo et al. 2013, Copeland et al. 2013), yet management actions that aim to bolster populations within priority areas will be critical for a species with declining distribution.

The purpose of our paper is to increase conservation effectiveness by exploring linkages between demography and implementable actions to benefit populations. Nest success is demonstrably important to λ, and enhancing this vital rate through management may benefit populations (Taylor et al. 2012). Variation in nest survival may in part be explained by grass height (DeLong et al. 1995), a feature influenced by grazing (Rickard et al. 1975), and a preeminent landuse in sagebrush systems. We used generalized linear models to

estimate the influence of vegetation and nest characteristics on sage-grouse nest survival within a landscape context (Dinsmore et al. 2002, Rotella et al. 2004). Findings will help guide the US Dept of Agriculture's Sage Grouse Initiative (SGI) in implementing rotational grazing systems designed to increase hiding cover for nesting grouse inside PACs on 847 000 ha of privately-owned rangelands (<www.sagegrouseinitiative.com/our-work/proactive-conservation/> under Grazing Systems).

## Material and methods

### Study area

We sampled sage-grouse in two distinct study areas in Johnson and Sheridan Counties in northeast Wyoming (southern region), and Bighorn, Rosebud, and Powder River Counties in southeast Montana (northern region), USA. Northern study areas were dominated by sagebrush, with conifer encroachment in more rugged landscapes and overall larger grassland areas. Southern study areas were also dominated by sagebrush, but had no conifers and exhibited smaller grassland areas. Shrub–steppe habitats were dominated by Wyoming big sagebrush *A. tridentata wyomingensis* with an understory of native and non-native grasses. Land use in both study areas was dominated by cattle ranching and land tenure was a mix of federal, state and private. Doherty et al. (2008) provides detailed descriptions of study areas. Because of the differences in landscape context, study area was included as a categorical blocking variable.

### Capture, radio-tracking and predictor variables

We captured sage-grouse in rocket-nets and walk-in traps (Giesen et al. 1982) and by spotlighting (Wakkinen et al. 1992) March–April and July–October in 2003–2007. We aged females, fitted them with necklace style VHF radio collars, and relocated sage-grouse to monitor nests by ground based radio-tracking throughout the breeding season. We used established protocols (Connelly et al. 2003) to quantify local vegetative features known to influence habitat selection within ≤15 m of nests (Connelly et al. 2000, Hagen et al. 2007; Table 1). Doherty et al. (2010b) provides a full description of nest monitoring.

### Statistical analyses and model selection

We used generalized linear models with a binomial likelihood and a log-link to estimate the influence nest age, study area and grass height on the daily survival rates (DSR) of nests (Dinsmore et al. 2002, Rotella et al. 2004). We derived nest survival rates by multiplying DSR together over the 28 day predicted incubation time for sage-grouse. We divided samples into nests used to build the model (n = 383 nests in 2004–2006) and those used to test model stability and predictive capability (n = 146 in 2003 and 2007).

We followed an iterative system for model selection. We first included a variable that controlled for the known effect of a spring snow storm in 2005 on DSR in all variable screenings and final model selection (Walker 2008).

Table 1. List of variables used in model selection explaining sage-grouse nest survival, Powder River Basin, Montana and Wyoming, USA, 2004–2006.

| Candidate variables | Description |
|---|---|
| Local scale habitat variables | |
| Shrub canopy cover | using the line-intercept method along two 30 m perpendicular transects centered at nest or random locations (Canfield 1941) |
| Shrub density | all shrubs > 15 cm within 1 m of transect line were counted, total /120 m$^2$ |
| Quadratic shrub canopy cover | shrub canopy cover + (shrub canopy cover × shrub canopy cover) |
| Nearest shrub height | height of nearest shrub to Daubenmire quadrant location. There were 10 Daubenmire quads on each of the two 30 m transects for a total of 20 Daubenmire quads. They were spaced 3 m apart and started at 0 m |
| Visual obstruction at nest | height density readings at 0, 1, 3 and 5 m from nest or available shrub in each cardinal direction (Robel et al. 1970) |
| Nearest grass height | average of the vegetative droop height for the nearest grass from the 20 Daubenmire quadrants |
| Tallest grass height | average of the vegetative droop height for the tallest grass from the 20 Daubenmire quadrants |
| Average grass height | (nearest grass height + tallest grass height)/2 |
| Nest characteristic variables | |
| Hen age | yearling or adult (Walker 2008) |
| Nest age | (nest age in days + nest age in days$^2$) (Walker 2008) |
| Snowstormmarker | grouped 7 nests that were abandoned following major snow event in May 2005 |
| Abiotic site variables | |
| Study area | north or south Powder River Basin |
| Year | year of observation |

We assigned predictor variables into 1 of 3 model categories: 1) habitat, 2) nest characteristic, and 3) site variables (Table 1). We first examined univariate selection for study area and the 8 habitat variables, and removed variables if 95% confidence intervals overlapped zero. If predictor variables were highly correlated ($r \geq |0.7|$), only the variable with the greatest biological merit was included in the model (Chatfield 1995). When variables were moderately correlated (i.e. $|0.3| \leq r < |0.7|$), we checked for stability and consistency of parameter estimates as predictor variables were added.

We allowed each variable that made it past variable screening to compete with all other combinations of variables to identify the most parsimonious model for habitat and study area. If variables made it past screening we determined if their addition improved model fit via Akaike's information criterion with a small sample size correction factor ($AIC_c$; Burnham and Anderson 2002). After obtaining the best habitat model using $AIC_c$ values, we then tested if inclusion of nest characteristic variables (Table 1) and an additional abiotic site variable (year effect) documented in Walker (2008) were still important predictor variables when included with

habitat covariates. We followed the exact variable screening and AIC methods described above to test if these variables improved model fit.

We tested the predictive strength of the final habitat model by grouping predicted nest survival probability from log-link analyses (2004–2006) into two bins with probabilities of nest survival, $<0.45$ and $>0.55$, generically representing low and high nest survival probabilities, respectively. We then compared observed nest success from independent data sets (2003 and 2007) between low and high validation bins, and calculated the ratio of observed nest success between the high and low bins. We reasoned that observed nest success should be higher in the top validation bin if the final model predicted nest success well across years, demonstrated by a ratio of observed nest success $>1$ between bins. We further evaluated the predictive model by comparing predicted nest success from our top model to observed nest success by year. Average grass height around nesting sage-grouse in a given year (Table 1) was the only continuous predictor variable included in our top model, thus we evaluated how well one variable served as an indicator of nest success. Statistical analyses were performed in program SAS ver. 8.0 (SAS Inst. <http://v8doc.sascom/sashtml/>).

We performed a bootstrap analysis to quantify precision and the effect size of grass height on nest survival, using beta coefficients from the best approximating model (Burnham and Anderson 2002). We used the logistic exposure equation (Rotella et al. 2004) to generate the predicted probability of successfully hatching a nest for each bootstrap dataset ($n = 5000$) by systematically varying grass height within the observed range of variation. We computed at each percentage the probability of successfully hatching a nest for each of 5000 simulations. We ordered these probabilities and used a rankit adjustment (Chambers et al. 1983) to estimate upper and lower 95% confidence intervals.

## Results

Nearest, tallest and average grass height were the only variables with significant coefficients when tested univariately. Nearest, tallest and average grass height were all positively associated with nest success, but were highly correlated and could not be included in the same model. Average and nearest grass height had virtually identical univariate coefficient estimates, however average grass height showed less variation around the estimate (average grass height $\beta = 0.034$, SE = 0.013, 95% CI = 0.008–0.060 vs nearest grass height $\beta = 0.039$, SE = 0.019, 95% CI = 0.001–0.076). Further, average grass height outcompeted nearest and tallest grass measures based on $AIC_c$ values, thus it was retained for additional modeling.

The addition of study area increased model fit, while hen age and year effects were removed from the model because they explained no additional variation in nest survival when included with habitat variables and confidence intervals around effect estimates overlapped zero. The inclusion of nest age increased model fit ($w_i = 0.974$; Table 2). Our final model included average grass height, nest age, study area and the variable that controlled for the known effect of a spring snow storm in 2005 on DSR.

Table 2. Comparisons of grass height, study area and nest age variables to identify the AICc best model explaining sage-grouse nest survival, Powder River Basin, Montana and Wyoming, 2004–2006[a].

| Model | K | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| Average grass height + study area + nest age | 6 | 834.418 | 0.000 | 0.974 |
| Average grass height + study area | 4 | 841.634 | 7.216 | 0.026 |
| Average grass height | 3 | 866.099 | 31.681 | 0.000 |
| Study area | 3 | 927.881 | 93.463 | 0.000 |

[a]all models included a categorical blocking variable which controlled for nests abandoned in a heavy spring storm in 2005 (Walker 2008).

Estimates of average grass height tracked annual trends in nest success (Fig. 1; northern region 2003–2007, beta estimate = 0.036, p = 0.023; southern region 2004–2007, beta estimate = 0.079, p = 0.001). Bootstrap analyses showed the positive relationship between average grass height and nest success (Fig. 2). Our final model including grass height and study area demonstrated large effect sizes (Fig. 2). Nests with probabilities $>0.55$ were 1.64 (2004–2006) to 3.11 (2007) times more likely to hatch than those $<0.45$ (Table 3), except in 2003 when average grass height (29.2 cm) and apparent nest success reached their highest recorded levels (68%, Fig. 1).

## Discussion

High predictive power of grass height illustrates its utility as a management tool to benefit sage-grouse populations. Findings show grass height is a strong predictor of nest survival inside intact landscapes, and increasing hiding cover can increase nest success, a demographic rate that explains a

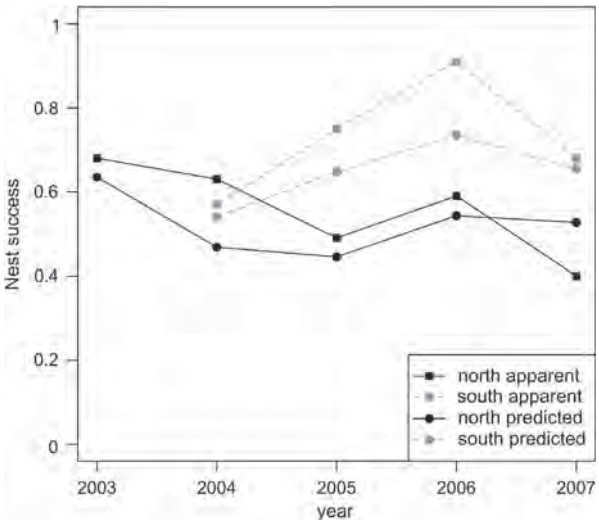



Figure 1. Apparent and predicted annual nest survival by year for sage-grouse in the Powder River Basin, Montana and Wyoming, US, 2003–2007. The final model included the effects of grass height, nest age, study area, and 2005 spring snow storm. Grass height measurements were averaged across nests within years to make annual predictions.

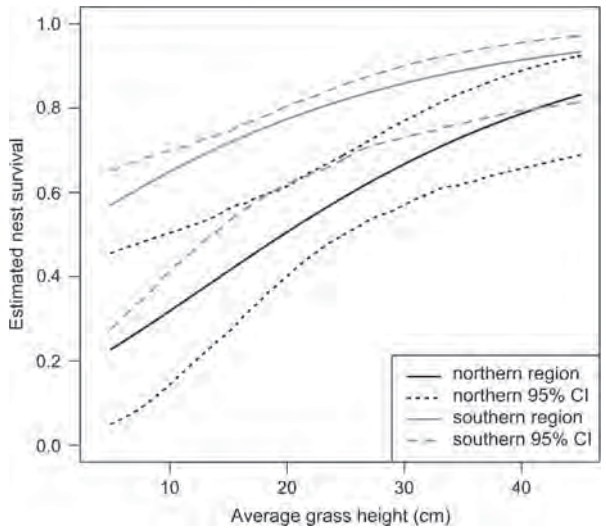



Figure 2. Relationship between average grass height and sage-grouse nest survival, Powder River Basin, Montana and Wyoming, USA, 2004–2006. Estimates of nest survival (95% confidence intervals [CIs]) in both study areas are based on 5000 bootstrap samples.

third of variation in $\lambda$ (Taylor et al. 2012). Moreover, grass height is a reliable management tool because it explained variation (Fig. 2) despite variability in absolute rates of nest success between study areas. Positive effects of grass height should be evaluated on other important demographic rates including adult female and chick survival (Taylor et al. 2012) to see if benefits extend beyond what is now known.

Managing grass height in large and intact landscapes with grazing is a tool that may benefit populations in eastern Montana and northeast Wyoming. Positive effects of grass height in our study areas explained variation in nest success between years with large and precise effect sizes. Differing intercepts prohibit extrapolating of results to novel sagebrush systems because absolute effects likely depend upon regional conditions that influence grass and shrub composition. South and west of our study areas where sagebrush rather than grass provides most hiding cover, grass height had only a weak effect on nest success, and nest fates were dominated by year and site effects (Holloran et al. 2005). Grass height is positively related to nest success for other prairie grouse species and subspecies (Attwater's prairie-chickens *Tympanuchus cupido attwateri*, Lehmann 1941; plains sharp-tailed grouse *T. phasianellus jamesi*, Hillman and Jackson 1973; greater prairie-chicken *T. cupido pinnatus*, McKee et al. 1998).

Table 3. Validation of grass height as a predictor for sage-grouse nest success, Powder River Basin, Montana and Wyoming, 2003–2007. We tested the AICc best model (Table 2) by calculating the predicted probability of hatching for each nest by applying grass height and region coefficients from log-link analysis (2004–2006) to observed grass heights at nests. We used the predicted probability (n is number of nests in each category) of hatching to group nests with probabilities of $<0.45$ and $>0.55$ and then compared apparent nest success ratios. We also validated the relationship with independent data sets (2003 and 2007). Nest age was excluded because we exponentiated daily survival rate for nests across the 28-day incubation period.

| Predicted probability | Observed nest success | | |
|---|---|---|---|
| | 2003 | 2004–2006 | 2007 |
| $p<0.45$ (low) | 0.714 (n = 7) | 0.486 (n = 70) | 0.200 (n = 5) |
| $p>0.55$ (high) | 0.667 (n = 30) | 0.796 (n = 184) | 0.623 (n = 52) |
| Ratio (high/low) | 0.93 | 1.64 | 3.11 |

Findings suggest that maintaining grass height during drought may provide the greatest benefits to populations. Average grass height and predicted nest success in this study is within the range of published literature (Schroeder et al. 1999, Connelly et al. 2000). Benefits may be negligible in years resembling 2003 when spring rains provided abundant grass and the correspondingly highest predicted nest success for the northern study area. High variation in pooled grass height by study area and years (11.4–29.2 cm) also suggested that modifying grazing practices to maintain nesting cover could improve a habitat feature that otherwise limits $\lambda$. We have identified a strong corollary of nest success in the Powder River Basin (PRB). If this relationship is validated in new study areas across different parts of the sage-grouse range, and if the relationship between grass height and nest success can be calibrated within these new areas, grass height may be useful as a surrogate to monitor nest success.

Findings emphasize the importance of an indirect effect of grazing on sage-grouse nest success. Results have broad implications because livestock grazing is the most widespread land use in the world (Holechek et al. 2003), affecting 70% of land area in the western US (Fleischner 1994). Effects of grazing on sage-grouse habitat may be wide-ranging depending upon current and historic timing and intensity of grazing, soil conditions, precipitation, plant communities and habitat features under consideration (Beck and Mitchell 2000, Connelly et al. 2000, 2004, Crawford et al. 2004). However, adjustments to duration and timing of grazing also may increase residual cover with the added benefit of increasing long-term rangeland health on which birds depend. For example, reducing the short-term stocking rate of sheep increased black grouse *Tetrao tetrix* numbers by 6% annually in Europe by increasing residual cover (Calladine et al. 2002). Replicated experiments to document sage-grouse response to different grazing systems are needed to help guide land managers to practices that are beneficial to sage-grouse and economically viable to producers (Krausman et al. 2011).

Habitat management within a PAC-based conservation strategy may benefit populations, but sage-grouse are a wildland species, and grass height is of little consequence if sagebrush systems continue to be replaced by anthropogenic land uses (Knick et al. 2013). Viability of ranching as a predominant land use may in part determine the future of sage-grouse conservation in the West. The SGI has increased by four-fold their implementation of rotational grazing systems by resting for up to 17 months the pastures used by nesting sage-grouse grouse within 488 000 ha inside Montana's PACs (J. Siddoway pers. comm.). Our findings suggest that these types of grazing systems that promote nest success may provide one mechanism to offset population losses by increasing bird numbers.

*Acknowledgements* – We thank landowners in the PRB that granted access to private lands. J. Hess, K. Keith, D. Nonne and F. Sutti provided outstanding leadership and assistance in the field. Major

funding for this work came from Bureau of Land Management (BLM) offices in Montana and Wyoming. Additional support came from the BLM (Washington DC), US Dept of Energy, Montana Dept of Fish, Wildlife and Parks, Wyoming Game and Fish Dept, National Fish and Wildlife Foundation, National Science Foundation (EPS–CORE program), Montana Cooperative Wildlife Research Unit, Petroleum Association of Wyoming, Western Gas Resources Inc., Wolf Creek Charitable Foundation, Bighorn Environmental Consulting, Anheuser-Busch Companies, Inc. and the Univ. of Montana. The views of the lead author are his own and do not necessarily represent the USFWS.

## References

Baruch-Mordo, S. et al. 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. – Biol. Conserv. 167: 233–241.

Beck, J. L. and Mitchell, D. L. 2000. Influences of livestock grazing on sage grouse habitat. – Wildl. Soc. Bull. 28: 993–1002.

Bukowski, B. E. and Baker, W. L. 2013. Historical fire regimes, reconstructed from land-survey data, led to complexity and fluctuation in sagebrush landscapes. – Ecol. Appl. 23: 546–564.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and inference: a practical information-theoretic approach. – Springer.

Calladine, J. et al. 2002. Effects of reduced grazing on population density and breeding success of black grouse in northern England. – J. Appl. Ecol. 39: 772–780.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. – J. For. 39: 388–394.

Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. – Sinauer.

Chambers, J. M. et al. 1983. Graphical methods for data analysis. – Duxbury Press, Boston, MA, USA.

Chatfield, C. 1995. Model uncertainty, data mining and statistical inference. – J. R. Stat. Soc. 158: 419–466.

Connelly, J. W. et al. 2000. Guidelines to manage sage grouse populations and their habitats. – Wildl. Soc. Bull. 28: 967–985.

Connelly, J. W. et al. 2003. Monitoring of greater sage-grouse habitats and populations. – College of Nat. Resour. Exp. Stn Bull. 80, Univ. of Idaho, Moscow, ID, USA.

Connelly, J. W. et al. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. – W. Ass. of Fish and Wildlife Agencies. Cheyenne, WY, USA.

Copeland, H. E. et al. 2013. Measuring the effectiveness of conservation: a novel framework to quantify the benefits of sage-grouse conservation policy and easements in Wyoming. – PLoS ONE 8:e67261.

Crawford, J. A. et al. 2004. Ecology and management of sage-grouse and sage-grouse habitat. – J. Range Manage. 57: 2–19.

DeLong, A. K. et al. 1995. Relationships between vegetational structure and predation of artificial sage grouse nests. – J. Wildl. Manage. 59: 88–92.

Dinsmore, S. J. et al. 2002. Advanced techniques for modeling avian nest survival. – Ecology 83: 3476–3488.

Doherty, K. E. et al. 2008. Greater sage-grouse winter habitat selection and energy development. – J. Wildl. Manage. 72: 187–195.

Doherty, K. E. et al. 2010a. Mapping breeding densities of greater sage-grouse: a tool for range-wide conservation planning. BLM Completion Report Interior Agency Agreement #L10PG00911. – US Bureau of Land Management.

Doherty, K. E. et al. 2010b. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. – J. Wildl. Manage. 74: 1544–1553.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. – Conserv. Biol. 8: 629–644.

Foley, J. A. N. et al. 2011. Solutions for a cultivated planet. – Nature 478: 337–342.

Giesen, K. M. et al. 1982. Methods for trapping sage-grouse in Colorado. – Wildl. Soc. Bull. 10: 224–231.

Hagen, C. A. et al. 2007. A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. – Wildl. Biol. 13: 42–50.

Hillman, C. N. and Jackson, W. W. 1973. The sharp-tailed grouse in South Dakota. – Pierre, South Dakota, USA, South Dakota Game, Fish, and Parks Tech. Bull. 3.

Holechek, J. et al. 2003. Range management: principles and practices. – Prentice Hall Publishing, Upper Saddle River, NJ, USA.

Holloran, M. J. et al. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. – J. Wildl. Manage. 69: 638–649.

Knick, S. T. et al. 2013. Modeling ecological minimum requirements or distribution of greater sage-grouse leks: implications for population connectivity across their western range, USA. – Ecol. Evol. 3: 1539–1551.

Knight, A. T. et al. 2008. Knowing but not doing: selecting priority conservation areas and the research-implementation gap. – Conserv. Biol. 22: 610–617.

Krausman, P. R. et al. 2011. An assessment of rangeland activities on wildlife populations and habitats. – In: Briske, D. D. (ed.), Conservation benefits of rangeland practices: assessment, recommendations and knowledge gaps. US Dept of Agriculture, Natural Resources Conservation Service, Washington, D.C., USA, pp. 253–290.

Lehmann, V. W. 1941. Attwater's prairie chicken: its life history and management. – US Fish and Wildlife Service, North American Fauna 57, US Government Printing Office, Washington D.C., USA.

McKee, G. et al. 1998. Predicting greater prairie-chicken nest success from vegetation and landscape characteristics. – J. Wildl. Manage. 62: 314–321.

Mills, L. S. 2012. Conservation of wildlife populations. – Wiley.

Millspaugh, J. J. and Thompson, III, F. R. 2009. Models for planning wildlife conservation in large landscapes. – Academic Press.

Murphy, T. et al. 2013. Trial by fire: improving our ability to reduce wildfire impacts to sage-grouse and sagebrush ecosystems through accelerated partner collaboration. – Rangelands 35: 2–10.

Naugle, D. E. 2012. Energy development and wildlife conservation in western North America. – Island Press.

Nicholson, E. et al. 2013. Testing focal species approach to making conservation decisions for species persistence. – Divers. Distrib. 19: 530–540.

Rickard, W. H. et al. 1975. Impact of cattle grazing on three perennial grasses in south–central Washington. – Soc. Range Manage. 28: 108–112.

Robel, R. J. et al. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. – J. Range Manage. 23: 295–297.

Rotella, J. J. et al. 2004. Extending methods for modeling heterogeneity in nest-survival data using generalized mixed models. – Stud. Avian Biol. 34: 34–44.

Schroeder, M. A. et al. 1999. Sage grouse *Centrocercus urophasianus*. – In: Poole, A. and Gill, F. (eds), The birds of North America. 610. Acad. Nat. Sci., Philadelphia, PA, USA.

Schroeder, M. A. et al. 2004. Distribution of sage-grouse in North America. – Condor 106: 363–376.

Schultz, C. 2010. Challenges in connecting cumulative effects analysis to effective wildlife conservation planning. – Bioscience 60: 545–551.
Taylor, R. L. et al. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. – J. Wildl. Manage. 76: 336–347.
US Fish and Wildlife Service 2010. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. – Federal Register 75: 13909–14014.
US Fish and Wildlife Service 2013. Sage-grouse Conservation Objectives Team completion report. – US Dept of the Interior, Washington, D.C., USA.
Walker, B. L. 2008. Greater sage-grouse response to coal-bed natural gas development and West Nile virus in the Powder River Basin, Montana and Wyoming, USA. – PhD thesis, Univ. of Montana, Missoula, MT, USA.
Wakkinen, W. L. et al. 1992. An improved spotlighting technique for capturing sage grouse. – Wildl. Soc. Bull. 20: 425–426.
Wilson, K. A. et al. 2007. Conserving biodiversity efficiently: what to do, where and when. – PLoS Biol. 5:e223.
Wisdom, M. J. et al. 2000. Life stage simulations analysis: estimating vital- rate effects on population growth for conservation. – Ecology 81: 628–641.

The Journal of Wildlife Management 80(2):266–274; 2016; DOI: 10.1002/jwmg.1001

*Research Article*

# Male Greater Sage-Grouse Detectability on Leks

**ALESHIA L. FREMGEN,**[1] *University of Missouri, 302 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA*
**CHRISTOPHER P. HANSEN,** *University of Missouri, 302 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA*
**MARK A. RUMBLE,** *United States Forest Service Rocky Mountain Research Station, 8221 S Highway 16, Rapid City, SD 57702, USA*
**R. SCOTT GAMO,** *Wyoming Game and Fish, 5400 Bishop Boulevard, Cheyenne, WY 82006, USA*
**JOSHUA J. MILLSPAUGH,** *University of Missouri, 302 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA*

**ABSTRACT** It is unlikely all male sage-grouse are detected during lek counts, which could complicate the use of lek counts as an index to population abundance. Understanding factors that influence detection probabilities will allow managers to more accurately estimate the number of males present on leks. We fitted 410 males with global positioning system and very high frequency transmitters, and uniquely identifiable leg-bands over 4 years in Carbon County, Wyoming. We counted male sage-grouse using commonly used lek-count protocols and evaluated variables associated with our ability to detect marked males using sightability surveys on 22 leks. We evaluated detection probabilities of male sage-grouse based on factors related to bird characteristics such as age or posture, lek and group size, lek characteristics such as vegetation cover or aspect, light conditions, weather, and observer. We then applied the detection probabilities to more accurately estimate male counts on leks. Detection probabilities were generally high ($\bar{x} = 0.87$) but varied among leks from 0.77 to 0.93. Male sage-grouse detection declined with increasing sagebrush height and bare ground and increased with more snow cover. Detection probabilities were also lower when observers counted from a higher elevation than the lek. Our sightability models predicted detection well and can be used to accurately estimate male abundance on leks from lek counts, which is especially useful where accurate abundance estimates are required or inference about population status is based on only 1 count. Further, it is important to consider lek attendance as a component of counts on leks because it affects availability of male sage-grouse for detection during lek counts. Detection can be maximized by conducting lek counts from 30 minutes before sunrise to 30 minutes after sunrise, although current protocols recommend lek counts can be performed up to 1 hour after sunrise. Detection can also be maximized by conducting lek counts $\geq$2 days after snowfall, which maximizes attendance and detection. © 2015 The Wildlife Society.

**KEY WORDS** abundance, *Centrocercus urophasianus*, detectability, detection, greater sage-grouse, index, lek counts, sightability, Wyoming.

Biologists and managers must be able to accurately monitor the status and trends of species that are declining in abundance, or under consideration for listing as endangered. For many species, detectability during surveys is an important factor affecting the accuracy and reliability of monitoring programs. When detection rates differ over time and space, observed trends in abundance may be biased unless they are corrected (Johnson 2008, Kéry and Schmidt 2008, Schmidt et al. 2013). Consequently, attempts have been made to identify factors affecting detectability of large mammals (Samuel et al. 1987, Bodie et al. 1995, Rice et al. 2009, Vander Wal et al. 2011, Walsh et al. 2011), songbirds (Farnsworth et al. 2002, Alldredge et al. 2007, Diefenbach et al. 2007, Kéry and Schmidt 2008, Schmidt et al. 2013), and other species to avoid bias in assessments of trends. Problems with detectability are a primary reason new analytical approaches, such as occupancy modeling (MacKenzie et al. 2003), have become so popular in recent years. For species such as the greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse), which was previously designated as warranted but precluded from listing as endangered under the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service [USFWS] 2010), careful monitoring is necessary to aid conservation efforts.

State and federal management agencies have been counting male sage-grouse on leks since the 1940s to evaluate sage-grouse population status and trends, and these data represent the only long-term data set available for sage-grouse abundance assessments (Connelly and Schroeder 2007, Johnson and Rowland 2007). Lek counts are also valuable because leks are relatively high concentrations of the population that can be easily and inexpensively surveyed every year in the same location (Patterson 1952, Dalke et al. 1963, Beck and Braun 1980, Walsh et al. 2004, Sedinger

Received: 13 May 2015; Accepted: 1 August 2015

[1]*E-mail: FremgenAL@missouri.edu*

2007). Lek locations and the timing of the breeding season are predictable because sage-grouse have high site fidelity to leks annually (Patterson 1952, Jenni and Hartzler 1978, Connelly et al. 2003) and within a breeding season (Campbell 1972, Dunn and Braun 1985, Schroeder and Braun 1992, Schroeder and Robb 2003, Walsh et al. 2010).

Although lek counts are used to survey male sage-grouse populations and may be useful to monitor relative abundance annually, lek counts may not provide a reliable index to population size if imperfect detection and variability in detection exist among leks or through time (Samuel et al. 1987, Anderson 2001, Johnson 2008). Lek counts may be unreliable estimates of relative abundance as well, if detection varies among survey events within a year. Birds that are not easily observed but are still present on the lek, such as foraging males or yearlings that do not actively display (Garton et al. 2007), may not be counted during a lek survey, and thus bias male abundance estimates. When detection is imperfect, detection probabilities can be used to estimate the number of males missed during a lek survey, and more accurately estimate the number of males present (White and Shenk 2001, White 2005). So-called sightability studies have been extensively applied to ungulates and other large game species (Samuel et al. 1987, Steinhorst and Samuel 1989, Bodie et al. 1995, Udevitz et al. 2006, Vander Wal et al. 2011) but have only recently been proposed for use on upland game birds (Walsh et al. 2004, Clifton and Krementz 2006, Baumgardt 2011). Sightability studies can be used with marked animals to determine factors influencing detection, including variables related to the marked animal and its immediate surroundings.

Factors that may affect sage-grouse sightability include light conditions (Vander Wal et al. 2011), bird behavior, bird location within the lek and in relation to other birds, observer experience and location in relation to the bird, and vegetative cover (Samuel et al. 1987, Vander Wal et al. 2011, Walsh et al. 2011). The physical size of the lek and group size of displaying birds on the lek may also affect an observer's ability to effectively search the area, and observers may have difficulty accurately counting males on leks with many birds (Samuel et al. 1987, Rice et al. 2009). Movement or posture of birds can increase an observer's ability to notice them (Bodie et al. 1995, Garton et al. 2007). Topography and vegetation at leks, or an observer's location in relation to the bird, could also influence detection (Bodie et al. 1995). Sightability studies determine the degree to which various factors influence detection, and can be used to estimate a detection probability for each lek based on characteristics of a lek, conditions of the count, and characteristics of male sage-grouse.

This research was part of a larger, long-term study using a before–after, control-impact design to assess relationships between wind energy development and sage-grouse ecology in Carbon County, Wyoming. We estimated detection probabilities on leks in the pre-construction phase of a wind energy development. Our objectives were to 1) evaluate how bird characteristics and activity, lek size, lek characteristics, vegetation, light conditions, and observer affected detection probabilities, 2) apply estimated detection probabilities to lek count data for an accurate estimate of male abundance on leks, and 3) determine optimal conditions for lek counts to maximize detectability of male sage-grouse on leks.

## STUDY AREA

The wind energy development was proposed on The Overland Trail Ranch (OTR), an approximately 1,295-$km^2$ mix of private and public land (Bureau of Land Management and Wyoming Office of State Lands and Investments) south of Rawlins, Wyoming. The OTR is a sagebrush steppe basin with foothills to the south and southwest and rocky ridges to the north and northeast with elevation ranging from 1,890 m to 2,590 m.

The climate is semiarid, with long, cold winters and short, hot summers (Bailey 1995). Highest temperatures are in July ($\bar{x}$ max. $= 31^\circ$ C) and lowest temperatures in December and January ($\bar{x}$ max. $= -1^\circ$ C; Western Regional Climate Center [WRCC] 2008). Annual precipitation is typically between 19 cm and 26 cm, with most precipitation occurring between April and October (WRCC 2008).

Vegetation in our study area was classified as intermountain semidesert province (Bailey 1995). Vegetation predominantly consisted of sagebrush or shadscale (*Atriplex confertifolia*) with short grasses (Bailey 1995). Greasewood (*Sarcobatus vermiculatus*) grew in moist alkaline flats, and willows (*Salix* spp.) and sedges (*Carex* spp.) lined streams and valley bottoms (Bailey 1995). Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) dominated lower elevations and mountain big sagebrush (*A. t. vaseyana*) dominated higher elevations, with silver sagebrush (*A. cana*) in lowlands and black sagebrush (*A. nova*) in rocky, exposed soils (Thatcher 1959, Chapman et al. 2004, Connelly et al. 2004, Welch 2005).

## METHODS

### Trapping and Marking

We trapped birds and distributed transmitters among active leks on and around the OTR. To avoid bias for dominant males roosting near leks (Walsh et al. 2004), we captured male sage-grouse in late fall and early spring to supplement the number of marked individuals and account for overwinter mortality. We captured male sage-grouse using spotlighting and hoop-netting techniques (Giesen et al. 1982, Wakkinen et al. 1992) facilitated by all-terrain vehicles. We weighed captured males and classified them based upon primary wing feather characteristics (Eng 1955, Crunden 1963) as adults ($\geq$2 years old) or yearlings (1–1.5 years old). Each bird received uniquely identifiable colored leg band combinations to facilitate resighting on leks (Walsh 2002; National Band and Tag Company, Newport, KY).

We deployed 20 transmitters in 2011, 20 in 2012, and 10 in 2013 using 30-g solar-powered platform transmitter terminal (PTT-100) global positioning system (GPS) transmitters (accuracy $\pm$ 18 m, Microwave Telemetry, Columbia, MD). The GPS–PTT transmitters had ultra high frequency (UHF) tracking. We marked an additional 50 males in

2011 with very high frequency (VHF) transmitters and attempted to maintain a sample size of 50 males with VHF transmitters every year by replacing expired transmitters and tagging new birds. Adult and yearling males tagged in spring with VHF transmitters usually received 30-g transmitters (Model A1150, Advanced Telemetry Systems [ATS], Isanti, MN), whereas juveniles tagged in fall with VHF transmitters received 15-g ATS transmitters (Model A1260, ATS) or 15-g Telonics (LB-35, Telonics, Mesa, AZ) transmitters. All GPS-PTT and VHF transmitters were <2% of grouse body weight and were attached using the Rappole and Tipton (1991) method. Trapping and handling procedures were approved through the University of Missouri Institutional Animal Care and Use Committee (Protocol #6750) and Wyoming Game and Fish Department (WGFD) Chapter 33 Permit (Permit #752).

**Sightability Surveys**

We monitored 58 leks throughout the study area (Fig. 1). Twenty-four to 33 leks were active each year of the study (2012–2014). We completed $2.65 \pm 0.06$ ($\bar{x} \pm$ SE) sightability surveys per lek on 20–22 active leks each spring (surveys per lek from 2012 to 2014 range = 1–11). Sightability surveys began 2 April 2012, 28 March 2013, and 19 March 2014 and continued until most leks were inactive or 3 lek counts were completed on each lek (22 May each year). We set up ground blinds at an observation point roughly 20–150 m from displaying males 1 week prior to lek counts to allow sage-grouse to habituate to its presence.

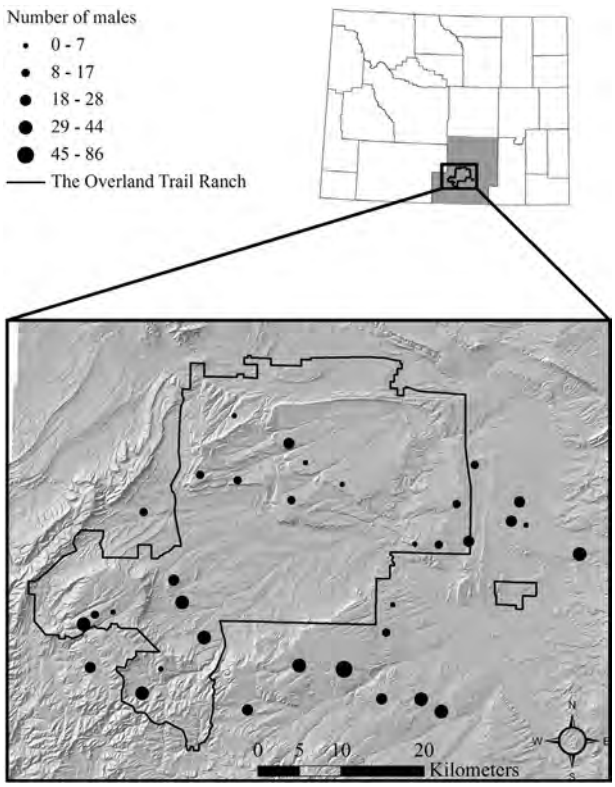



**Figure 1.** The Overland Trail Ranch in Carbon County, Wyoming, with all active greater sage-grouse leks in the study area. Active leks had ≥1 male from 2012 to 2014. Symbol size represents relative lek size based on 2013 count data. Because leks were active and inactive different years, we had 34 active leks total throughout the study.

We used a protocol with 2 observers to conduct sightability surveys. One observer (observer 1) recorded numbers of displaying males on leks and noted the occurrence and location of marked birds on the lek, facilitated by telemetry. Observer 1 was in a blind on the lek perimeter, able to observe marked birds and use telemetry to locate unseen marked birds. Observer 1 entered the blind 2 hours before sunrise and counted sage-grouse at 15-minute intervals starting as soon as light was sufficient, approximately 30 minutes before sunrise, until all birds left the lek (usually before 1000 hours). Between counts, observer 1 used telemetry equipment to scan UHF and VHF radio frequencies and detect unseen radio-marked birds on the lek. Once a male was visually confirmed to be present on the lek, observer 1 would note the marked male's location. Once a bird was detected by observer 1, it was not considered again.

A second observer (observer 2) independently recorded numbers of displaying males and the occurrence and location of marked individuals with no prior knowledge of marked individuals on the lek. Observer 2 counted sage-grouse on foot, using WGFD protocols for lek surveys simultaneously with observer 1. Observer 2 conducted lek counts from a location approximately 50–200 m from the lek boundary, and the location was independently chosen by observer 2 on the observation morning to imitate a WGFD observer's location choice during conventional lek counts. Observer 2 recorded male and female birds on the lek, color band identities, locations, and associated covariates for marked males. Observer 2 noted time spent surveying for marked individuals and total time observers were present at the lek.

Once the survey was complete, observers immediately compared data. We considered grouse that observer 2 located to be detected. We considered grouse that observer 1 noted, but observer 2 failed to detect as undetected. We used covariates recorded by observer 2 when the marked male was detected by observer 2, and covariates recorded by observer 1 when the marked male was not detected by observer 2.

For lek counts, we recorded date, observer location (Universal Transverse Mercator), time, wind speed, and sky condition. We recorded sky conditions as a code including clear or a few clouds (0), partly cloudy (1), cloudy or overcast (2), fog or haze (3), drizzle (4), showers (5), flurries (6), or snow showers (7). For each marked bird, observers recorded the bird's activity (sitting, foraging or standing without strutting, or strutting), time the bird was observed, group size (no. grouse within 5 m of the marked bird), number of males present on the lek at the time of detection, and time spent searching for the marked male (i.e., sampling intensity). We determined marked bird locations using a compass and rangefinder (accuracy ± 1 m from 5 m to 686 m away, Leupold RX-750, Beaverton, OR) to determine an azimuth and distance from a known location of the observer.

After grouse left the lek, we recorded microsite vegetation measurements on the day of the sightability survey at the location where the grouse was detected. We established 2,

10-m perpendicular bisecting transects in cardinal directions that were centered over the sage-grouse's location. We measured visual obstruction (VOR) using a modified Robel pole with 1.27-cm increments (Robel et al. 1970, Benkobi et al. 2000) at the plot center and every meter up to 5 m from the plot center, with a VOR reading in each cardinal direction ($n = 84$). We recorded the lowest height at which an increment on the Robel pole was completely obscured. We estimated canopy cover using a 0.1-$m^2$ quadrat placed parallel to the transect (Daubenmire 1959, Hanley 1978) at 1-m intervals out to 5 m along each transect and plot center ($n = 24$). Observers estimated canopy cover classes (1 = 0–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–95%, 6 = 95–100%) for sagebrush, other non-sagebrush shrubs, grasses and forbs, snow, and bare ground in each quadrat (Daubenmire 1959). We measured natural droop height (cm) of sagebrush, other shrubs, and grasses or forbs by selecting the plant in each category closest to the corner of the frame. We averaged Robel pole and vegetation height measurements for each sage-grouse location, and recoded canopy cover classes to the midpoints of the intervals and calculated average percent coverage for all cover classes at each sage-grouse location.

We calculated lek attendance rates, surrounding sagebrush cover, and elevation differences from observer to grouse as additional covariates. We calculated a seasonal lek attendance rate for each male sage-grouse by dividing the number of days the bird attended a lek by the number of days he was available to attend the lek throughout the season (Walsh et al. 2004, Fremgen 2014). We used ArcMap 10.0 (Environmental Systems Research Institute, Redlands, CA) with a $30 \times 30$-m categorical land cover layer based on Landsat ETM+ data (Driese and Nibbelink 2004), which we reclassified as sagebrush or other cover to calculate the percent of sagebrush within 50 m of the marked male. The 50-m radius provided a larger-scale representation of surrounding sagebrush cover on the lek, whereas the 5-m microsite vegetation measurements characterized sagebrush cover surrounding the male. We used a $30 \times 30$-m digital elevation model (DEM) to determine elevation for observation points and marked males, and we subtracted the elevation of the marked male's location from observer 2's elevation to model effects of the observer's position in relation to the lek. After the lek season ended, observers mapped leks using known locations of marked and unmarked birds noted during lek counts, and sign such as feathers, cecal tar, and droppings (Fremgen 2014). We calculated lek area ($m^2$) in ArcMap 10.0 using mapped lek perimeters.

**Sightability Model Data Analysis**

We created a priori models related to observer characteristics, lek size, vegetation characteristics, environmental conditions, and bird characteristics. We created models using biologically reasonable combinations of variables (Fremgen 2014: appendix D). We tested for correlation among covariates using PROC CORR in SAS 9.3 (SAS Institute, Cary, NC) and eliminated 1 variable of the pair when they were correlated ($r > 0.8$); we kept the variable that was most biologically meaningful. We evaluated whether data could be combined across years by comparing model rank with and without year as a covariate for multiple models; because year did not influence detection, we analyzed data pooled across years.

We modeled sightability of male sage-grouse using covariates for birds that were and were not detected using logistic regression in a generalized linear mixed model with observers modeled as a random effect using PROC GLIMMIX in SAS 9.3. We used second-order small sample size Akaike's Information Criterion ($AIC_c$; Burnham and Anderson 2002) to identify the most parsimonious model. Our model selection process involved 2 stages, including a screening process first to select the structural form of each variable that best represented its effect on detection, and then fitting a priori models using the best structural form (Franklin et al. 2000, Washburn et al. 2004). We tested structural forms of each variable using $AIC_c$ to rank linear, quadratic, and pseudothreshold forms with the quadratic term centered on its mean to avoid multicollinearity between linear and quadratic terms in the polynomial (Bonnot et al. 2011). For simplicity we selected linear structural forms unless a nonlinear form was >2 $\Delta AIC_c$ units less than the linear form for that variable. We fit our a priori model set and averaged parameter estimates for all models with an Akaike weight ($w_i$) >12.5% the weight of the top model (Burnham and Anderson 2002). We did not consider interactions among variables because it would be complex for our many categorical variables. Initially, top models included sampling intensity and time since 30 minutes before sunrise, but those variables were not interpretable because they were strongly related to their sample distribution, with most males being recorded early in the morning. We removed models including those variables from analysis.

We evaluated goodness-of-fit using the Pearson $\chi^2$ statistic divided by degrees of freedom (Pearson $\chi^2$/DF). We evaluated the predictive ability of the most-supported model using 10-fold cross validation (Boyce et al. 2002) by dividing data into 10 random subsets and removing 1 subset for testing data, and refitting the model set using the remaining 9 subsets as training data. We estimated detection probabilities for testing sets based on model parameter estimates from the corresponding training set, and found the average difference between predicted probability of detection and observed detection. We also evaluated predictive ability using the Spearman-rank correlation coefficient by dividing our observations of detected males into 10 equal size bins based on the range of predicted probability of detection, and calculated the Spearman-rank correlation between the predicted probability and frequency of observed detections in each bin.

We used averaged model parameter estimates, weighted by model probability, to calculate detection probabilities at each lek using characteristics of the lek observed during the lek count with the highest male count, and we estimated an average detection probability by averaging characteristics

across leks. Once we calculated the detection probability ($\hat{y}$) for each lek, we used it to obtain an accurate estimate of males present on the lek from count data. The estimated number of males on the lek ($\widehat{N}$) was:

$$\widehat{N} = \sum_{1}^{t} \frac{l_i}{\hat{y}_i}$$

where $l_i$ is the maximum number of birds counted on lek $i$ throughout the season by any observer, and $\hat{y}_i$ is the detection probability on lek $i$. We calculated variance for the corrected abundance using bootstrap methods. At each active lek, we sampled from the estimated detection probability and used the male high count to calculate abundance for 1,000 iterations. We summed the estimated numbers of males at each lek for the corrected male abundance at all leks. Male sage-grouse move among leks, but the probability that a male would move to a new lek and be double counted during lek counts was low because lek counts were completed near the peak of attendance, when interlek movements are less likely (Fremgen 2014). Therefore, lek counts are not likely to overestimate total male abundance from double counting males if counts are completed at an appropriate time of year, near the peak of male attendance.

## RESULTS

We deployed an average of $85 \pm 27$ ($\bar{x} \pm$ SE) transmitters each year ($37 \pm 9$ GPS-PTT transmitters and $48 \pm 19$ VHF transmitters) to assist with lek counts and sightability survey effort (Table 1). From 2012 to 2014, we detected 222 marked birds; 44 birds were not detected by observer 2 but present on the lek. Most of the marked male sage-grouse were recorded as detected between 30 minutes before sunrise to 1 hour after sunrise (Fig. 2). Only 12 (5%) marked individuals were detected >1 hour after sunrise.

The top sightability model included sagebrush height and snow cover, which were the most important factors for detection, but we model-averaged parameter estimates across the top 3 models because of model uncertainty (Table 2). Detection of marked males increased with greater snow cover and lower sagebrush height (Fig. 3). Although detection also had a negative relationship with bare ground and elevation difference between observer and the observed grouse, the effects were not as strong, with little change in predicted detection across the range of data we observed (Table 3; Fig. 3).

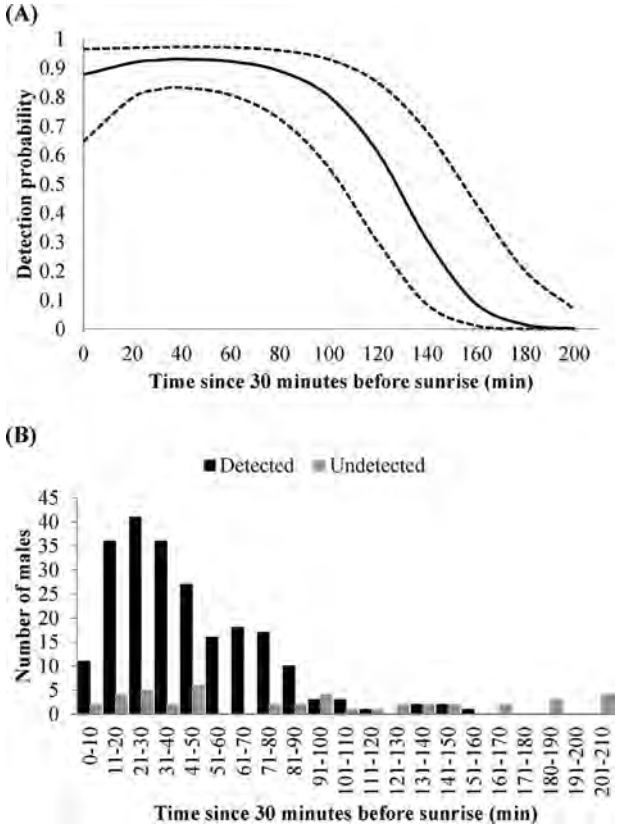



**Figure 2.** Detection of greater-sage grouse across time (since 30 min before sunrise) during sightability surveys in Carbon County, Wyoming from 2012 to 2014 including A) the probability of detection (with 95% CI) predicted from logistic regression with a random effect for observer identity, modeled across the range of times we observed and B) counts of males that were detected or undetected through different time intervals. We calculated time since 30 minutes before sunrise for males that were not detected by observer 2 (undetected) as time spent searching the lek without finding the marked male. Time since 30 minutes before sunrise was initially the top model, and the effect is shown in panel A, but we removed the variable from model selection because it was highly correlated with the rate at which we recorded marked males.

The model-averaged probability of bird detection across all leks was generally high (0.87 [95% CL: 0.78, 0.93]), but the model-predicted, lek-specific detection probabilities varied

**Table 1.** Lek sizes and sightability survey effort to assess male greater sage-grouse detectability in Carbon County, Wyoming in 2012–2014.

| | 2012 | 2013 | 2014 |
|---|---|---|---|
| Start date of sightability surveys | 2 Apr | 28 Mar | 19 Mar |
| End date of sightability surveys | 22 May | 22 May | 22 May |
| No. leks counted | 49 | 56 | 58 |
| No. occupied leks | 24 | 29 | 33 |
| High count of males on occupied leks ($\bar{x} \pm$ SE) | $20 \pm 3.09$ | $17 \pm 2.35$ | $23 \pm 3.03$ |
| Range of number of males on an occupied lek | 1–63 | 1–48 | 1–86 |
| Lek high counts (total for leks with sightability surveys) | 408 | 428 | 540 |
| No. sightability surveys completed | 48 | 56 | 60 |
| Leks with sightability surveys | 20 | 20 | 22 |
| No. observations of marked males | 33 | 112 | 121 |
| No. marked males that were detected by observer 2 (without telemetry equipment) | 23 (70%) | 99 (88%) | 100 (83%) |
| No. unique marked males observed | 28 | 67 | 67 |

**Table 2.** Top 3 sightability models, ranked by second order Akaike's Information Criterion ($AIC_c$) predicting male sage-grouse detectability in Carbon County, Wyoming, 2012–2014. All other models had a model weight ($w_i$) <12.5% of the top model.

| Model[a] | −2 LL[b] | $K$[c] | $AIC_c$ | $\Delta AIC_c$ | $w_i$[d] |
|---|---|---|---|---|---|
| *ln*(sagebrush height + 0.05) + snow cover | 221.8 | 4 | 229.9 | 0.0 | 0.420 |
| *ln*(elevation difference + 0.05) | 226.9 | 3 | 233.0 | 3.1 | 0.089 |
| *ln*(sagebrush height + 0.05) + *ln*(bare ground + 0.05) | 225.1 | 4 | 233.3 | 3.3 | 0.079 |
| Null model | 233.0 | 2 | 237.0 | 49.2 | 0.000 |

[a] Parameters with +0.05 indicate we added 0.05 to linear structural forms to make values non-zero before natural logarithm transformation into the pseudo-threshold structural form. Elevation difference is between the observer and the grouse detected (i.e., observer elevation − grouse elevation).
[b] LL, log likelihood.
[c] No. parameters in model.
[d] Model weight.

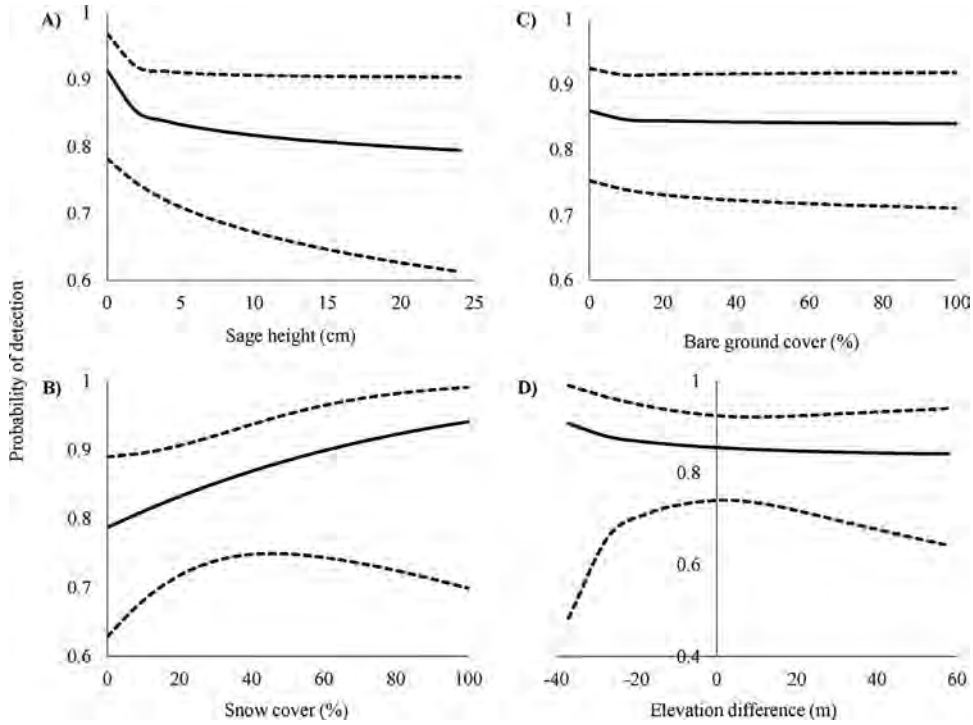



**Figure 3.** Variables included in the model-averaged top models for male greater sage-grouse detectability in Carbon County, Wyoming from 2012 to 2014. Variables are graphed across the range observed throughout the study, and include 95% upper and lower confidence limits as dotted lines. Detection was influenced by A) sagebrush height, B) snow cover, C) bare ground cover, and D) elevation difference between the observer and the bird (i.e., observer elevation − grouse elevation).

from 0.77 (95% CL: 0.58, 0.89) to 0.93 (95% CL: 0.73, 0.98). The Pearson $\chi^2$/DF statistic indicated adequate model fit for the top 3 models, ranging from 0.81 ($\chi^2_{266} = 216.15$) to 0.83 ($\chi^2_{266} = 220.05$). The difference between observed detection and predicted detection probabilities averaged $0.27 \pm 0.28$ ($\bar{x} \pm$ SE) and the Spearman rank correlation coefficient indicated the model predicted well ($\rho_{10} = 0.96$, $P \leq 0.001$).

**Table 3.** Model-averaged parameter estimates with unconditional standard errors (SE), odds ratios, and 95% confidence intervals (LCL, UCL) for detection probabilities of male greater sage-grouse on leks in Carbon County, Wyoming, 2012–2014.

| Parameter[a] | Estimate | SE | Odds ratio | LCL | UCL |
|---|---|---|---|---|---|
| *ln*(bare ground + 0.05) | −0.0202 | 0.0375 | 0.9800 | −0.0937 | 0.0533 |
| *ln*(elevation difference + 0.05) | −0.2174 | 0.3967 | 0.8046 | −0.9949 | 0.5600 |
| Intercept | 2.3693 | 1.6479 | 10.6902 | −0.8606 | 5.5993 |
| *ln*(sagebrush height + 0.05) | −0.1639 | 0.1145 | 0.8488 | −0.3883 | 0.0605 |
| Snow cover | 0.0146 | 0.0112 | 1.0147 | −0.0074 | 0.0366 |

[a] Parameters with +0.05 indicate we added 0.05 to linear structural forms to make values non-zero before natural logarithm transformation into the pseudo-threshold structural form. Elevation difference = observer elevation − grouse elevation.

Detection probabilities and associated male population estimates varied throughout the study area. When accounting for undetected males during lek counts on leks with sightability surveys, abundance in 2012 differed by 17% between the raw count (408) and estimated ($478 \pm 6.31$, $\bar{x} \pm$ SD) number of males; the male population in 2013 differed by 18% between raw (428) and estimated ($503 \pm 5.79$) abundance; and the male abundance in 2014 differed by 19% between raw (540) and estimated ($644 \pm 6.75$) number of male sage-grouse. Counts were corrected by as much as 14 males on a relatively large lek with tall and dense sagebrush where the detection probability was 0.79.

## DISCUSSION

Detection probabilities for male sage-grouse on leks in Carbon County, Wyoming were generally high and the most important factors affecting detection were sagebrush height and snow cover, although bare ground and the elevation difference between the observer and sage-grouse were also included in supported models. Our hypothesis that vegetation cover inhibits detection of male sage-grouse on leks was corroborated by the most strongly supported model. Vegetation is consistently an important variable influencing detection of wildlife during surveys because increasing vegetative cover can conceal animals and decrease detection (Samuel et al. 1987, Anderson and Lindzey 1996, Rice et al. 2009, Vander Wal et al. 2011). Less bare ground and shorter sagebrush predicted higher detection probabilities for male sage-grouse. However, bare ground may have been a spurious variable because it had wide confidence intervals, and although bare ground was never included in a priori models with snow cover because they were negatively correlated, they were in the same model after model averaging (Cade 2015). Higher snow cover increased our ability to observe male sage-grouse on leks. Most snowfall during our study occurred as several heavy storms, creating a white background on the lek that contrasted the male's dark plumage, making them more easily visible. Samuel et al. (1987) also reported snow cover increased contrast and detection rates of animals in surveys. There was a slight trend toward low detection when observers were higher than the lek, possibly because some males were obscured in small depressions in the landscape such as drainages.

Sage-grouse behavior, lek size, topographic characteristics of the lek, light conditions, and number of birds on the lek did not affect our ability to detect marked individuals in our study. Movement by animals or posture increased an observer's ability to detect some animals (Samuel et al. 1987, Bodie et al. 1995). In our study, observers had similar resight probabilities for all sage-grouse postures, possibly because male sage-grouse can be completely obscured by vegetation irrespective of activity. We expected better light conditions, with clear skies and direct sunlight later in the morning, to yield higher detection probabilities (Bodie et al. 1995, Baumgardt 2011, Vander Wal et al. 2011). However, this expectation was not supported in our data and we did not conduct lek counts during heavy precipitation (Connelly et al. 2003) that would have resulted in low-light and high-cloud cover and likely low detection probabilities. During light precipitation, few males were present on leks and observers often located marked males within 30 minutes before or after sunrise. We also anticipated males would be difficult to detect at larger leks resulting in lower detection probabilities (Baumgardt 2011), but marked males were visible regardless of the number of birds present or the lek's physical area. High detection rates for sage-grouse on leks resulted from the relatively flat, open landscapes (Patterson 1952) with less habitat diversity and landscape diversity than areas surveyed for other wildlife.

Several factors complicate use of lek counts as a population index and should be quantified, because lek counts are the only long-term population trend data available for sage-grouse across their range. Not all leks are known and those that are known may not be a representative sample of all leks (Anderson 2001, Johnson and Rowland 2007). Further, not all leks are counted every year because of logistical constraints (Johnson and Rowland 2007), although some state agencies monitor male abundance trends using only leks that have been surveyed consistently through time (R. S. Gamo, Wyoming Game and Fish, personal observation). Often, not all males will be present on the lek during counts because date, time of day, weather, and predators affect lek attendance (Jenni and Hartzler 1978, Emmons and Braun 1984, Walsh et al. 2004, Johnson and Rowland 2007, Fremgen 2014), and occasionally birds visit different leks (Emmons and Braun 1984, Schroeder and Robb 2003, Fremgen 2014). Most bird surveys, including lek counts, have issues with availability of birds for counting such as lek attendance or interlek movements, which should be considered in addition to detectability (Farnsworth et al. 2002, Alldredge et al. 2007, Diefenbach et al. 2007, Kéry and Schmidt 2008, Schmidt et al. 2013). Finally, despite being present, not all males are accurately counted (Walsh et al. 2004). We quantified accuracy of counts given birds were present on the lek, but other aspects of lek counts should be assessed for their influence on the validity of lek counts.

Because sage-grouse population estimates are often based on the highest count observed on a lek during a season (Walsh et al. 2004, Johnson and Rowland 2007, Garton et al. 2011), accurate estimates of abundance should maximize detection and attendance by males. Many bird species are less active during high winds and precipitation, and, therefore, not available for detection during count-based surveys (Robbins 1981). Male sage-grouse attendance rates are lower on days with precipitation and increasing wind speeds and can remain low for an additional day (Bradbury et al. 1989, Fremgen 2014). Precipitation in our study had a stronger effect on attendance than high winds, with substantial declines in attendance the day of a precipitation event and the subsequent day (Fremgen 2014). However, detection on leks increased with increasing snow cover immediately after precipitation, creating a challenge to balance maximum detection and availability. To accurately estimate population abundance, managers must identify the highest count of males available on the lek, which should be done by maximizing detectability and availability for detection and performing at least 3 lek counts on active leks (Connelly et al. 2003).

Counts are a good index to the population when detection is constant through time and space and independent of population size (Johnson 2008). In our preliminary data analysis, we found that detectability on leks did not vary annually and substantially from one lek to another. Therefore, lek counts can be a reasonable index to population abundance assuming all other components of detection listed above are also constant. Additionally, we found detectability on leks was independent of the lek size and number of males present on the lek, indicating lek counts may be adequate indices to population abundance at a larger scale.

## MANAGEMENT IMPLICATIONS

If accurate estimates of male abundance on leks are desirable for small regional populations, especially if there is great variation in vegetation or snow cover among leks or surveys within a year, we recommend concurrent sightability surveys to estimate and correct for detection probabilities. If detection on leks is not accounted for, lek counts can underestimate regional abundance of males on leks by 17–19%. However, because detectability on leks is constant spatially and temporally, and independent of population size, lek counts may be an adequate index for broader scale population trends unless other components of detection vary. Current lek count protocols recommend avoiding lek counts during precipitation or high winds but do not incorporate any lag effect after precipitation (Connelly et al. 2003). We found snow cover increased detection, but we recommend waiting to perform lek counts until 2 days after snow storms in areas with severe storms to maximize availability of grouse (Fremgen 2014). Current lek count protocols recommend performing lek counts 30 minutes before sunrise to 1 hour after sunrise (Connelly et al. 2003). We found the rate of recording marked males was highest within the recommended time frame but most efficient in the first hour. We do not advocate observers performing lek counts from a lower elevation than the birds; rather we suggest counters consider visibility of birds in relation to landscape features such as drainages. Although we were able to determine variables that can be manipulated to maximize detection probabilities during lek counts, other factors contributing to detection may be beyond the control of observers. For example, detection improved with shorter sagebrush near males on the lek, but vegetation cannot be controlled during lek counts. Modeling detection probabilities based on sightability surveys are critical to accounting for these factors when estimating abundance.

## ACKNOWLEDGMENTS

F. R. Thompson, III, H. S. He, N. J. Wojcik, and A. M. Widmer provided comments on earlier drafts of this manuscript. We thank the OTR, Power Company of Wyoming, LLC, J. M. Theesfeld, and other Carbon County landowners for land access. J. C. Brockman, A. N. Coleman, M. E. Doherty, C. A. Doyle, A. Foster, J. A. Fox, R. L. Golden, M. B. Gonnerman, A. M. Miller, M. J. Peterson, S. L. Robatcek, B. N. Towery, and M. P. Womack provided technical field assistance. M. J. Paul, N. J. Wojcik, J. W. Kehmeier, R. Hay, R. B. Duncan, and T. Grosch assisted with lek counts. Primos Hunting provided financial assistance for ground blinds. F. R. Thompson, III and T. W. Bonnot assisted with analyses. Funding was provided by federal and state wildlife agencies, and wind energy partners under the oversight of the National Wind Coordinating Collaborative. Funding sponsors include the University of Missouri, U.S. Department of Energy Office of Energy Efficiency and Renewable Energy, Wind and Water Power Technologies (DE-AC36-08GO28308), National Renewable Energy Laboratory (subcontract XFT-1-11321-01), National Fish and Wildlife Foundation, U.S. Forest Service Rocky Mountain Research Station (10-JV-11221632-215 and 13-JV-11221632-046), and Western Association of Fish and Wildlife Agencies (11-CO-11221632-068, 12-CO-11221632-181, and 13-CO-11221632-007). We thank C. L. Aldridge and D. D. Musil for providing helpful comments on an earlier draft that improved our manuscript.

## LITERATURE CITED

Alldredge, M. W., K. H. Pollock, T. R. Simons, J. A. Collazo, and S. A. Shriner. 2007. Time-of-detection method for estimating abundance from point-count surveys. Auk 124:653–664.

Anderson, C. R., Jr., and F. G. Lindzey. 1996. Moose sightability model developed from helicopter surveys. Wildlife Society Bulletin 24:247–259.

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294–1297.

Bailey, R. G. 1995. Description of the ecoregions of the United States: 342 intermountain semidesert province. United States Department of Agriculture, U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Baumgardt, J. A. 2011. Probability of attendance and sightability of greater sage-grouse on leks: relating lek-based indices to population abundance. Dissertation, University of Idaho, Moscow, USA.

Beck, T. D. I., and C. E. Braun. 1980. The strutting ground count: variation, traditionalism, management needs. Proceedings of the Western Association of Fish and Wildlife Agencies and the Western Division American Fisheries Association 60:558–566.

Benkobi, L., D. W. Uresk, G. Schenbeck, and R. M. King. 2000. Protocol for monitoring standing crop in grasslands using visual obstruction. Journal of Range Management 53:627–633.

Bodie, W. L., E. O. Garton, E. R. Taylor, and M. McCoy. 1995. A sightability model for bighorn sheep in canyon habitats. Journal of Wildlife Management 59:832–840.

Bonnot, T. W., M. L. Wildhaber, J. J. Millspaugh, A. J. DeLonay, R. B. Jacobson, and J. L. Bryan. 2011. Discrete choice modeling of shovelnose sturgeon habitat selection in the Lower Missouri River. Journal of Applied Ichthyology 27:291–300.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Bradbury, J. W., S. L. Vehrencamp, and R. M. Gibson. 1989. Dispersion of displaying male sage grouse: I. Patterns of temporal variation. Behavioral Ecology and Sociobiology 24:1–14.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Cade, B. S. 2015. Model averaging and muddled multimodel inference. Ecology 96:2370–2382.

Campbell, H. 1972. A population study of lesser prairie chickens in New Mexico. Journal of Wildlife Management 36:689–699.

Chapman, S. S., S. A. Bryce, J. M. Omernik, D. G. Despain, J. ZumBerge, and M. Conrad. 2004. Ecoregions of Wyoming (color poster with map, descriptive text, summary tables, and photographs). U.S. Geological Survey, Reston, Virginia, USA.

Clifton, A. M., and D. G. Krementz. 2006. Estimating numbers of greater prairie-chickens using mark-resight techniques. Journal of Wildlife Management 70:479–484.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats.

Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.
Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station Bulletin 80. University of Idaho, Moscow, USA.
Connelly, J. W., and M. A. Schroeder. 2007. Historical and current approaches to monitoring greater sage-grouse. Pages 3–9 *in* K. P. Reese, and R. T. Bowyer, editors. Monitoring populations of sage-grouse. College of Natural Resources Experiment Station Bulletin 88. University of Idaho, Moscow, USA.
Crunden, C. W. 1963. Age and sex of sage grouse from wings. Journal of Wildlife Management 27:846–849.
Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. Journal of Wildlife Management 27:810–841.
Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43–64.
Diefenbach, D. R., M. R. Marshall, J. A. Mattice, and D. W. Brauning. 2007. Incorporating availability for detection in estimates of bird abundance. Auk 124:96–106.
Driese, K. L., and N. Nibbelink. 2004. Database development for analysis of cumulative impacts in southeast Wyoming. University of Wyoming, Wyoming Geographic Information Science Center, Laramie, USA.
Dunn, P. O., and C. E. Braun. 1985. Natal dispersal and lek fidelity of sage grouse. Auk 102:621–627.
Emmons, S. R., and C. E. Braun. 1984. Lek attendance of male sage grouse. Journal of Wildlife Management 48:1023–1028.
Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal of Wildlife Management 19:267–272.
Farnsworth, G. L., K. H. Pollock, J. D. Nichols, T. R. Simons, J. E. Hines, and J. R. Sauer. 2002. A removal model for estimating detection probabilities from point-count surveys. Auk 119:414–425.
Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in Northwestern California. Ecological Monographs 70:539–590.
Fremgen, A. L. 2014. Lek ecology of male greater sage-grouse in Carbon County, Wyoming. Thesis, University of Missouri, Columbia, USA.
Garton, E. O., J. W. Connelly, J. S. Horne, C. A. Hagen, A. Moser, and M. A. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Studies in Avian Biology 38:293–379.
Garton, E. O., D. D. Musil, K. P. Reese, J. W. Connelly, and C. L. Anderson. 2007. Sentinel lek-routes: an integrated sampling approach to estimate greater sage-grouse population characteristics. Pages 31–41 *in* K. P. Reese, and R. T. Bowyer, editors. Monitoring populations of sage-grouse. College of Natural Resources Experiment Station Bulletin 88, University of Idaho, Moscow, USA.
Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.
Hanley, T. A. 1978. A comparison of the line-interception and quadrat estimation methods of determining shrub canopy coverage. Journal of Range Management 31:60–62.
Jenni, D. A., and J. E. Hartzler. 1978. Attendance at a sage grouse lek: implications for spring censuses. Journal of Wildlife Management 42:46–52.
Johnson, D. H. 2008. In defense of indices: the case of bird surveys. Journal of Wildlife Management 72:857–868.
Johnson, D. H., and M. M. Rowland. 2007. The utility of lek counts for monitoring greater sage-grouse. Pages 15–23 *in* K. P. Reese, and R. T. Bowyer, editors. Monitoring populations of sage-grouse. College of Natural Resources Experiment Station Bulletin 88, University of Idaho, Moscow, USA.
Kéry, M., and B. R. Schmidt. 2008. Imperfect detection and its consequences for monitoring for conservation. Community Ecology 9:207–216.
MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.
Patterson, R. L. 1952. The sage grouse in Wyoming. Sage Books, Denver, Colorado, USA.
Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.
Rice, C. G., K. J. Jenkins, and W. Chang. 2009. A sightability model for mountain goats. Journal of Wildlife Management 73:468–478.
Robbins, C. S. 1981. Bird activity levels related to weather. Studies in Avian Biology 6:301–310.
Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–297.
Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. Journal of Wildlife Management 51:622–630.
Schmidt, J. H., C. L. McIntyre, and M. C. MacCluskie. 2013. Accounting for incomplete detection: what are we estimating and how might it affect long-term passerine monitoring programs? Biological Conservation 160:130–139.
Schroeder, M. A., and C. E. Braun. 1992. Greater prairie-chicken attendance at leks and stability of leks in Colorado. Wilson Bulletin 104:273–284.
Schroeder, M. A., and L. A. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildlife Biology 9:291–299.
Sedinger, J. S. 2007. Improving understanding and assessment of greater sage-grouse populations. Pages 43–56 *in* K. P. Reese, and R. T. Bowyer, editors. Monitoring populations of sage-grouse. College of Natural Resources Experiment Station Bulletin 88, University of Idaho, Moscow, USA.
Steinhorst, R. K., and M. D. Samuel. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. Biometrics 45:415–425.
Thatcher, A. P. 1959. Distribution of sagebrush as related to site differences in Albany County, Wyoming. Journal of Range Management 12:55–61.
U.S. Fish and Wildlife Service. 2010. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered; proposed rule. Federal Register 75:13909–13958.
Udevitz, M. S., B. S. Shults, L. G. Adams, and C. Kleckner. 2006. Evaluation of aerial survey methods for Dall's Sheep. Wildlife Society Bulletin 34:732–740.
Vander Wal, E., P. D. McLoughlin, and R. K. Brook. 2011. Spatial and temporal factors influencing sightability of elk. Journal of Wildlife Management 75:1521–1526.
Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.
Walsh, D. P. 2002. Population estimation techniques for greater sage-grouse. Thesis, Colorado State University, Fort Collins, USA.
Walsh, D. P., H. Campa III, D. E. Beyer, Jr., and S. R. Winterstein. 2011. Measurement error and survey design in sightability model development. Journal of Wildlife Management 75:1228–1235.
Walsh, D. P., J. R. Stiver, G. C. White, T. E. Remington, and A. D. Apa. 2010. Population estimation techniques for lekking species. Journal of Wildlife Management 74:1607–1613.
Walsh, D. P., G. C. White, T. E. Remington, and D. C. Bowden. 2004. Evaluation of the lek-count index for greater sage-grouse. Wildlife Society Bulletin 32:56–68.
Washburn, B. E., D. J. Tempel, J. J. Millspaugh, R. J. Gutiérrez, and M. E. Seamans. 2004. Factors related to fecal estrogens and fecal testosterone in California spotted owls. Condor 106:567–579.
Welch, B. L. 2005. Big sagebrush: a sea fragmented into lakes, ponds, and puddles. United States Department of Agriculture, U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
Western Regional Climate Center [WRCC]. 2008. Local climate data, Rawlins Municipal Airport. Western Regional Climate Center, Reno, Nevada, USA.
White, G. C. 2005. Correcting wildlife counts using detection probabilities. Wildlife Research 32:211–216.
White, G. C., and T. M. Shenk. 2001. Population estimation with radio-marked animals. Pages 329–350 *in* J. J. Millspaugh, and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

*Associate Editor: Michael Morrison.*

# Greater Sage-Grouse Population Dynamics and Probability of Persistence

Final Report to Pew Charitable Trusts
18 March 2015

*Edward O. Garton*[1]*, Adam G. Wells*[2]*, Jeremy A. Baumgardt*[3] *and John W. Connelly*[4]

***Abstract***. We updated our earlier comprehensive analysis of Greater Sage-Grouse (*Centrocercus urophasianus*) population dynamics and probability of persistence from 1965 to 2007 throughout the species range by accumulating and analyzing additional counts of males from 2008 to 2013. A total of 89,749 counts were conducted by biologists and volunteers at 10,060 leks from 1965 through 2013 in 11 states occupied by Greater Sage-Grouse. In spite of survey effort increasing substantially (12.6%) between 2007 and 2013 in 10 of the 11 states, the reconstructed estimate for minimum number of breeding males in the population fell by 55% from 98,616 (SE 3,736) to 44,297 (SE 1,019). Using standard approximations for missing values from Colorado suggests that the range-wide population fell 56% from109,990 breeding males in 2007 to 48,641 breeding males in 2013. The best model of annual rates of change of populations estimated across the Sage-Grouse Management Zones was a stochastic density dependent Gompertz model with 1-year time lags and declining carrying capacities through time. Weighted mean estimates of carrying capacity for the minimum number of males counted at leks for the entire range-wide distribution, excepting Colorado, were 40,505 (SE 6,444) in 2013 declining to 19,517 (SE 3,269) in 30 years and 8,154 (SE 1,704) in 100 years. Starting with the estimated abundance of males counted at leks in 2007 a simple effort to evaluate the validity of future forecasts of abundance was conducted by forecasting abundance in 2013 from Gompertz density dependent models with 1-year time lag and declining carrying capacity models of 6 of the 7 management zone populations. Estimated mean abundance in 2013 predicted 97.8% of the variation in true abundance in management zones. Concerted efforts across both public and private land ownerships that are intended to benefit Greater Sage-Grouse show little current evidence of success but more will be required to stabilize these declining populations and ensure their continued persistence in the face of ongoing development and habitat modification in the broad sagebrush region of western North America.

---

[1] Emeritus Professor, University of Idaho, Moscow; [2] Washington State University, Vancouver; [3] Texas A&M University, Kingsville; [4] Retired Research Scientist, Idaho Department of Fish and Game, Blackfoot

## Introduction

The Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) is considered a "landscape species" with annual ranges that can encompass > 2,700 $km^2$ (Leonard et al. 2000, Holloran and Anderson 2005, Knick and Connelly 2011). Movements within breeding habitat can exceed 25 km, and seasonal ranges can be > 80 km apart (Connelly et al. 1988, Holloran and Anderson 2005). Populations throughout the species' range have been negatively affected by loss and fragmentation of habitat largely due to wildfire, invasive species and energy development (Doherty et al. 2008, Miller et al. 2011). Moreover, some populations have declined as a result of west Nile virus (Walker et al. 2004, 2007). Schroeder et al. (2004) estimated that sage-grouse have been extirpated from 44% of the species' likely historic range.

Despite substantial evidence indicating population declines and habitat loss (Braun 1998, Connelly et al. 2004, Schroeder et al. 2004), in 2005, the U.S. Fish and Wildlife Service (USFWS) determined that listing greater sage-grouse under the Endangered Species Act (ESA) was not warranted (Stiver 2011). However, a complaint filed in July 2006 by Western Watersheds alleged the 2005 finding was incorrect, arbitrary, and unwarranted (Ashe 2010). The U.S. District Court for Idaho subsequently ruled the USFWS determination was arbitrary and capricious and remanded the finding to the USFWS. In March 2010, the USFWS concluded that the sage-grouse was warranted for protection under ESA, but listing was precluded because of higher priorities (Ashe 2010); this agency agreed to issue a final determination by September 2015. The listing decision identified habitat loss/fragmentation, including habitat treatments, and lack of adequate regulatory mechanisms as the major factors contributing to declines in sage-grouse populations (Connelly 2014).

In addition to the work by Schroeder et al. (2004), other publications have assessed sage-grouse population change. Connelly and Braun (1997) concluded that by 1994 breeding populations had declined by 17-47% from long-term averages. Connelly et al. (2004) reported that sage-grouse populations declined at an overall rate 2.0% per year from 1965-2003. Similarly, an analysis by the Western Association of Fish and Wildlife Agencies (WAFWA 2008) indicated range wide declining trends for sage-grouse from 1965-2007. The most recent analysis (Garton et al. (2011) assessed long-term changes in sage-grouse populations by sage-grouse management zone (Stiver et al. 2006), reconstructed population abundance, and evaluated the likelihood of long-term persistence of populations. These authors' findings generally agreed with previous studies documenting declining populations of sage-grouse. Moreover, Garton et al. (2011) generated models that suggested at least 3 of 23 populations but no Sage-Grouse Management Zones (SMZs) may decline below effective population size of 50 within the next 30 years and at least 18 of 23 populations and 2 of 7 SMZs are likely to decline below effective population size of 500 within 100 years if current conditions and trends persist.

Recently, state and federal agencies have implemented a variety of conservation plans and programs to improve sage-grouse populations and habitats (NTT 2011, Baruch-Mordo et al. 2013, Copeland et al. 2013, Connelly 2014). Although federal conservation actions have been criticized (Connelly 2014) and some positive impacts of CRP on sage-grouse populations in Washington had been documented through 2010 (Schroeder and Vander Haegen 2011), no current evaluations of the status of sage-grouse at the population, SMZ, or range-wide scales exist that provide insight into current status of sage-grouse or that may allow an evaluation of effectiveness of conservation actions to date. If implementation of current conservation programs were effective and sufficient, we would expect that trends for many sage-grouse over the last 6 years would have begun to stabilize or in some cases may have begun to increase. With availability of 6 additional years of data since the Garton et al. (2011) publication, our objectives were to update the analyses of Garton et al. (2011) and evaluate our predictions. Thus, we 1) assess recent changes (2007-2013) in sage-grouse populations by SMZ; 2) reconstruct population abundance back to 1965 for each population, SMZ and range-wide; 3) evaluate the probability of persistence of sage-grouse populations; and 4) validate forecasts of future sage-grouse population abundance critical to estimating probability of persistence. We then examine these findings for evidence of stabilizing or increasing populations that could be attributed to recent conservation programs.

## Methods

We obtained lek counts from 2007 to 2013 from each state fish and game agency except Colorado to reconstruct the sage-grouse populations for 6 additional years and use these estimates of the minimum number of males attending leks to model population changes and project probabilities of persistence for each population, SMZ population and the entire metapopulation using an analogous approach to that presented in Garton et al. (2011) and in a similar analysis for Lesser Prairie Chickens (Garton et al. in press). All states except Colorado contributed data on lek surveys that were combined with earlier data (Garton, et al. 2011:293) yielding a total of 89,749 surveys conducted from 1965 to 2013 at 10,060 individual leks. Detailed descriptions of each population and SMZ are provided in Garton et al. 2011.

### *Population Reconstruction*

Leks surveyed in previous years (1965-2007) as well as leks added to the counts or discovered since 2007 were used to reconstruct an index of population abundance for each population (Fig. 1) and SMZ population ($N(t)$) based on the maximum count of males out of 3 or more surveys at each lek. The population index was estimated from the total number of males counted and the associated standard error from mean counts in 2007 to 2013, finite rates of change ($\lambda(t)$) and relative sizes of the previous years' populations ($\theta(t)$) in each pair of years using ratio estimators (Garton et al. 2011:301) to extend earlier estimates from 1965 to 2013. Only repeated counts of

leks from consecutive years were included in the estimates to insure that they produce unbiased estimates of population size and rates of change. New leks added to the surveys or missed leks were included in estimation once they had been counted in successive years. New leks substantially increased the precision of the most recent estimates of minimum male abundance because of a 50% increase in the number of leks counted in most areas over the last 10 years of surveys. Confidence intervals for the reconstructed populations were calculated from the variance of mean lek counts in 2013 combined with the variances of successive ratios of previous year to current year abundance ($\theta(t)$) back to the year in question as in Garton et al. (2011:302). Thus we began at 2013 and reconstructed population sizes for each population and SMZ back to the earliest lek counts available to us, typically 1965. Finite rates of change ($\lambda(t)$) were transformed to instantaneous rates of change ($r(t)=\ln\lambda(t)$) to model population growth. These estimates provided an index of population abundance from 1965-2013 for modeling changes in population, population projections, and identifying the probability of the species persistence.

*Modeling Population Growth*

We fit the same suite of 26 stochastic population growth models as described by Garton et al. (2011:302) to the time series of reconstructed minimum male population indices for each SMZ and population. The first 2 models are a more efficient and realistic version of the classic trend models (WAFWA 2008) assuming no density dependence in the rates of population change but either a single trend through time portraying exponential growth with process error (EGPE; Dennis et al. 1991) or exponential growth with differing mean rates of change between two time periods (period 1 = 1967–1987, period 0 = 1987–2013). We also fit density-dependent models of annual rates of change based on either Ricker-type density dependence in population growth (Dennis and Taper 1994) in which rates of change decline in proportion to abundance, or Gompertz-type density dependence in population growth (Dennis et al. 2006) in which rates of change decline logarithmically in proportion to abundance. Because of the apparent cyclic pattern of population growth observed in come populations and management zones (Rich 1985, Garton et al. 2011) we incorporated either 0,1 or 2 year time lags ($\Delta$)into the density dependent Ricker and Gompertz models. To portray the apparent difference in growth patterns through time as either a difference between the 2 time periods identified above or as a continuously changing carrying capacity, each density dependent model was combined with a period effect (period, as described above), and a time trend in population carrying capacity (year) or both (Garton et al. 2011:302). Letting $N(t)$ be the observed population index at time $t$ ,$Y(t) = \log[N(t)]$, and the annual growth rate $r(t) = Y(t+1) - Y(t)$. The global stochastic model incorporating Ricker-type density dependence was

$$r(t) = a + b \times N(t-\Delta) + c \times Year + d \times Period + E(t), \qquad (1)$$

and the analogous model for Gompertz-type density dependence was

$$r(t) = a + b \times \ln\left(N(t-\Delta)\right) + c \times Year + d \times Period + E(t) \quad (2)$$

where $Y(t) = \log[N(t)]$, the annual growth rate $r(t) = Y(t + 1) - Y(t)$.

The global statistical model incorporated a difference in time periods by setting Period = 1 if Year = 1965 – 1996 and Period = 0 if Year = 1997 – 2013. $E$(t) represented environmental (i.e., process) variation in realized growth rates and was a normally distributed random deviate with mean = 0 and variance = $\sigma^2$. These models yielded five parameters (i.e., *a, b, c, d,* and $\sigma^2$) that were estimated via maximum likelihood using the indices to past abundance data estimated from the population reconstruction.

The only difference between the Ricker and Gompertz models is that the Ricker assumes growth rates are a linear function of population size and the Gompertz assumes growth rates are a linear function of the natural log of population size. Density dependent models such as Gompertz and Ricker provide an objective approach to estimate a carrying capacity or quasi-equilibrium (hereafter carrying capacity), which is defined as the population size at which the growth rate is 0. This carrying capacity represents a turning point in abundance below which population size tends to increase and above which population size tends to decrease. Adding period or year effects to these density dependent models evaluate the possibility that carrying capacity varied between the early time period and more recently or that it has changed through the years or both. This set of 24 density dependent models produce an efficient approach to evaluate and estimate 2 types of density dependence (arithmetic vs logarithmic for Ricker vs Gompertz) with 3 lags (0, 1 or 2 years) with potential differences in periods of time (2 periods) with constant or continuously changing carrying capacities (changing or constant, i.e. year or no year effect) yielding 2 by 3 by 2 by 2 combinations or 24 total density dependent models that we would hypothesize might best describe the observed reconstructed population abundance indices through time. Note that the 2 density independent models appear superficially similar to classic trend models obtained by simply converting reconstructed annual abundance indices to logarithms and regressing log abundance on year to "fit a trend line" through the data or as done by WAFWA (2008) fitting separate trend lines to the 2 time periods but at the conceptual level they differ fundamentally. Fitting a single or 2 trend lines is far less efficient (Humbert et al. 2009) and falsely treats error around the regression line as errors in observation, while our approach to estimating trend estimates logarithmic rates of change *r(t)* in each year and then estimates the average or an average for each time period as an efficient estimator of trend, treating errors in the estimates as estimates of process error rather than observation error. Estimating process error in this way provides a straight-forward approach to forecast future abundance incorporating process error (see below) whereas observation error estimated by regression is not useful for forecasting future patterns of abundance.

*Parameter Estimation*

To each set of observed abundance data, we fit these 26 models using general linear mixed models in the statistical computing program R (R Development Core Team 2014) and mixed procedure of Program SAS (SAS Institute 2003) in the same manner as applied earlier to sage-grouse (Garton et al. 2011:303 eq. 15.10) and applied to Lesser Prairie Chicken (*Tympanuchus pallidicinctus*, Garton et al. in press). These stochastic growth models treat annual rates of

change ($r_t$) as mixed effects of fixed effects (year and period) and random effects (reconstructed population index with or without log transformation and time lags). Residual annual rates of change ($r_t$) were consistently described well by a normal distribution. We used Akaike's Information Criteria corrected for small sample size (AICc) to rank the relative performance (i.e., predictive ability) of each model (Burnham and Anderson 2002). Likewise, we followed Akaike (1973,), Buckland et al. (1997) and Burnham and Anderson (2002:75) in calculating AICc weights ($w_i$), which we treated as relative likelihoods for a model given the data

$$w_i = \frac{\exp(-0.5 \times \Delta_i)}{\sum_{i=1}^{R} \exp(-0.5 \times \Delta_i)} \quad (3)$$

where Δi was the difference between the AICc for model i and the lowest AICc of all R models. For a given analysis unit, we report a 95% confidence set of models based on the best model using the sum of model weights ≥0.95 (Burnham and Anderson 2002). This approach reduced the number of models reported for all analysis units to those models with some potential of explaining the data but did not necessarily drop all models with ΔAICc less than 2 or 3. All models and resulting parameter estimates are reported in Appendices 1 and 2.

We used this same approach based on maximum likelihood estimation of general linear mixed models to estimate a weighted mean carrying capacity for each population where weights were based on Akaike weights defined above. We combined SMZ population estimates into a range-wide estimate by treating SMZ populations as strata within a stratified random population estimate of range-wide abundance and carrying capacity. From these base models, several plausible scenarios for population growth can be realized. Models involving time trends (+ Year) and period differences (+ period) can be interpreted as inferring that the carrying capacity is changing through time (i.e., negative slopes imply declines through time) or differs between time periods. For example, the parameter estimates from the Ricker model with a time trend (Year) and period effect (Period) can be used to estimate a carrying capacity as follows:

$$\hat{K} = -\hat{b}^{-1}(\hat{a} + \hat{c}Year + \hat{d}Period) \quad (4)$$

The hat (^) notation over a parameter indicates this value was the maximum likelihood estimate for that parameter when fit to past abundance data. When parameters *b* and *c* are set to 0, these models reduce to the EGPE model (Dennis et al. 1991) and including Period simply allows for differing carrying capacities between the two time periods. All forecasts assume that period effects estimated for the final time period and future year effects continue into the future at constant annual rates of change.

*Stochastic population projections*

For each population, we used parametric bootstraps in SAS and R by projecting 4,000 replicate abundance trajectories for 30 and 100 years post 2013 using

$$N(t+1) = N(t) + e^{\hat{r}(t)} \quad (5)$$

where $\hat{r}(t)$ was the stochastic growth rate calculated using maximum likelihood parameter estimates for the given model. For example, to project based on the Ricker model with no time lag, a time trend in carrying capacity and a difference between periods, we used

$$N(t+1) = N(t) \times e^{\hat{a}+\hat{b}N(t)+\hat{c}Year+\hat{d}Period+E(t)} \quad (6)$$

where $N(0)$, the initial abundance for the projections, was the final observed population size index (i.e., male sage-grouse counted in 2013), Period = 0 indicating that future change (growth or decline) would be analogous to what occurred from 1987 to 2013 and $E(t)$ was a random deviate drawn from a normal distribution with mean 0 and standard deviation equal to $\hat{\sigma}$ (square root of maximum likelihood estimate of mean squared error remaining from mixed model). These parametric bootstraps (replicate stochastic time series) were then used to calculate the probability that the population would decline below a quasi-extinction threshold corresponding to minimum counts of 20 and 200 males for comparison to earlier estimates (Garton et al. 2011) or 77 and 767 males at leks (effective population sizes of 50 and 500 of Franklin (1980) and Soule (1980); see next paragraph for details). Probability of quasi-extinction was the proportion of replications in which population abundance fell below the quasi-extinction threshold at some point during the time horizon (30 or 100 years).

We calculated thresholds for estimation of probability of persistence in two different manners for this analysis. First, for comparison to earlier bootstraps of probability of persistence we used the same thresholds of quasi-extinction of 20 and 200 males representing breeding lek attendance of 50 and 500 sage-grouse (Garton et al. 2011:304). Secondly, we estimated persistence defined as probability of falling below effective population size ($N_e$) of 50 and 500 as proposed by Franklin (1980) and Soule (1980), respectively. We used the average of three independent approaches to estimating breeding sex ratio applied to Sewall Wright's (1938) estimator of effective population size:

$$N_e = \frac{1}{\frac{1}{N_m} + \frac{1}{N_f}} \qquad (7)$$

where $N_m$ = number of males successfully breeding and $N_f$ = female breeders. Patterson's (1952) historic work in Wyoming suggested that sex ratio at leks is 2.5 adult plus yearling females per male producing an estimate of 70 males counted at leks corresponding to an effective population size of 50 or 699 males for $N_e$ of 500. Aldridge (2001) estimated $N_e$ of 88 for sage-grouse in Alberta based on estimates of breeding success applied to his counts of 140 males and 280 females attending 8 leks. This suggests a count of 79 males required for an effective population size of 50 and 795 for $N_e$ of 500. Schroeder et al. (1999) reviewed banding data on 3671 females and 5468 males banded in Colorado, Idaho and Wyoming indicating average annual survival rates of yearlings and adults combined of 61.7% for females and 49.2% for males. Applying these average rates in a simple lifetable for yearlings and adults yields an estimate of 1.64 females per male in the populations of breeding age sage-grouse. Using Wright's formula, this sex ratio implies 80 males are required at leks for an effective population size of 50 and 804 males for an effective population size of 500. Averaging these 3 independent estimates of effective population size yields thresholds of counts of 77 males at leks required for an effective population size of 50 and 767 for $N_e$ of 500.

Based on our comparison of AICc values, most populations had >1 model that could be considered a competing best model by scoring within the 95% set; this generally meant $\Delta$AICc < 3. Therefore, to incorporate model selection uncertainty into forecasts of population viability, we projected future population abundances using each of the 26 models and used model averaging (Burnham and Anderson 2002:159) to generate an overall (i.e., based on all fitted

models) estimate of the probability of quasi-extinction. Generally, a "model averaged" prediction can be obtained by calculating the predicted value of a parameter of interest (e.g., probability of quasi-extinction) for each model and taking a weighted average of the predictions where the weights are the relative likelihoods of each model,

$$\hat{\Pr}(Extinction) = \sum_{i=1}^{R} \left\langle \hat{\Pr}(Extinction \left| Model_i \right\rangle \times w_i \right) \quad (8)$$

Probability of extinction under a particular model is conditional on that model and its maximum likelihood parameter estimates. To assess the precision of model averaged probabilities of quasi-extinction, we calculated a weighted variance for these probabilities of extinction (Krebs 1999:276) similar to the variance of a mean for grouped data (Remington and Schork 1970:46)

$$\hat{Var}\left[\hat{\Pr}(Extinction)\right] = \sum_{i=1}^{R} w_i^2 \times [\hat{\Pr}(Extinction) - \hat{\Pr}(Extinction \left| Model_i \right.)]^2 \quad (9)$$

*Metapopulation Analyses*

We analyzed viability of the metapopulation of sage-grouse across all 6 management zones similarly to the analysis for individual SMZs with three exceptions. First, instead of basing population projections on all 26 models, we used only the highest ranked AICc model across all 6 SMZ populations, Gompertz density dependent models with one year time lag and declining trend in carrying capacity through time. Second, the metapopulation model required estimated dispersal rates among SMZs. Movements were modeled using the same approach developed in earlier work (Garton et al. 2011:367) with the modification that Colorado Parks and Wildlife's failure to participate required dropping those potential movements and connections. Lastly, correlated dynamics among SMZs were modeled by including a covariance in the random deviates used to portray environmental stochasticity.

Specifically, the metapopulation was projected through time using

$$N_{Meta}(t+1) = \sum_{j=1}^{7} N_j(t+1) \quad (10)$$

where *Nj* is the abundance of SMZj. Abundance of each SMZ was projected using

$$N_j(t+1) = N_j(t) \times e^{r_j(t)} + \sum_{i=1 \neq j}^{7} N_i(t) \times D_{ij} - \sum_{i=1 \neq j}^{7} N_j(t) \times D_{ji} \quad (11)$$

where *Dij* is the dispersal rate between SMZ i and j. We followed the approach developed by Knick and Hanser (2011) to estimate dispersal rates between populations within SMZs. The probability of connectivity between every pair of leks was estimated using graph theory, based on distance between known leks, the difference in size between adjacent leks, and the product of all probable steps (dispersal limited to 27 km) between the pair of leks (Knick and Hanser 2011). We expressed the estimated number of probable connective links between leks in adjacent SMZs, based on graph theory, as a proportion of all the links shown between any pair of SMZs

(N = 112). These proportions were standardized to an estimated maximum dispersal rate at a distance of 27 km of 0.05 (Knick and Hanser, 2011). The random deviate, *Ej(t)*, for the growth rate of the jth SMZ, $r_j(t)$, was drawn from a multivariate normal distribution with mean = 0 and the six by six variance/covariance matrix estimated from past abundance trajectories. We obtained estimates of covariance by correlating the residuals of the information-theoretic best model for each management zone pair. We used a program similar to the SAS and R routines performing parametric bootstraps in SAS for metapopulation projections.

*Data Considerations and Limitations*

A key issue in analyzing lek data concerns the magnitude of sampling error in sage-grouse lek counts as sampling error could inflate estimates of process error leading to stochastic forecasts of future population viability that are excessively conservative. We evaluated this question by analyzing each reconstructed population time series using an approach that simultaneously estimates observation and process error (Dennis et al. 2006) and found that the population reconstruction time series provide unbiased estimates of process error just as they did for sage-grouse and for Lesser Prairie Chicken in earlier analyses (Garton et al. 2011, Garton et al. in press) with sampling error from combining counts at tens to hundreds of leks approaching 0. Only 3 small populations with limited numbers of leks indicated a non-zero value for observation error and those were exceedingly small ($\sigma^2$<0.002). Thus, we were able to take the same approach applied successfully to sage-grouse earlier (Garton et al. 2011) of estimating parameters and likelihoods for models including observation error within a single error term combining both process (stochastic environmental and demographic) error and sampling error. Consequently, forecasts from these models of probability of persistence will be slightly conservative, implying that probability of persistence is at least as large as our estimates or slightly larger.

All US states supporting populations of sage-grouse (Fig. 1) provided results of lek surveys they conducted except Colorado. Colorado Parks and Wildlife denied requests for results of lek counts (email from Jeffrey M. Ver Steeg, Assistant Director Research, Policy and Planning, Colorado Parks and Wildlife, dated 19 January 2015) making it necessary to substitute the best reasonable estimate of current numbers of breeding males counted at leks in 2013 in Colorado for the observed counts. We used a standard approach for missing values by replacing them with the best available estimate closest in time to the missing value. For 307 leks in Colorado included in the Wyoming Basin population and Wyoming Basin SMZ, we used the last available abundance of sage-grouse counted at these 307 leks: 4103 males were counted in Colorado at 213 of the leks in 2007 (Garton et al. 2011:35). The final estimate for abundance of males in this region in 2013 was then corrected to include both the total number of males observed in surveys in Wyoming and Utah in 2013 plus this estimated number of males present on the Colorado leks not reported, 4103 in 2007. This corrected estimate of male attendance at surveyed leks in 2013 was used as the base survey for population reconstruction back to 2007 and beyond to the earliest surveys in 1965 for Wyoming Basins population and SMZ II. For the Colorado Plateau (SMZ VII) we noticed that the earlier analysis of lek data (Garton et al. 2011:363) identified 2 best models of stochastic growth with no time trend, i.e., stochastic density dependent Ricker and

Gompertz models. Therefore we used an average of the predicted stochastic carrying capacity from each of these models and the last population estimate in 2007 at 73 leks as a best estimate of the missing abundance for this SMZ in 2013.

## Results

Great Plains Management Zone

*Dakotas Population*

Sampling effort for leks in this population occupying western portions of North and South Dakota and small parts of southeastern Montana and northeastern Wyoming increased 16.5%. The average number of leks counted per year from 2008-2013 was 83 leks, up from 56 leks counted per year on average from 2000-2007. The estimated minimum population size was 311 males (SE = 55) which represented a 72% decline from the reconstructed estimate of 1,112 males (SE = 307) based on counts at 85 leks in 2007. The last 6 years showed a continuous (Fig. 2a) decline to reach abundances lower than ever observed before and approximately 16% of average values of about 1,917 males counted in the 1970s and 1980s (Fig. 2a). The best model characterizing the dynamics of this population was a Gompertz model ($r_t$ = 35.8948 – 0.3942 ln($N_t$ )– 0.017 year, $r^2$ = 0.189) with a declining year trend of 1.7% per year which successfully portrayed 19% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 32%. Quasi-equilibriums were estimated at 280 males (SE 79.2) in 2013, 97 males (SE 30.6) in 30 years and 45 males (SE 17.7) in 2113. Parametric bootstraps imply that the minimum count of males has a 21.5% (SE 7.7%) chance of declining below 20 males in 30 years, lower than estimated with data through 2007 (29%) but not significantly lower. Model weighted probabilities of declining below effective population sizes of 50 (35.4%, SE 7.4%) in 30 and 100 years (72.5%, SE 8.5%) were higher.

*Northern Montana Population*

Sampling effort for leks in this population occupying parts of north-central Montana, southeast Alberta, and southwest Saskatchewan declined 11.4 %. This is partially due to Canadian counts included in the 2007 data and analysis but excluded from our current data set. If Canadian counts are removed, sampling effort increased by 6.2%. The average number of leks counted per year from 2008-2013 was 138 leks per year, down from 162 leks counted per year on average from 2000-2007. The estimated minimum population size was 1,667 males (SE = 165) which represented a 54% decline from the reconstructed estimate of 3,615 males (SE = 573) based on counts at 175 leks in 2007. The last 6 years showed a continuous (Fig. 2b) decline to reach abundances as low as those in the 1970s and early 1980s of approximately 1,600 males. Current estimates are about 40% lower than the average counts shown from 1984-2007, which showed a slight increase in abundance males over the preceding 10 years (Fig. 2b). The best model for the dynamics of this population was a Gompertz model with a one year time-lag and a period effect ($r_t$ = 2.8591 – 0.3347 ln($N_{t-1}$ )– 0.3066 period, $r^2$ = 0.352) and showed a probability of being the correct model of 36%. Quasi-equilibrium estimated at 4353 (SE 1,394) in 2013, 3,714 (SE 1,122) in 30 years and 3,380 (SE 992) in 2113. Parametric bootstraps imply that the minimum count of males has a 2.7% (SE 2.1%) chance of declining below 20 males in 30 years. Model

weighted probabilities of declining below effective population sizes of 50 (5.6%, SE 4.4%) in 30 and 100 years (7.2%, SE 5.1%) are all quite low.

*Powder River Basin Population*

Sampling effort for leks in this population, occupying parts of southeastern Montana and northeastern Wyoming, remained fairly steady between 2007 and 2013, with only a 2.1% increase in the number of leks counted. The average number of leks counted per year, however, from 2008-2013 was 395 leks per year, up from 239 leks counted per year on average from 2000-2007, a 65% increase between the 2 periods. The estimated minimum population size was 1651 males (SE = 155) which represented a 76% decline from the reconstructed estimate of 6804 males (SE = 919) based on counts at 384 leks in 2007. The last 6 years showed a continuous (Fig. 2c) decline to reach abundances lower than ever observed before and approximately 4% of average values close to 38,500 males counted in the 70s and 80s. The best model for the dynamics of this population was a Gompertz model with a one-year time lag and an effect of year ($r_t = 67.1015 – 0.396 \ln(N_{t-1}) – 0.0318$ year, $r^2 = 0.317$) with a declining year trend of 0.3% per year which successfully portrayed 32% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 63%. Quasi-equilibriums were estimated about 2,273 (SE 618) in 2013, 240 (SE 78) in 30 years and 36 (SE 24) in 2113. Parametric bootstraps imply that the minimum count of males has a 2.9% (SE 2.3%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (98.7%, SE 2.2%) in 30 and 100 years (98.8%, SE 2.1%) suggest that is fairly certain to happen.

*Yellowstone Watershed Population*

Sampling effort for leks in this population occupying southeastern Montana and northeastern Wyoming increased 83% from 327 leks in 2007 to 625 leks counted in 2013. The estimated minimum population size was 3045 males (SE = 106) which represented a 29% decline from the reconstructed estimate of 8747 males (SE = 949) based on counts at 327 leks in 2007. The last 6 years showed a continuous (Fig. 2d) decline to reach abundances lower than ever observed before and approximately one quarter of average values close to 12,000 males estimated in the 70s and 80s. The best model for the dynamics of this population was a Ricker model ( $r_t = 32.4125 – 0.00006027 N_t – 0.016$ year, $r^2 = 0.364$) with a declining year trend of 1.6% per year as in earlier analyses (Garton et al. 2011:313) which successfully portrayed 36% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 68%. An estimate of carrying capacity for the population in 2013 is 3,087 (SE =788) but the estimate for 2043 indicates a decline to 241 (SE =172) and to 136 (SE =97) in 2113. Compared to results in 2007 when there was negligible chance of the population count falling below 20 males at leks in the short term (30 years, Garton et al. 2011:313) declines during the last 6 years have increased the probability to 15.6% (SE = 2.1%) with the probability of declining below effective population size of 50 now above half (54.5 % with SE = 7.2%). Long term probabilities (in 100 years) of declining below counts of either 20 or 200 males attending leks or effective population sizes of 50 or 500 all exceed 89% (Table 6).

*Great Plains Management Zone Comprehensive Analysis*

Biologists dramatically increased their efforts (33% increase) to count sage-grouse leks from 2007 (957 leks) to 2013 (1,271 leks) producing a reconstructed population estimate of the minimum number of male sage-grouse of 20,016 (SE = 1462) in 2007 which was almost 50% larger than the estimate obtained from counting fewer leks earlier (Garton et al. 2011:314). In spite of this dramatic increase in effort, the estimated minimum male numbers attending leks fell by two-thirds to 6,674 (SE = 312) in the 6-year interval to 2013. This population is continuing its downward trajectory (Figure 2e) with an irregular pattern of peaks separated by periods varying in length from 3 to 16 years. As before (Garton et al. 2011:315) the 4 best models all include Gompertz and Ricker models with declining time trends with and without 1-year time lags that are not significantly better than each other by likelihood ratio tests (Appendix 1). The very top model by information criteria was a Ricker with decreasing time trend (($r_t$ = 30.2053 – 0.0.00001673 $N_t$ – 0.015 year, $\sigma$ = 0.148, $r^2$ = 0.239) implying a 1.5% decrease in carrying capacity each year. Across the best models carrying capacity was estimated as a minimum count of males of 3798 (SE 1378) currently, declining to 1,444 (SE 546) in 2043 and further to 481 (SE 193) in 100 years. With 6 additional years of declining counts at leks the estimates of carrying capacity for this management zone have decreased by half. Forecasts of probability of persistence suggest likelihood of falling below counts of 20 or 200 males have risen to almost 50% (Table 6) while long term probability of falling below effective population sizes of 50 or 500 are now in the range 55% (SE 9.8%) to 93% (SE 5.1%).

Wyoming Basin Management Zone

*Wyoming Basin Population*

Sampling effort to count leks in this population occupying much of Wyoming, part of southern Montana, northeast Utah and northern Colorado increased by 5% excluding Colorado data. The estimated population size was 15,767 males (SE = 644) in 2013 based on counts at 1158 leks which represented a 63% decline from the reconstructed estimate of 43,040 males (SE = 2727) based on counts at 1,106 leks in 2007, again excluding Colorado. The last 6 years showed a continuous (Fig. 3c) decline to reach abundances lower than ever observed before and approximately 25% of average values approximating 63,000 males counted in the 70s and 80s. The best model for the dynamics of this population was a Gompertz model with a one year time lag and a year effect ($r_t$ = 23.619 – 0.2946 ln($N_{t-1}$ )– 0.0103 year, $r^2$ = 0.246) indicating a declining trend of 1.0% per year which successfully portrayed 25% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 36%. Quasi-equilibriums were estimated about 16,078 (SE 4,982) in 2013, 6,158 (SE 2,020) in 30 years and 2,209 (SE 913) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.1% (SE 0.06%) chance of declining below 20 males in 30 years but model weighted probabilities of declining below effective population sizes of 50 (4.7%, SE 1.9%) in 30 and 100 years (21.0%, SE 8.1%) are somewhat higher though still well below 50%.

*Wyoming Basin Management Zone Comprehensive Analysis*

This enormous population constituting a minimum of 54,282 (SE 2636) males in 2007 has dropped precipitously (63% decline) through 2013 to a minimum of 20,006 males (SE 646) counted at 1258 leks if we replace the missing surveys of Colorado leks with the last count available to us in 2007 of 4103 males counted at 213 leks. Alternately, simply ignoring the missing lek surveys from Colorado produces an estimate for this SMZ of 43,149 males declining 63% to 15,903 males in 2013. Sampling effort appeared to decrease by 5.2% between 2007 and 2013 due to failure to report by Colorado, but excluding the 213 Colorado leks counted in 2007 reveals effort in the other states actually increased by 13%. The average number of leks counted from 2007-2013 was 1,161 leks per year a decrease from 1,321 from 2000-2007, again due to failure to report by Colorado. Excluding the 307 total Colorado leks suggests increased effort of 14% in average number of leks surveyed in the recent time interval. The last 6 years showed a continuous (Fig. 3d) decline to reach abundances lower than ever observed before and approximately 33% of average values close to 62,368 males counted in the 70s and 80s. From a reconstructed minimum male population estimate approaching 175,000 birds in the late 1960s the last minimum male population estimate has fallen by an order of magnitude (Fig. 3d). The 10-year interval between peaks in this population appears to have shortened to an 8 or 9 year interval and the low estimate in 2013 is approximately 2000 males below the previous low in the cycle in 1996 though this difference is not statistically significant because of the large SE (4,798) of that earlier low estimate in the cycle.

The best stochastic growth model for this management zone population is a Gompertz model with one year time lag and a carrying capacity declining at approximately 1% per year ($r_t$ = 23.58 – 0.298 ln($N_{t-1}$) – 0.0102 year, $\sigma$ = 0.148, $r^2$ = 0.247). This model has a relative likelihood of 37% followed closely by the comparable Ricker model with declining year trend in carrying capacity. The best stochastic growth models imply that the population of sage-grouse will fluctuate around the current carrying capacity of 18,899 (SE 5518) which will decline to 8,285 (SE 2,619) in 2043 and 2,798 (SE 1,147) in 2113 if this yearly rate of decline persists. Parametric bootstraps forecasting the likelihood of this management zone population falling below 20 or 200 males attending leks are less than 25% (Table 7) but chances for declines below effective population sizes of 50 and 500 in 100 years have grown to 22.1% (SE 8.2%) and 65.3% (SE 7.6%) respectively. These probabilities of extinction are two to three times as large as they were at the end of 2007.

Southern Great Basin Management Zone

*Mono Lake, California-Nevada, Population*

Sampling effort for leks in this small population straddling the California-Nevada border increased by 138% to 50 leks in 2013. The average number of leks counted increased to 46 leks per year, up from 24 leks per year from 2000-2007. The estimated minimum population size was 543 males (SE = 157) which represented a 25% increase from the reconstructed estimate of 435 males (SE = 266) based on counts at 21 leks in 2007. The last 6 years showed an increase until 2013 (Fig. 4a) to reach abundances approximately 83% larger than average values close to 300 males counted in the 1970s and 1980s. The best model for the dynamics of this population was the Gompertz model ($r_t$ = 3.1176 – 0.5521 ln($N_t$ ), $r^2$ = 0.267) and showed a probability of being

the correct model of 37%. Quasi-equilibriums reached about 330 (SE 120) in 2013, 576 (SE 216) in 30 years and 4,059(SE 1,678) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.09% (SE 0.25%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (7.7%, SE 1.6%) in 30 and 100 years (21.5%, SE 4.3%) are low.

*South Mono Lake, California, Population*

Sampling effort for leks in this small population in eastern California increased 16.7% from 12 leks in 2007 to 14 leks in 2013. The estimated minimum population size was 264 males (SE = 102) which represented a 6% decline from the reconstructed estimate of 282 males (SE = 161) based on counts at 12 leks in 2007. The last 6 years showed slight overall (Fig. 4b) decline to reach abundances approximately equal with average values close to 270 males counted in the 1970s and 1980s. The best model for the dynamics of this population was a Gompertz model ($r_t = 2.491 – 0.4528 \ln(N_t)$, $r^2 = 0.228$) and garnered a 38% probability of being the correct model. Quasi-equilibriums reached about 258 (SE 84.5) in 2013, 275 (SE 91.7) in 30 years and 336 (SE 118.3) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.26% (SE 0.42%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (7.9%, SE 2.1%) in 30 and 100 years (21.3%, SE 3.9%) are fairly low.

*Northeast Interior Utah Population*

Sampling effort for leks in this population decreased 18% from 32 leks in 2007 to 26 leks in 2013. The average number of leks counted from 2007-2013 was 27 leks per year an increase from 25 from 2000-2007. The estimated minimum population size was 241 males (SE = 71) which represented a 42% decline from the reconstructed estimate of 412 males (SE = 192) based on counts at 32 leks in 2007. The last 6 years showed a continuous (Fig. 4c) decline to reach abundances 50% of average values close to 486 males counted in the 1970s and 1980s. The best model for the dynamics of this population was a Ricker model with period effect ($r_t = 0.2812 – 0.0012(N_t) + 0.3498$ period, $r^2 = 0.222$) and showed a probability of being the correct model of 19%. Quasi-equilibriums reached about 241 (SE 67) in 2013, 304 (SE 85) in 30 years and 705 (SE 204) in 2113. Parametric bootstraps imply that the minimum count of males has a 1.4% (SE 1.0%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (13.9%, SE 4.5%) in 30 and 100 years (27.5%, SE 6.7%) are fairly low.

*Sanpete-Emery Counties, Utah, Population*

From 2007 to 2013, only 2 to 3 leks were counted, consistent with counts since approximately 1987. The estimated minimum population size was 48 males (SE = 19) which represented a 100% increase from the reconstructed estimate of 24 males (SE = 26) based on counts at 2 leks in 2007. The last 6 years showed a slight increase (Fig. 4d) for this small, isolated population.

*South-Central Utah Population*

Sampling effort for leks in this population decreased 18% from 51 leks in 2007 to 42 leks in 2013. The average number of leks counted from 2007-2013 was 51 leks per year, an increase from 38 from 2000-2007. The estimated minimum population size in 2013 was 737 males (SE = 208) which represented a 51% decline from the reconstructed estimate of 1501 males (SE = 570) based on counts at 51 leks in 2007. The last 6 years showed an overall (Fig. 4e) decline to reach abundances approximately 53% of average values close to 1382 males counted in the 1970s and 1980s. The best model characterizing the dynamics of this population was a Gompertz model ($r_t = 2.2129 – 0.3196 \ln(N_t)$, $r^2 = 0.186$) and garnered a probability of being the correct model of 19%. Quasi-equilibriums reached about 944 (SE 248.1) in 2013, 802 (SE 209.4) in 30 years and 680 (SE 177.2) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.11% (SE 0.16%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (0.9%, SE 0.7%) in 30 and 100 years (18.7%, SE 7.6%) are low.

*Summit-Morgan Counties, Utah, Population*

Sampling effort for leks in this population decreased 14% from 7 leks in 2007 to 6 leks in 2013. The average number of leks counted from 2007-2013 was 8 leks per year, a decrease from 9 from 2000-2007. The estimated minimum population size was 65 males (SE = 19) which represented a 25% decline from the reconstructed estimate of 87 males (SE = 67) based on counts at 7 leks in 2007. The last 6 years showed a decline (Fig. 4f) to reach abundances approximately 85% of average values close to 77 males counted in the 1970s and 1980s.

*Toole-Juab Counties, Utah, Population*

Sampling effort for leks in this population increased 29% from 7 leks in 2007 to 9 leks in 2013. The average number of leks counted from 2007-2013 was 9 leks per year an increase from 6 from 2000-2007. The estimated minimum population size was 57 males (SE = 18) which represented a 78% decline from the reconstructed estimate of 257 males (SE = 237) based on counts at 7 leks in 2007. The last 6 years showed a decline (Fig. 4g) to reach abundances approximately 23% of average values close to 244 males estimated in the 2000.

*Southern Great Basin Population*

Sampling effort for leks in this population decreased in 2013 by 12.1% to 269 leks, down from 306 in 2007. Since 2007 however, the average number of leks counted per year increased from 233 leks per year from 2000-2007 to 281 leks per year from 2008-2013 and overall showed a greater sampling effort. The estimated minimum population size was 3,388 males (SE = 259) which represented a 33% decline from the reconstructed estimate of 5,084 males (SE = 691) based on counts at 306 leks in 2007. The last 6 years showed an overall (Fig. 4h) decline to reach abundances approximately 43% of average values close to 7,855 males counted in the 1970s and 1980s. The best model for the dynamics of this population was a Gompertz model with a 2-year time lag and a year effect ($r_t = 28.088 – 0.4317\ln(N_{t-2}) – 0.0123$ year, $r^2 = 0.357$) with a declining year trend of 1.2% per year which successfully portrayed 36% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 50%. Quasi-equilibriums reached about 2,702 (SE 961) in 2013, 1,417 (SE 551) in 30 years and 543

(SE 267) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.14% (SE 0.16%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 are 1.3% (SE =1.5%) and 10.4% (SE =3.5%) in 30 and 100 years.

*Southern Great Basin Management Zone Comprehensive Analysis*

The population estimate for the entire Southern Great Basin Management Zone declined from a peak in the 6-9 year cycle exceeding 15,000 males in 1970 to a low point of less than 4,000 males in mid-1990s. The 33% decline from an estimated minimum number of males of 8202 (SE 971) in 2007 to 5485 males (SE 382) in 2013 exemplifies the observed declines over the last 2 decades (Fig. 4i). Sampling effort fell 4.0% in that same period. The best stochastic growth model of dynamics of this management zone population was a Gompertz model of density dependence with a 1-year time lag and declining carrying capacity through time ($r_t$ = 15.2114 – 0.3777 ln($N_{t-1}$) – 0.006 year, $\sigma$ = 0.13, $r^2$ = 0.34). This best model implies that the carrying capacity for sage-grouse in the Southern Great Basin Management Zone is declining very slowly at 0.6% per year. Weighted mean estimates of carrying capacity for the management zone across all 24 density dependent models is 4862 (SE 1514) for 2013, 3722 (1175) for 2043 and 2649 (SE 875) for 2113. Parametric bootstraps of probability of declining below counts of 20 and 200 males in 30 years are nil (0%) but grow somewhat for declining below effective population sizes of 50 and 500 in100 years (10.0% with SE 6.0% and 25.3% with SE 6.3%).

Snake River Plain Management Zone

*Baker, Oregon, Population*

Sampling effort for leks in this small population in eastern Oregon increased by 6.3% to 49 leks in 2013. The average number of leks counted per year increased to 21 leks per year from 2008-2013 up from 15 leks per year from 2000-2007. The estimated minimum population size was 49 males (SE = 18) which represented a 64% decline from the reconstructed estimate of 137 males (SE = 92) based on counts at 16 leks in 2007. The last 6 years showed a continuous (Fig. 5a) decline to reach abundances lower than ever observed before and approximately 25% of average values close to 200 males counted from 1993-2007.

*Bannack, Montana, Population*

The small population in Bannack, Montana, estimated at a minimum of 219 (SE 81) males in 2007 declined 19% to a minimum of 177 (SE 35) males observed at 15 leks in 2013, a 37.5% decline in leks counted since 2007 (Fig. 5b). The best models of the dynamics of this small population were Gompertz models with a combination of Period and Year effects ($r_t$ = 16.2963 – 0.4031 ln($N_t$ ) –0.0071 year– 0.1995 period, $r^2$ = 0.212) indicating a very slow decline at approximately 0.7% per year to a quasi-equilibrium about 146 (SE 40.1) in 2013, 109 (SE 30.2) in 30 years and 86 (SE 24.6) in 2113. Parametric bootstraps imply that the minimum count of males has a 6.6% (SE 4.2%) chance of declining below 20 males in 30 years but is already below 200. Model weighted probabilities of declining below effective population sizes of 50 (37.3%, SE 8.3%) in 30 and 100 years (48%, SE 9.0%) are uncomfortably large while long-term persistence based on probability of declining below an effective population size of 500 is nil.

*Red Rocks Lake, Montana, Population*

Sampling effort for leks in this small population occupying southwestern Montana just north of the Idaho border decreased by 30% from 30 leks counted in 2007 to 21 leks counted in 2013. The average number of leks counted per year from 2008-2013 was 18 leks per year, down slightly from 20 leks counted per year on average from 2000-2007. The estimated minimum population size was 357 males (SE = 113) which represented a 37% increase from the reconstructed estimate of 260 males (SE = 202) based on counts at 30 leks in 2007 (Fig. 5c). The last 6 years showed an increase (Fig. 5c) to reach abundances approximately 35% larger than average values of 265 males counted in the 1970s and 1980s.

*Snake-Salmon-Beaverhead, Idaho, Population*

Sampling effort for leks in this population increased by 67.1% to 620 leks up from 321 leks in 2007. The average number of leks counted per year from 2008-2013 was 505 leks, up from 323 leks counted per year on average from 2000-2007. The estimated minimum population size was 6,126 males (SE = 229) which represented a 30% decline from the reconstructed estimate of 8,734 males (SE = 1157) based on counts at 371 leks in 2007 (Fig. 5e). The last 6 years showed a decline (Fig. 5e) to reach abundances approximately 39% of average values of approximately 16,000 males counted in the 70s and 80s. The best model characterizing the dynamics of this population was a Gompertz model with a one-year time lag and a period effect ($r_t = 3.0269 - 0.3423 \ln(N_{t-1}) + 0.2949$ period, $r^2 = 0.371$) and showed a probability of being the correct model of 36%. Estimated quasi-equilibriums reached about 5,727 (SE 1,823) in 2013, 5,074 (SE 1,538) in 30 years and 4,719 (SE 1394) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.36% (SE 0.3%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (3.3%, SE 2.7%) in 30 and 100 years (16.5%, SE 7.4%) are low.

*Northern Great Basin Population*

Sampling effort for leks in this population occupying portions of Nevada, southeastern Oregon, southwestern Idaho, and Northwestern Utah declined by 9.4% to 951 leks down from 1,008 in 2007. The average number of leks counted per year from 2008-2013 was 951 leks per year, up from 595 leks counted per year on average from 2000-2007. The estimated minimum population size was 6,580 males (SE = 376) which represented a 34% decline from the reconstructed estimate of 9,927 males (SE = 1,144) based on counts at 1,008 leks in 2007. The last 6 years showed a decline (Fig. 5f) to reach abundances lower than ever observed before and approximately 23% of average values close to 28,618 males counted in the 1970s and 1980s. The best model for the dynamics of this population was a Gompertz model with a one-year time lag and a year effect ($r_t = 49.056 - 0.5015\ln(N_{t-1}) - 0.0222$ year, $r^2 = 0.514$) with a declining year trend of 0.2% per year which successfully portrayed 51% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 77%. Quasi-equilibriums reached about 6,214 (SE 1,565) in 2013, 1,664 (SE 424) in 30 years and 77 (SE 20.3) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.05% (SE 0.4%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (0.06%, SE 0.5%) in 30 and 100 years (83.6%, SE 2.8%) differ dramatically.

*Snake River Plain Management Zone Comprehensive Analysis*

The estimated minimum number of males attending leks in the Snake River Plain Management Zone declined 31% from 2007 (19,510 SE 1404) to an estimated 13,371 (SE 550) in 2013 (Figure 5h). Sampling effort in this interval increased 9.9% from counting 1480 leks in 2007 to 1,627 leks in 2013 and this increased effort substantially increased the estimated minimum number of males attending leks from the population reconstruction by almost 4,000 males compared to the earlier population estimate (Garton et al. 2011:351). The best stochastic growth model for the reconstructed population was a Gompertz with 1-year time lag and both year and period effects on carrying capacity ($r_t = 25.4738 - 0.4124 \ln(N_{t-1}) - 0.0107\ year + 0.1566\ period$, $\sigma = 0.1319$, $r^2 = 0.448$) which estimated carrying capacities for the management zone declining at 1.07% per year from 13,275 (SE 4,008) in 2013, to 6,420 (SE 2,083) in 2043 and further to 2,330 (SE 1,111) in 100 years.

Northern Great Basin Management Zone

*Central Oregon Population*

The Central Oregon population of sage-grouse has declined 33% since 2007 to a minimum estimated number of males attending leks of 559 (SE 95) along with a 17% decrease in number of leks counted to 80 down from 97 in 2007. The average number of leks counted per year from 2008-2013 was 86.8 leks per year, down from 96 leks counted per year on average between 2000 and 2007. The last 6 years showed a decline to reach abundances lower than ever observed before and approximately 23% of average values close to 2,424 males counted in the 1970s and 1980s (Fig 6a). This final survey is less than one tenth of the peak estimates for the late 1960s which reflects fairly continuous declines through time. The best models characterizing dynamics of this population were Gompertz density-dependent models with either period or year or both parameters indicating a 1.1% decline per year but the best of these models only described slightly more than 20% of the variation in annual estimates of abundance and suggested a carry-capacity currently less than half of current numbers (146, SE 40). Consequently parametric bootstraps imply a 6.6% (SE 4.2%) probability of falling below male counts of 20 and 100% probability below 200 in the short term. Probabilities of declining below effective population sizes of 50 in the long term climb to 48% (SE 9%) while long-term persistence is unlikely if the population continues this pattern of decline.

*Northwest-Interior Nevada Population*

Sampling effort for leks in this small, scattered population, occurring in north-central Nevada decreased by 23.1% to 50 leks down from 65 leks counted in 2007. The average number of leks counted per year from 2008-2013 was 30.2 leks per year, down from 40 leks counted per year on average from 2000-2007. The estimated minimum population size was 79 males (SE = 29) which represented a 32% decline from the reconstructed estimate of 117 males (SE = 102) based on counts at 65 leks in 2007. The last 6 years showed a decline (Fig. 6b) to reach abundances

lower than ever observed before and approximately 52% of average values close to 153 males counted from 1999-2007 (Fig. 6d). The best model for the dynamics of this population was a Gompertz model ($r_t = 4.9614 – 1.0683 \ln(N_t)$, $r^2 = 0.70$) and showed a probability of being the correct model of 69%. . Parametric bootstraps imply that the minimum count of males has a 100% (SE 0%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (100%, SE 0%) in 30 and 100 years (100%, SE 0%) imply that is certain.

*Western Great Basin Population*

Sampling effort for leks in this population decreased by 1.7% to 396 leks in 2013 down from 403 leks in 2007. The average number of leks counted per year from 2008-2013 was 330 leks per year, up from 285 leks counted per year on average from 2000-2007. The estimated minimum population size was 1,934 males (SE = 212) which represented a 69% decline from the reconstructed estimate of 6,327 males (SE = 1,345) based on counts at 403 leks in 2007 (Fig. 6d). The last 6 years showed a decline (Fig. 6c) to reach abundances lower than ever observed before and approximately 16% of average values close to 11,765 males counted in the 1970s and 1980s. The best model characterizing the dynamics of this population was a Gompertz model with a one-year time lag and period effect ($r_t = 2.5868 – 0.3036 \ln(N_{t-1}) + 0.2514$ period, $r^2 = 0.241$) and showed a probability of being the correct model of 44%. Quasi-equilibriums reached about 2,548 (SE 812) in 2013, 701 (SE 228) in 30 years and 40 (SE 14.8) in 2113. Parametric bootstraps imply that the minimum count of males has a 13.1% (SE 6.7%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (13.1%, SE 6.75%) in 30 and 100 years (96.2%, SE 1.1%) are polar opposites.

*Northern Great Basin Management Zone Comprehensive Analysis*

From an abundance of an estimated 40,000 males attending leks in 1965 this management zone population has shown a continuing decline overlaid on 10-year or longer cycles which extended dramatically in length in the most recent period (Figure 6d). The estimated minimum abundance in 2007 of 7,429 (SE 1,312) males, declined 65% by 2013 to 2,573 (SE 468) males even though sampling effort was close to 500 leks counted in both of those years. The best stochastic growth model for the Great Basin management zone population is again a Gompertz model with 1-year lag and a decreasing trend through time ($r_t = 27.4378 – 0.33 \ln(N_{t-1}) – 0.0123$ year, $\sigma = 0.1947$, $r^2 = 0.221$). Weighted mean estimates of carrying capacity for this management zone suggest that the abundance will fluctuate around 2,796 (SE 835) males in 2013, 1,027 (SE 330) males in 2043 and 382 (SE 152) males in 2113. Parametric bootstraps forecast that chances of declining below male attendance at leks of 20 and 200 in the short term (30 years) are only 9.9% (SE 5.3%) and 13.6% (SE 6.7%) but long term extinction defined as falling below effective population sizes of 50 and 500 are very likely at 72.2% (SE 6.2%) and 92.3% (SE 4.9%).

Columbia Basin Management Zone

*Moses Coulee, Washington, Population*

Sampling effort for leks in this small population decreased by 46.9% to 17 leks in 2013, down from 32 leks in 2007. The average number of leks counted per year from 2008-2013 was 20.2 leks per year, down from 33 leks counted on average from 2000-2007. The estimated minimum population size was 202 males (SE = 39) which represented a 12% decline from the reconstructed estimate of 230 males (SE = 84) based on counts at 32 leks in 2007. The last 6 years showed a decline (Fig. 7a) to reach abundances approximately 33% of average values of approximately 609 males counted in the 1970s and 1980s. The best model for the dynamics of this population was a Gompertz model with a one-year time lag and a year effect ($r_t$ = 27.7956 – 0.3647 ln($N_{t-1}$ )– 0.0129 year, $r^2$ = 0.199) with a declining year trend of 1.2% per year which successfully portrayed 20% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 31%. Quasi-equilibriums were about 172 (SE 49.9) in 2013, declining to107 (SE 34.6) in 2043 years and 77 (SE 27.7) in 2113. Parametric bootstraps imply that the minimum count of males has a 7.4% (SE 3.6%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (71.6%, SE 7.8%) in 30 and 100 years (81.0%, SE 6.2%) are both greater than 50%.

*Yakima, Washington, Population*

Sampling effort for leks in this small population increased by 55% to 17 leks in 2013, up from 11 leks in 2007. The average number of leks counted per year from 2008-2013 was 13 leks per year, up from 10 leks counted per year on average from 2000-2007. The estimated minimum population size was 89 males (SE = 36) in 2013 which represented an 11.7% increase from the reconstructed estimate of 80 males (SE = 50) based on counts at 10 leks in 2007. The last 6 years showed small fluctuations (Fig. 7b) but typical numbers of males attending leks reached abundances lower than ever observed before and approximately 24% of average values close to 350 males counted in the 1970s and 1980s.

*Columbia Basin Management Zone Comprehensive Analysis*

Estimated numbers of males attending leks in the Columbia Basin management zone were close to 2,000 in 1965 but showed an approximately 10-year cyclic pattern imposed over a continuous decline to the present. From a 2007 reconstructed, male population estimate of 310 (SE 98) the population declined approximately 6% to an estimated 291 (SE 56) males in 2013 (Fig. 7c). Surveying effort fell to 34 leks counted in 2013 compared to 43 counted in 2007. The best stochastic growth model for the Columbia Basin management zone population is again a Gompertz model with 1-year time lag and declining year trend in carrying capacity ($r_t$ = 27.8921 – 0.3956 ln($N_{t-1}$) – 0.0128 year, $\sigma$ = 0.209, $r^2$ = 0.208). Weighted mean estimates of carrying capacity for this management zone suggest that the abundance will fluctuate around 233 (SE 69.7) males in 2013, 12 (SE 38.9) males in 2043 and 64 (SE 24.2) males in 2113. Parametric bootstraps forecast that chances of declining below male attendance at leks of 20 and 200 in the short term (30 years) are only 11.8% (SE 6.1%) and 85.2% (SE 6.0%) but long term extinction,

defined as falling below effective population sizes of 50 and 500 in 100 years are almost certain at 80.2% (SE 7.5%) and 100% (SE 0%).

Colorado Plateau Management Zone

*Colorado Plateau Management Zone Comprehensive Analysis*

Colorado Parks and Wildlife denied our requests for results of lek counts on 4 separate occasion because of a decision of the leadership team (3 emails and 1 conversation with Kathy Griffin on 1/6/15) making it necessary to substitute the best reasonable estimate of current numbers of breeding males counted at leks in 2013: 244 calculated as average of last count (241 in 2007), estimated carrying capacity from best model (248 from Ricker model, Garton et al. 2011:381) and second best model (241 from Gompertz model, Garton et al. 2011:381) based on earlier studies (Garton et al. 2011:363). This lack of cooperation makes it impossible to provide any improved estimates or discussion of changes from 2007 to 2013.

*Range-wide Summary Including All Sage-Grouse Management Zones*

Comparing the estimated minimum male population size between 2007 and 2013 from population reconstructions of all evaluated populations showed declines in population size from 6% to 100% except for 4 small populations of less than 500 males which exhibited increases of 2% to 100% (Table 1). The total numbers estimated by summing across all 27 populations with sufficient data to analyze but excluding Colorado leks, suggest a minimum total of 98,740 males breeding in 2007 declined 55% to a total of 44,209 males breeding in 2013 (Table 1) whereas corrected total estimates including Colorado suggest a 56% decline from 109,990 in 2007 to 48,641 in 2013 (Figure 8). Placing the declines during these last 6 years in proper perspective requires looking more broadly at range-wide population changes over the last 5 decades (Fig. 9) which strongly suggests that this last 6-7 years represent the latest downward swing in the cycles of approximately 10-11 year intervals (statistically significant lows in 1965, 1975, 1985, 1996, 2002 and 2013) with the periodic low in 2002 coming 4 years early. The last 3 decades period appear to represent a multi-decadal periodic pattern where relative magnitude of change between highs and lows has decreased during an overall decline until 2013 where lek counts reached their lowest magnitude (48,641 males counted) in 50 years of records. Examination of SMZ population reconstructions reveal fairly, but not perfectly, simultaneous peaks and lows at 9-11 year intervals excepting the missing peak around 2000.

Estimated minimum male sage-grouse attending leks in various SMZs declined from 6% to 67% between 2007 and 2013 with largest declines occurring in the more northern regions excepting the Columbia Basin where numbers were already quite low in 2007(Table 2). Combining estimates across all the regions except Colorado Plateau the range-wide population declined 55% from an estimated 98,603 (SE 3,736) males in 2007 to 44,252 (SE 1,019) males in 2013.

The best stochastic growth model to describe annual changes in sage-grouse populations (Appendix 1) and SMZ populations (Appendix 2) was a stochastic density dependent Gompertz model with 1-year time lag and declining yearly trend in most cases (36% of populations and 66% of SMZ populations). Combining information theoretic measures across SMZs for all 26

models (Table 3) identified this model as significantly better than any of the alternative models (AICc difference > 2.0 indicates significant difference by likelihood ratio test at $\alpha$=0.05, Burnham and Anderson 2002). When these best models are used to forecast present and future carrying capacity of each population (Table 4) and SMZ (Table 5) they estimate that current populations of SMZs exceed carrying capacity by 3,800 males and that future SMZ carrying capacities will decline from approximately 40,000 males to 20,000 in 30 years and 8,000 males in 100 years if current trends portrayed by stochastic growth models hold that far into the future (Table 5).

*Validation*

Results of a validation test comparing predicted abundances in 2013 ($Z_{2013}$) to observed abundances ($N_{2013}$)based on forecasts from Gompertz models with one-year lag and long-term annual trend in carrying capacities (Gompertz t-1 with year models) for each SMZ starting with abundances in 2007 (Fig. 8) indicated that the models ($Z_{2013}$=256 + 0.9585 $N_{2013}$, $r^2$=0.978) predicted 97.8% of the variation in 2013 SMZ population abundances.

Parametric bootstraps forecasting future abundance of each population (Table 6) and SMZ population (Table 7) yielded higher probabilities of the minimum count of males attending leks falling below 20 or 200 compared to earlier projections based on models and parameters estimated in a previous analysis for lek surveys through 2007 (Garton et al. 2011:293 ff.). Only the Great Plains and Columbia Basin SMZs showed high probability of declining below these levels of abundance but the likelihoods increase for effective population sizes of 50 and 500 for both of these SMZs. Long-term (100 year) probability of abundance less than these levels are higher than 50% for the Wyoming Basin and Northern Great Basin as well as for the Great Plains and Columbia Basin management zones.

*Metapopulation Persistence*

Metapopulation projections of the probability of persistence depended on the level of independence in demographic rates amongst SMZ populations (Table 8) which were similar to measures in earlier studies (Garton et al. 2011:369) and imply that the Columbia Basin SMZ effectively fluctuates independently of the remaining portions of the metapopulation. Most of the highest correlations in population changes amongst SMZs were associated with the Snake River Plain which was utilized as the primary SMZ to generate correlated rates for other zones. Movements were modeled using the same approach developed in earlier work (Garton et al. 2011:367) with the modification that Colorado Parks and Wildlife's failure to participate required dropping those potential movements and connections (Table 9). The Columbia Basin SMZ population was effectively independent of other SMZs. Parametric bootstraps to forecast individual SMZ population persistence and overall persistence of the metapopulation consisting of all the populations produced more extreme forecasts (Table 7) in which probability of declining below effective population sizes of 50 in either short of long term approach 0, excepting the already low Columbia Basin, while long term (100 year) probabilities of declining below effective population sizes of 500 were 100% or close to it. The metapopulation model forecasts virtually no chance of the entire metapopulation declining below effective population sizes of 50 or 500 in either short- or long-term periods.

**Discussion**

All previously published analyses of sage-grouse populations have documented decreases throughout the species' range (Connelly and Braun 1997, Connelly et al. 2004, Schroeder et al. 2004, WAFWA 2008, Garton et al. 2011). Our results support these findings and provide compelling evidence that most populations have continued to decline over the last 6 years reaching a low in 2013 below 50,000 males attending leks range-wide, an 8 fold decline from the late 1960s. Moreover, our findings compliment conclusions of a recent USFWS report (U.S. Fish and Wildlife Service 2013) and other recent research that document ongoing threats to sage-grouse populations.

Great Plains Management Zone

This zone contains four sage-grouse populations (Garton et al. 2011), including the Dakotas, Northern Montana, Powder River Basin, and Yellowstone Watershed populations. Sage-grouse populations within the Great Plains management zone declined by two-thirds in the last 6 years with the entire management zone most likely declining below effective population sizes of both 50 and 500 within 30 years and with 90% certainty within 100 years. Individual populations all declined more than 50% in the last 6 years with both the Dakotas and Powder River Basin declining more than 70% raising a concern that they may be dropping into an extinction vortex. Even the largest population within the Yellowstone watershed fell by two-thirds with parametric bootstraps implying that every population except Northern Montana is virtually certain to go extinct (96% to 100% probabilities) unless recent patterns of decline change.

The Dakotas population is strongly influenced by energy development; moreover conversion of native rangeland to cropland is a major threat to the persistence of this sage-grouse population. Overall, this population is small and at high risk (U.S. Fish and Wildlife Service 2013). Additionally, Taylor et al. (2012) reported that sage-grouse viability in the Powder River Basin is impacted by multiple stressors including West Nile virus and energy development. Their research suggested that if development continues, future viability of sage-grouse populations in northeast Wyoming will be compromised. The expanding threat of energy development across the Powder River Basin and declining sage-grouse numbers makes this overall an at-risk population (U.S. Fish and Wildlife Service 2013). Finally, cropland conversion continues to take place in the Yellowstone Watershed and this population is potentially at risk (U.S. Fish and Wildlife Service 2013).

Wyoming Basin Management Zone

The Wyoming Basin management zone, containing the largest population of sage-grouse in the United States, has declined 60% in the last 6 years from almost 50,000 males attending leks in 2007 to less than 20,000 in 2013. Nevertheless the likelihood of the management zone population declining below effective population sizes of 50 or 500 are all less than 50% except for a three-quarters chance of declining below an effective population size of 500 in 100 years.

Here again we wonder about the role of drought in addition to fires and expanding oil and gas development on sage-grouse habitat as primary drivers behind these precipitous declines. Primary threats to sage-grouse populations in this zone are energy development and transfer, drought, and sagebrush eradication programs (U.S. Fish and Wildlife Service 2013). Sage-grouse population declines near energy developments in this area have been well documented (Lyon 2000; Holloran 2005; Holloran and Anderson 2005; Kaiser 2006). Residential development has also been identified as a threat (U.S. Fish and Wildlife Service 2013).

Southern Great Basin Management Zone

The Southern Great Basin is one of two major management zones showing the least precipitous population declines of only one-third. This management zone includes populations in California, Nevada, and Utah. A large portion of this zone is managed by the Bureau of Land Management. However, large areas of sagebrush habitat are at considerable risk due to wildfire, cheatgrass (*Bromus tectorum*) invasion, drought, and conifer expansion (U.S. Fish and Wildlife Service 2013) and many areas have burned over the last 10 years. Some of the historic habitat available to sage-grouse within this zone has transitioned to pinyon-juniper woodlands. The area of pinyon-juniper woodlands has increased approximately 10-fold throughout the western United States since the late 1800s (Miller and Tausch 2001).

Snake River Plain Management Zone

The Snake River Plain is the other major management zone showing relatively small population declines of only one-third. This zone contains one of the largest landscapes of connected sage-grouse habitat, and supports the largest sage-grouse population outside of the Wyoming Basin (Garton et al. 2011, U.S. Fish and Wildlife Service 2013). However, the Southern Great Basin and Snake River Plain combined represent a decline of almost 9,000 less males attending leks across the region over the last six years. Three small populations representing less than 500 males counted on leks in Sanpete-Emory Counties, Utah, Mono Lake, California-Nevada and Red-rock Lakes, Montana showed increases in males counted. In contrast, most of the remaining populations within these two zones had moderate declines except Toole-Juab Counties, Utah and Weiser, Idaho which may be dropping into extinction vortices. However every population is so low that its long-term probability of persistence is low except for the Snake-Salmon-Beaverhead population in Idaho which has high probability of persistence over both long- and short-term periods. The Snake River Plain Zone contains a large amount of land managed by BLM and USFS. Within some areas, wildfires and invasive species have continued to reduce the quality of habitat. The mountain Valley portions of this population appear to have relatively stable habitats (U.S. Fish and Wildlife Service 2013). Thus far, energy development is very limited and there are few wild horses.

The Northern Great Basin population of the Snake River Plain SMZ represents a large sage-grouse population in Oregon, Idaho, Nevada, and Utah. Wildfires and invasive species have

reduced the quality and quantity of habitat in many portions of this area. The Murphy Fire Complex in Idaho and Nevada recently burned about 600,000 acres of habitat. The 2012 Long Draw fire in Oregon affected 582,000 acres. Since 2000, over 800,000 acres of sagebrush habitats have burned in the Nevada portion of this zone. In conjunction with fire, invasive weeds are also one of the greatest risks (U.S. Fish and Wildlife Service 2013). Other threats in this region include mining development, renewable energy development, transmission, and juniper encroachment at higher elevations (U.S. Fish and Wildlife Service 2013). West Nile virus has also been consistently detected in this region and in 2006 the population was subjected to the largest known West Nile virus mortality event involving sage-grouse in Oregon (U.S. Fish and Wildlife Service 2013).

Northern Great Basin Management Zone

BLM lands comprise a major portion of sagebrush landscapes in the Northern Great Basin (62%) followed by private (21%). This zone has experienced a 65% decline over the last six years with a 9.9% chance of falling below effective population size of 50 and a 72.2% chance of falling below effective population size of 500. These populations are subject to a broad suite of threats, including juniper encroachment, invasive weeds, renewable energy development, transmission lines, roads, OHV recreation, and residential development (U.S. Fish and Wildlife Service 2013). The central Oregon population within this zone is estimated to have only 53 percent of historic sagebrush habitat (U.S. Fish and Wildlife Service 2013) and its extinction appears likely. The Western Great Basin population within this zone is shared among southeastern Oregon, northeastern California and northwestern Nevada. Invasive weeds, fire, and juniper encroachment (particularly on the western edge) represent the greatest risks to this population (U.S. Fish and Wildlife Service 2013). In 2012, the Rush Fire burned more than 313,000 acres of key sage-grouse habitat in California and Nevada. Most of the largest leks and important nesting habitats were within the fire perimeter (U.S. Fish and Wildlife Service 2013). The Western Great Basin population has declined by 69% over the last 6 years and appears to be experiencing an extinction vortex.

Columbia Basin Management Zone

This zone contains two extant populations, Moses Coulee and Yakima Training Center. The Moses Coulee population has been maintaining its population for about the last 30 years, largely due to the Conservation Reserve Program. Major issues in Moses Coulee are the lack of habitat stability due to the abundant private land, habitat fragmentation, and dependence on farm programs (U.S. Fish and Wildlife Service 2013). The Yakima population is much smaller than Moses Coulee, but occurs mostly on public land. A substantial amount of the sage-grouse habitat on the area has been negatively affected by military activities and resulting wildfires. Despite efforts to manage wildfire risks, wildfires have continued to reduce the quantity of habitat for this population (U.S. Fish and Wildlife Service 2013). This zone declined by 6% over the last

year and has an 82% chance of falling below effective populations sizes of 50 and 500. Extinction is probable for both the Moses Coulee and Yakima populations.

Colorado Plateau Management Zone

This management zone contains two populations; Parachute-Piceance Basin and Meeker-White River Colorado. Risks to sage-grouse in the zone include small size of existing populations, energy development and associated infrastructure, as well as pinyon-juniper. The USFWS considers these populations to be at high risk but no current data were provided by Colorado so population analyses were not possible.

*Sage-grouse and Cycles*

The range-wide and SMZ population reconstructions suggest that the dynamics of sage-grouse may be another example of the widely reported 10-year cycle in wildlife populations (Keith 1987, Blasius et al. 1999, Watson et al. 2000, Krebs et al. 2001) that are widely believed to result from time delays in the dynamics of herbivores and their interactions with their plant resources and/or predator populations. Blasius et al. (1999) found from a model based on a spatial lattice of patches that only small amounts of local migration are required to induce broad-scale phase synchronization with all patches locking onto the same collective rhythm. This phase synchronization leads to emergence of complex chaotic travelling wave synchronization which may be crucial to species persistence. Watson et al. (2000) found similar approximately 10-year cycles in Rock Ptarmigan (*Lagopus mutus*) and Red Grouse (*Lagopus lagopus scoticus*) synchronous over landscapes in Scotland that were successfully modeled without plant or predator community interactions from one-year lagged weather events combined with fourth-order delayed density dependence with emigration critical to synchrony across regions.

The figures plotting population reconstruction estimates suggest that every SMZ population is apparently at the bottom of an approximately 10-year cycle. What does this mean in terms of future sage-grouse population trends? In 3-4 years these populations could increase again or the cycle may be disappearing and the precipitous drops since 2007 may be the start of a complete population collapse. Biologists from Idaho, Oregon, Nevada, Utah and Wyoming felt that 2013 was a particularly bad year for lek counts as it followed multiple years of poor productivity due to the multi-year drought along with the associated wildfires.

*Modeling Population Dynamics*

With 6 more years of data every single SMZ population analysis picked the Gompertz model with a one year time lag and annually-declining carrying capacity as the best or second best model (Appendix 2). Zeng et al. (1998) demonstrated the power of the stochastic growth models we applied in detecting density dependence, complex dynamics and time lags. Lande et al. (2002) demonstrated that interpreting the coefficients of delayed density dependence are quite complex involving the negative elasticity of population growth rate per generation with respect to change in population size. Brook and Bradshaw (2006) found that Gompertz density dependent models were most frequently selected in a similar multi-model inferential analysis

across 1198 species including birds, mammals, fish, insects and invertebrates. A similar comprehensive analysis was conducted for Lesser Prairie-Chicken populations throughout this species range. Garton et al. (In press) accumulated and analyzed counts of mostly males from 504 individual leks and 28 lek routes conducted from 1964 to 2012 (Garton et al. In press) and found a similar 57% decline in range-wide estimates of abundance from 80,000 in 2008 to 34,000 in 2012. Three of four ecoregional populations (analogous to SMZs for sage-grouse) showed precipitous declines with only the most northern population remaining approximately stable during that period. Even that population which has been supported by habitat improvements under the CRP program may now be at risk because of major cut-backs in funding for CRP in the region and conversion of habitat into corn fields.

The Powder River population in Wyoming represents one of the large populations early in the data set that has declined most dramatically within the last 6 years (-76%). In 2013 it reached a low of approximately 1600 males attending leks, a figure roughly 4% of the estimates in 1970-1990. Dave Naugle and his students have documented the impact of a "perfect storm" of habitat loss and disturbances through energy development combined with impacts of added water sources spreading West Nile Virus (Naugle, et al. 2004, 2005 Walker, et al. 2004, 2007a) in this population that portends serious negative consequences for sage-grouse populations experiencing expanded energy development throughout the multistate region containing minable energy sources (Doherty et al. 2008, Naugle, et al. 2011, Walker et al. 2007b).

*Evidence for Stabilized or Increasing Populations*

Every management zone and almost all populations have declined substantially except the sage-grouse population in Washington which exhibited a relatively small overall decline associated with reasonably stable populations in north-central Washington that was likely the result of more extensive development and use of CRP lands (Schroeder and Vander Haegen 2011). In contrast, the Yakima population continued a long-term decline. Beck et al. (2012) advocated eliminating sagebrush control management actions in sagebrush communities until new studies can demonstrate their positive consequences for sage-grouse and other wildlife species yet these still persist (Connelly 2014).

Given continued populations declines and ongoing loss of habitat quality and quantity in every SMZ, the conclusion seems pretty straightforward that current policies and programs are accomplishing little. Claims to the contrary notwithstanding (Connelly 2014), our analyses suggest it is far too early to proclaim various conservation programs are "successful". However, it is possible that it is still too early to detect effects of habitat improvement and that efforts cast in an experimental framework with random assignment of treatments and controls will demonstrate substantial positive effects in the future. Connelly (2014) noted that current sage-grouse conservation efforts appear to be getting sage-grouse conservation "nowhere fast", largely because of bureaucratic approaches and continued reliance on rhetoric and dogma. Similarly, Braun (2014) stated conservation plans overall in Colorado have been ineffective. Copeland et al. (2013) predicted that the core area policy of Wyoming plus a targeted $250 million easement investment could reduce possible population losses to 9–15% (95% CI: 3–32%), decreasing anticipated losses by roughly half statewide and nearly two-thirds within core areas. However, this finding apparently means the population will continue to decline, just at a slower rate. Many conservation efforts (e.g., fence marking, conifer control, enhanced fire protection) have recently

been put in place. It may be too early to detect effects and this population analysis should be repeated at approximately 5-year intervals to broadly assess success of conservation efforts. Treating the entire sage-grouse population as a single metapopulation suggests that loss of the entire species across this enormous range is extremely unlikely over the short term though loss of individual populations is very likely. Overall persistence of the species into the far distant future is not assured or even likely without maintenance of the essential connectivity amongst populations and without substantial changes in the current trajectories of the populations occupying this broad region.

**Management Implications**

Studies of widely distributed species reinforce the extreme importance of collaborative studies across multiple land ownerships, political entities, and spatial scales in assessing the cumulative effects of myriad factors impacting natural communities and their key wildlife components. Failure of Colorado Parks and Wildlife to support this collaborative effort has placed substantial barriers to successful completion of a solid population assessment. Likewise no single governmental or private entity has the financial resources to devote to critical large-scale experimental research to evaluate the causal factors determining persistence of landscape species such as sage-grouse but multiple organizations, together, might succeed in developing solid understanding of the causal pathways required to maintain productive sage-steppe communities while simultaneously supporting productive rural communities in the landscape. Regular assessment of the status and prospects for landscape species such as sage-grouse will provide an invaluable assessment of the success of conservation actions throughout the region. Application of classic adaptive management would move this process forward substantially but is nowhere in evidence at present.

The total number of sage-grouse estimated by summing across all 27 populations with sufficient data to analyze but excluding Colorado leks, indicate a minimum total of 98,740 males in 2007 declined 55% to a total of 44,209 males in 2013. Overall, our results combined with findings from other recent studies suggest sage-grouse populations that are quite small or exposed to continuing severe threats (wildfire, energy development) are faring poorly. The evidence is clear that these populations continue to decline in spite of various conservation efforts. Populations occupying landscapes where wildfire is relatively rare and energy development limited have fared better over the last 6 years but nowhere have we found evidence that any larger populations are stable to increasing. Conservation efforts that emphasize protecting remaining habitats over broad landscapes are necessary to insure sage-grouse persistence on these lands.

**Acknowledgements**

We thank first the myriad state and federal biologists and volunteers that spent countless early morning hours counting male sage-grouse at leks and compiling these data for use in monitoring sage-grouse populations across the region. We especially thank biologists (Scott Gardner, Don Kemner, Adam Messer, Shawn Espinosa, Aaron Robinson, Dave Budeau, Jackie Cupples, Travis Runia, Avery Cook, Mike Schroeder and Tom Christiansen) in every state except Colorado who provided results of lek surveys from 2007 to 2013. Courtney Conway, J. Michael Scott and Dale Goble provided invaluable counsel on treatment of missing data from Colorado. Michael A. Schroeder and Clait E. Braun provided critical reviews of the manuscript to Pew Charitable Trusts that substantially improved the report.

**Literature cited**


Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 in B. N. Petrov, and F. Csaki, (eds.) Second International Symposium on Information Theory. Akademiai Kiado, Budapest.

Aldridge, C. L., 2001. Do Sage Grouse have a future in Canada? Population dynamics and management suggestions. Proceeding of the 6th Prairie Conservation and Endangered Species Conference, Winnipeg, MB, Canada.

Aldridge, C. L., and R. M. Brigham. 2003. Distribution, status and abundance of Greater Sage-Grouse, Centrocercus urophasianus, in Canada. Canadian Field Naturalist 117:25-34.

Ashe, D. M. 2010. Endangered and Threatened Wildlife and Plants:; 12-Month findings for petitions to list the Greater Sage-Grouse (*Centrocercus urophasianus*) as Threatened or Endangered. Federal Register 50 CRF Part 17.

Baruch-Mordo, S., J. S. Evans, J. P. Severson, D. E. Naugle, J. D. Maestas, J.M. Kiesecker, M. j. Falkowski, C. A. Hagen, K. P. Reese. 2013. Saving sage-grouse from the trees: A proactive solution to reducing a key threat to a candidate species. Biological Conservation 167 (2013) 233–241.

Blasius, B., A. Huppert & L. Stone. 1999. Complex dynamics and phase synchronization in spatially extended ecological systems. Nature 399:354-359.

Braun, C. E. 1998. Sage Grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139-156.

Braun, C. E. 2014. In My Opinion: Conservation plans and the future of sage-grouse in Colorado, USA. Grouse News 47:6-7.

Brook, B.W. and C.W.A. Bradshaw. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. Ecology 87:1445–1451.

Beck, J. L., J. W. Connelly, and C. L. Wambolt. 2012. Consequences of treating Wyoming big sagebrush to enhance wildlife habitats. Rangeland Ecology and Management. 65:444-455.

Buckland, S. T., K. P. Burnham, and N. H. Augustine. 1997. Model selection: an integral part of of inference. Biometrics 53:603–618.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, WY.

Connelly, J. W., and C. E. Braun. 1997. A review of long- term changes in sage grouse populations in western North America. Wildlife Biology 3:123-128.

Connelly, J. W. 2014. Federal agency responses to Greater Sage-grouse and the ESA: Getting nowhere fast. Northwest Science 88:61-64.

Copeland, H. E. et al. 2013. Measuring the effectiveness of conservation: a novel framework to quantify the benefits of sage-grouse conservation policy and easements in Wyoming. – PLoS ONE 8:e67261.

Dennis, B. and M. L. Taper. 1994. Density dependence in time series observations of natural populations: estimation and testing. Ecological Monographs 64:205-224.

Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs 61:115-143.

Dennis, B., J. M. Ponciano, S. R. Lele and M. Taper. 2006. Estimating density dependence, process noise and observation error. Ecological Monographs 76:323–341.

Doherty, K.E., D.E. Naugle, B.L. Walker, and J.M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187-195.

Franklin, I. R . 1980. Evolutionary change in small populations. Pp. 135-139 In M. E. Soule and B. A. Wilcox, eds. Conservation Biology: an Ecological-Evolutionary Perspective. Sinauer Associates, Sunderland, MA.

Garton, E. O., J. W. Connelly, J. S. Horne, C. A. Hagen, A. Moser, and M. A. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Studies in Avian Biology 38: 293-382.

Garton, E. O., C. A. Hagen, G. M. Beauprez, D. S. Klute, S. C. Kyle, J. C. Pitman, D. S. Schoeling, and W. E. Van Pelt. 2015 (In press). Population dynamics of the Lesser Prairie-Chicken. In D. A. Haukos and C. W. Boal (eds.) Ecology and Conservation of Lesser Prairie-Chicken. Studies in Avian Biology.

Holloran, M.J. 2005. Greater sage-grouse (Centrocercus urophasianus) population response to natural gas field development in western Wyoming. Ph.D Dissertation, University of Wyoming, Laramie, WY. 215pp.

Holloran, M.J. and S. H. Anderson 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742-752.

Kaiser, R.C. 2006. Recruitment by greater sage-grouse in association with natural gas development in western Wyoming. M.S. Thesis, University of Wyoming, Laramie, WY. 102pp.

Keith, L. B. 1983. Role of food in hare population cycles. Oikos 40: 385-395.

Knick, S. T., and J. W. Connelly. 2011. Greater sage-grouse and sagebrush: an introduction to the landscape. Studies in Avian Biology 38: 1-9.

Knick, S. T., and S. E. Hauser. 2011. Connecting pattern and process in Greater Sage-Grouse population and sagebrush landscapes. Studies in Avian Biology 38:383-405.

Krebs, C. J. 1979. Ecological Methodology, 2nd ed. Addison-Welsey Educational Publishers, Menlo Park, CA.

Krebs, C. J., R. Boonstra, S. Boutin and A.R.E. Sinclair. 1999. What drives the 10-year cycle of snowshoe hares? Bioscience 51:25-

Lande,R., S. Engen, B.E. Saether, F. Fille, E. Matthysen and H. Weimerskirch. 2002. Estimating density dependence from population time series using demographic theory and life-history data. American Naturalist 159:321-37.

Leonard, K. M., K. P. Reese, and J. W. Connelly. 2000. Distribution, movements, and habitats of sage grouse Centrocercus urophasianus on the Upper Snake River Plain of Idaho: changes from the 1950's to the 1990's. Wildlife Biology 6:265-270.

Lyon, A.G. 2000. The potential effects of natural gas development on sage grouse (Centrocercus urophasianus) near Pinedale, Wyoming. M.S. Thesis, University of Wyoming, Laramie, WY. 129pp.

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S.E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Studies in Avian Biology 38:145-184.

Miller, R.F. and R.J. Tausch. 2001. The role of fire in juniper and pinyon woodlands: a descriptive analysis. Pages 15-30 In Galley, K.E.M. and T.P. Wilson (eds). Proceedings of the invasive species workshop: The role of fire in the control and spread of invasive species. Fire Conference 2000: The First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, FL. 146pp.

Naugle, D. E., C. A. Aldridge, B. L. Walker, K. E. Doherty, M. R. Matchett, J. McIntosh, T. E. Cornish, and M. S. Boyce. 2005. West Nile virus and sage-grouse: What more have we learned? Wildlife Society Bulletin 33:616-623.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtman, R. T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: Pending crisis for Greater Sage-Grouse. Ecology Letters 7:704-713.

Naugle DE, KE Doherty, BL Walker, MJ Holloran, and HE Copeland. 2011. Energy development and greater-grouse. Studies in Avian Biology 38: 505-516.

National Technical Team (NTT). 2011. A report on greater sage-grouse conservation measures. Bureau of Land Management, Washington, DC.

Patterson, R. L. 1952. The Sage Grouse in Wyoming. Sage Books, Denver, CO.

R Development Core Team. 2014. R: A language and environment for statistical computing, reference index version 3.0.3. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org .

Remington, R. D. and M. A. Schork. 1970. Statistics with Application to the Biological and Health Sciences. Prentice-Hall, Englewood Cliffs, NJ.

Rich, T. 1985. Sage grouse population fluctuations: evidence for a 10-year cycle. U.S. Department of Interior, Bureau of Land Management Technical Bulletin 85-1. Boise, ID.

SAS Institute. 2003. Version 9.1.3. SAS Institute, Cary, North Carolina, USA.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. Condor 106:363-376.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage Grouse (Centrocercus urophasianus). In A. Poole, and F. Gill (editors.) The Birds of North America, No. 425.

The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, DC.

Schroeder, M. A., and W. M. Vander Haegen. 2011. Response of Greater Sage-Grouse to the conservation reserve program in Washington State. Studies in Avian Biology 38: 517-529.

Soule, M.E. 1980. Thresholds for survival: Maintaining fitness and evolutionary potential. Pp. 151-169 In M. E. Soule and B. A. Wilcox, eds. Conservation Biology: an Ecological-Evolutionary Perspective. Sinauer Associates, Sunderland, MA.

Stiver, S. J., A.D. Apa, J.R. Bohne, D.D. Bunnell, P.A. Deibert, S.C. Gardner, M.A. Hilliard, C.W. McCarthy, and M. A. Schroeder. 2006. Greater Sage-Grouse comprehensive conservation strategy. Western Association of Fish and Wildlife Agencies, Cheyenne, WY. http:/www.wafwa.org/pdf/GreaterSage-grouseConservationStrategy2006.pdf (21 August 2009).

Stiver, S. J. 2011. The legal status of Greater Sage-Grouse. Studies in Avian Biology 38: 33-49.

Taylor, R.T., D.E. Naugle, and L.S. Mills. 2012. Viability analysis for the conservation of sage-grouse populations: Buffalo Field Office, Wyoming. Final Report. 27 February 2012. Prepared for BLM. 46pp.

U.S. Fish and Wildlife Service. 2013. Greater Sage-grouse (*Centrocercus urophasianus*) Conservation Objectives: Final Report. U.S. Fish and Wildlife Service, Denver, CO. February 2013.

WAFWA. 2008. Greater Sage-Grouse population trends: an analysis of lek count databases 1965-2007. Unpublished report from the Sage- and Columbian Sharp-tailed Grouse Technical Committee, Western Association of Fish and Wildlife Agencies, Cheyenne, WY.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2004. From the field: outbreak of west Nile Virus in greater sage-grouse and guidelines from monitoring, handling, and submitting dead birds. Wildlife Society Bulletin 32:1000-1006.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2007a. West Nile Virus and Greater Sage-Grouse: Estimating infection rate in a wild bird population. Avian Diseases 51:691-696.

Walker, B.L., D.E. Naugle, and K.E. Doherty. 2007b. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644-2654.

A. Watson, R. Moss and P. Rothery. 2000. Weather and synchrony in 10-year population cycles of rock ptarmigan and red grouse in Scotland. Ecology 81:2126-2136.

Wright, S. 1938. Size of population and breeding structure in relation to evolution. Science 87:430-431.

Zeng, Z., R.M.N. Owierski, M.L. Taper, B. Dennis, and W.P.Kemp. 1998. Complex population dynamics in the real world: modeling the influence of time-varying parameters and lags. Ecology 79:2193–2209.

List of Tables

Table 1. Summary of estimated minimum male population attending leks in each population

Table 2. Summary of estimated minimum male population attending leks in each Sage-Grouse Management Zone

Table 3. Information Theoretic Measures of Best Models Across All SMZs

Table 4. Estimated minimum number of males counted at leks in 2013 compared to estimated carrying capacities for individual populations in 2013, 2043 and 2113.

Table 5. Estimated minimum number of males counted at leks in 2013 compared to estimated carrying capacities in 2013, 2043 and 2113.

Table 6. Summary Presentation of results of parametric bootstraps to forecast probability of populations falling below N of 20 and 200 and Ne of 50 and 500

Table 7. Probabilities of extinction with standard errors (SE) estimated by parametric bootstraps across all models weighted by the probability that each models is the correct (best) model within the set of 26 models and the probability of extinction under a metapopulation model based on the best stochastic growth model across all SMZs incorporating movement between SMZ populations and correlated environmental perturbations amongst SMZ populations.

Table 8. Correlations in residuals among sage-grouse management zones from predictions of the overall best AICc Gompertz type model of density dependence in annual rates of change with 1-year time lag and declining trend in carrying capacity through time.

Table 9. Dispersal rates among sage-grouse management zones representing the proportion of the population dispersing to another management zone each year.

Appendices

Appendix 1. Top models of annual rates of change with estimates of carrying capacity in 2013, 2043 and 2113 for Populations.

Appendix 2. Top models of annual rates of change with estimates of carrying capacity in 2013, 2043 and 2113 for SMZs

Table 1. Summary of estimated minimum male population attending leks in each population

| Sage-Grouse Population | Estimated Minimum No. Males 2007 | SE | No. Males 2013 | SE | Change |
|---|---|---|---|---|---|
| I Great Plains Management Zone | | | | | |
| Dakotas | 1,112 | 307 | 311 | 55 | -72% |
| Northern Montana | 3,615 | 573 | 1,667 | 165 | -54% |
| Powder River Basin | 6,804 | 919 | 1,651 | 155 | -76% |
| Yellowstone Watershed | 8,747 | 949 | 3,045 | 196 | -65% |
| II Wyoming Basin Management Zone | | | | | |
| Jackson Hole | 133 | 82 | 136 | 44 | 2% |
| Wyoming Basin | 43,040 | 2,727 | 15,767 | 644 | -63% |
| III Southern Great Basin Management Zone | | | | | |
| Mono Lake, Californai-Nevada | 435 | 266 | 543 | 157 | 25% |
| South Mono Lake, California | 282 | 161 | 264 | 102 | -6% |
| Northeast Interior Utah | 412 | 192 | 241 | 71 | -42% |
| Sanpete-Emery Counties, Utah | 24 | 26 | 48 | 19 | 100% |
| South-Central Utah | 1,501 | 570 | 737 | 208 | -51% |
| Summit-Morgan Counties, Utah | 87 | 67 | 65 | 19 | -25% |
| Toole-Juab Counties, Utah | 257 | 237 | 57 | 18 | -78% |
| Southern Great Basin | 5,087 | 691 | 3,388 | 259 | -33% |
| IV Snake River Plain Management Zone | | | | | |
| Baker, Oregon | 137 | 92 | 49 | 18 | -64% |

| | | | | | |
|---|---|---|---|---|---|
| Bannack, Montana | 219 | 81 | 177 | 35 | -19% |
| Red Rocks Lake, Montana | 260 | 202 | 357 | 113 | 37% |
| East Central Idaho | 179 | NA | 86 | 35 | -52% |
| Snake-Salmon-Beaverhead, Idaho | 8,734 | 1,157 | 6,126 | 229 | -30% |
| Northern Great Basin | 9,927 | 1,144 | 6,580 | 376 | -34% |
| Weiser, Idaho | 153 | 73 | 51 | 15 | -67% |
| | | | | | |
| V Northern Great Basin Management Zone | | | | | |
| Central Oregon | 829 | 222 | 559 | 95 | -33% |
| Klamath-Oregon-California | 11 | NA | 0 | 0 | -100% |
| Northwest-Interior Nevada | 117 | 102 | 79 | 29 | -32% |
| Western Great Basin | 6,327 | 1,345 | 1,934 | 212 | -69% |
| | | | | | |
| VI Columbia Basin Management Zone | | | | | |
| Moses-Coulee, Washington | 230 | 84 | 202 | 39 | -12% |
| Yakima, Washington | 81 | 50 | 89 | 36 | 10% |
| | | | | | |
| VII Colorado Plateau Management Zone | NA | NA | NA | NA | NA |
| | | | | | |
| Total Across All Zones except CO | 98,740 | | 44,209 | | |

Table 2. Summary of estimated minimum male population attending leks in each Sage-Grouse Management Zone

| Sage-Grouse Management Zone | Estimated Minimum No. Males 2007 | SE | No. Males 2013 | SE | Change |
|---|---|---|---|---|---|
| I Great Plains | 20,016 | 1,462 | 6,674 | 312 | -67% |
| II Wyoming Basin[1] | 54,282 | 2,636 | 20,006 | 646 | -63% |
| III Southern Great Basin | 8,202 | 1,085 | 5,485 | 38 | -34% |
| IV Snake River Plain | 19,510 | 1,404 | 13,371 | 550 | -32% |
| V Northern Great Basin | 7,429 | 1,312 | 2,573 | 468 | -65% |
| VI Columbia Basin | 310 | 98 | 291 | 56 | -6% |
| VII Colorado Plateau[1] | 241 | 52 | 241 | NA | NA |
| Total Across All Zones except CO | 98,616 | 3,736 | 44,297 | 1,019 | -55% |
| Total Across All Zones | 109,990 | | 48,641 | | -56% |

[1] Missing estimates for Colorado portions of range replaced by last available estimates from 2007.

Table 3. Information Theoretic Measures of Best Models Across All SMZs

| Model | K | Total AICc | ΔAICc |
|---|---|---|---|
| EGPE | 3 | -911.2 | 47.6 |
| Period | 4 | -885.5 | 73.3 |
| Gompertz | 4 | -894 | 64.8 |
| Ricker | 4 | -894 | 64.8 |
| Gompertz + Year | 5 | -910.6 | 48.2 |
| Ricker + Year | 5 | -905.8 | 53 |
| Gompertz + Period | 5 | -893.5 | 65.3 |
| Ricker + Period | 5 | -891 | 67.8 |
| Gompertz + Year, Period | 6 | -900.7 | 58.1 |
| Ricker + Year, Period | 6 | -894 | 64.8 |
| Gompertz t-1 | 4 | -907.6 | 51.2 |
| Ricker t-1 | 4 | -906.5 | 52.3 |
| Gompertz t-1 + year | 5 | -958.8 | 0 |
| Ricker t-1 + Year | 5 | -941 | 17.8 |
| Gomperz t-1 + Period | 5 | -929.1 | 29.7 |
| Ricker t-1 + Period | 5 | -921 | 37.8 |
| Gomperz t-1 + Year,Period | 6 | -951 | 7.8 |
| Ricker t-1 + Year,Period | 6 | -930 | 28.8 |
| Gompertz t-2 | 4 | -903.4 | 55.4 |
| Ricker t-2 | 4 | -901.4 | 57.4 |
| Gompertz t-2 + Year | 5 | -935.5 | 23.3 |
| Ricker t-2 + Year | 5 | -918.2 | 40.6 |
| Gomperz t-2+ Period | 5 | -918.8 | 40 |
| Ricker t-2+ Period | 5 | -909.6 | 49.2 |
| Gomperz t-2 + Year,Period | 6 | -926.5 | 32.3 |
| Ricker t-2 + Year,Period | 6 | -907.9 | 50.9 |

Table 4. Estimated minimum number of males counted at leks in 2013 compared to estimated carrying capacities for individual populations in 2013, 2043 and 2113.

| Sage-Grouse Population | Estimated Males | | Estimated Carrying Capacity of Minimum No. of Males | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 2013 | SE | 2013 | SE | 2043 | SE | 2113 | SE |
| I Great Plains Management Zone | | | | | | | | |
| Dakotas | 311 | 55 | 280 | 79 | 97 | 31 | 45 | 18 |
| Northern Montana | 1,667 | 165 | 4,353 | 1,394 | 3,714 | 1,123 | 3,380 | 992 |
| Powder River Basin | 1,651 | 155 | 2,273 | 618 | 240 | 78 | 36 | 24 |
| Yellowstone Watershed | 3,045 | 106 | 3,087 | 14,671 | 241 | 1,138 | 136 | 644 |
| II Wyoming Basin Management Zone | | | | | | | | |
| Jackson Hole | NA | NA | NA | NA | NA | NA | NA | NA |
| Wyoming Basin | 15,767 | 644 | 16,078 | 4,983 | 6,158 | 2,021 | 2,209 | 913 |
| III Southern Great Basin Management Zone | | | | | | | | |
| Mono Lake, Californai-Nevada | 543 | 157 | 330 | 120 | 576 | 216 | 4,059 | 1,679 |
| South Mono Lake, California | 264 | 102 | 258 | 84 | 275 | 92 | 336 | 118 |
| Northeast Interior Utah | NA | NA | NA | NA | NA | NA | NA | NA |
| Sanpete-Emery Counties, Utah | NA | NA | NA | NA | NA | NA | NA | NA |
| South-Central Utah | 737 | 208 | 944 | 248 | 802 | 209 | 680 | 177 |
| Summit-Morgan Counties, Utah | NA | NA | NA | NA | NA | NA | NA | NA |
| Toole-Juab Counties, Utah | NA | NA | NA | NA | NA | NA | NA | NA |
| Southern Great Basin | 3,388 | 259 | 2,702 | 962 | 1,417 | 551 | 543 | 268 |
| IV Snake River Plain Management Zone | | | | | | | | |
| Baker, Oregon | NA | NA | NA | NA | NA | NA | NA | NA |
| Bannack, Montana | 177 | 35 | 146 | 40 | 109 | 30 | 86 | 25 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Red Rocks Lake, Montana | NA | NA | NA | NA | NA | NA | NA | NA |
| East Central Idaho | NA | NA | NA | NA | NA | NA | NA | NA |
| Snake-Salmon-Beaverhead, Idaho | 6,126 | 229 | 5,727 | 1,823 | 5,074 | 1,539 | 4,719 | 1,394 |
| Northern Great Basin | 6,580 | 376 | 6,214 | 1,566 | 1,664 | 425 | 77 | 20 |
| Weiser, Idaho | NA | NA | NA | NA | NA | NA | NA | NA |
| | | | | | | | | |
| V Northern Great Basin Management Zone | | | | | | | | |
| Central Oregon | 559 | 95 | 509 | 178 | 148 | 58 | 28 | 17 |
| Klamath-Oregon-California | NA | NA | NA | NA | NA | NA | NA | NA |
| Northwest-Interior Nevada | 79 | 29 | | | | | | |
| Western Great Basin | 1,934 | 212 | 2,548 | 812 | 701 | 228 | 40 | 15 |
| | | | | | | | | |
| VI Columbia Basin Management Zone | | | | | | | | |
| Moses-Coulee, Washington | 202 | 39 | 172 | 50 | 107 | 35 | 77 | 28 |
| Yakima, Washington | NA | NA | NA | NA | NA | NA | NA | NA |
| | | | | | | | | |
| VII Colorado Plateau Management Zone | NA | NA | NA | NA | NA | NA | NA | NA |
| | | | | | | | | |
| Total Across All Populations* except CO | 43,030 | | 43,349 | | 21,084 | | 16,416 | |
| *(> 25 leks counted) | | | | | | | | |

Table 5. Estimated minimum number of males counted at leks in each management zone in 2013 compared to estimated carrying capacities in 2013, 2043 and 2113.

| | Estimated Males | | Estimated Carrying Capacity of Minimum No. of Males | | | | | |
|---|---|---|---|---|---|---|---|---|
| Sage-Grouse Management Zone | 2013 | SE | 2013 | SE | 2043 | SE | 2113 | SE |
| I Great Plains | 6,674 | 312 | 3,798 | 1,378 | 1,444 | 546 | 481 | 193 |
| II Wyoming Basin | 15,903 | 646 | 15,541 | 4,536 | 6,784 | 2,135 | 2,248 | 918 |
| III Southern Great Basin | 5,485 | 38 | 4,862 | 1,514 | 3,722 | 1,175 | 2,649 | 875 |
| IV Snake River Plain | 13,371 | 550 | 13,275 | 4,008 | 6,420 | 2,083 | 2,330 | 1,111 |
| V Northern Great Basin | 2,573 | 468 | 2,796 | 835 | 1,027 | 330 | 382 | 152 |
| VI Columbia Basin | 291 | 56 | 233 | 70 | 120 | 39 | 64 | 24 |
| VII Colorado Plateau | NA | NA | NA | NA | NA | NA | NA | NA |
| Total Across All Zones except CO | 44,297 | 1,019 | 40,505 | 6,444 | 19,517 | 3,269 | 8,154 | 1,704 |

Table 6. Summary Presentation of results of parametric bootstraps to forecast probability (percentage) of populations falling below counts (N) of 20 and 200 and effective population sizes (Ne) of 50 and 500.

| | 30-year | | | | 100-year | | | |
|---|---|---|---|---|---|---|---|---|
| Sage-Grouse Population | N< 20 | N< 200 | Ne< 50 | Ne< 500 | N< 20 | N< 200 | Ne< 50 | Ne< 500 |
| I Great Plains Management Zone | | | | | | | | |
| Dakotas | 21.5 | 73.1 | 35.4 | 100.0 | 69.1 | 77.1 | 72.4 | 100.0 |
| Northern Montana | 2.7 | 6.2 | 5.6 | 11.5 | 16.7 | 24.0 | 7.2 | 13.7 |
| Powder River Basin | 2.9 | 77.6 | 5.8 | 99.0 | 98.7 | 98.9 | 98.8 | 99.3 |
| Yellowstone Watershed | 15.6 | 68.6 | 54.5 | 74.9 | 89.5 | 95.6 | 89.5 | 96.0 |
| II Wyoming Basin Management Zone | | | | | | | | |
| Jackson Hole | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Wyoming Basin | 0.1 | 14.4 | 4.7 | 20.3 | 20.7 | 21.4 | 21.0 | 74.9 |
| III Southern Great Basin Management Zone | | | | | | | | |
| Mono Lake, Californai-Nevada | 0.1 | 65.2 | 7.7 | 100.0 | 0.3 | 67.1 | 21.5 | 100.0 |
| South Mono Lake, California | 0.3 | 87.5 | 7.9 | 100.0 | 0.8 | 88.8 | 21.3 | 100.0 |
| Northeast Interior Utah | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Sanpete-Emery Counties, Utah | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| South-Central Utah | 0.1 | 8.2 | 0.9 | 100.0 | 17.9 | 36.9 | 18.7 | 100.0 |
| Summit-Morgan Counties, Utah | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Toole-Juab Counties, Utah | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Southern Great Basin | 0.1 | 2.6 | 1.3 | 36.8 | 3.3 | 77.0 | 10.4 | 90.5 |
| IV Snake River Plain Management Zone | | | | | | | | |
| Baker, Oregon | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Bannack, Montana | 6.6 | 100.0 | 37.2 | 100.0 | 34.8 | 100.0 | 47.9 | 100.0 |
| Red Rocks Lake, Montana | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| East Central Idaho | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Snake-Salmon-Beaverhead, Idaho | 0.4 | 5.3 | 3.3 | 6.7 | 16.1 | 18.6 | 16.5 | 20.7 |
| Northern Great Basin | 9.9 | 13.6 | 12.6 | 46.7 | 35.3 | 90.2 | 72.2 | 92.3 |
| Weiser, Idaho | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| V Northern Great Basin Management Zone | | | | | | | | |
| Central Oregon | 2.7 | 49.7 | 3.4 | 100.0 | 50.1 | 51.2 | 50.5 | 100.0 |
| Klamath-Oregon-California | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Northwest-Interior Nevada | | | | | | | | |
| Western Great Basin | 13.1 | 13.2 | 13.1 | 78.1 | 54.6 | 99.9 | 96.2 | 99.9 |
| VI Columbia Basin Management Zone | | | | | | | | |
| Moses-Coulee, Washington | 13.1 | 13.2 | 13.1 | 78.1 | 54.6 | 99.9 | 96.2 | 99.9 |
| Yakima, Washington | | | | | | | | |
| VII Colorado Plateau Management Zone | n/a | | n/a | | n/a | | n/a | n/a |
| Average Across All Zones except CO | 6 | 37 | 14 | 68 | 33 | 68 | 46 | 85 |

Table 7. Probabilities of extinction with standard errors (SE) estimated by parametric bootstraps across all models weighted by the probability that each models is the correct (best) model within the set of 26 models and the probability of extinction under a metapopulation model based on the best stochastic growth model across all SMZs incorporating movement between SMZ populations and correlated environmental perturbations amongst SMZ populations.

| | | | | | | Probability Under Metapopulation | |
|---|---|---|---|---|---|---|---|
| | Time | Probability (as %) for each SMZ individually (SE) | | | | | |
| Sage-Grouse Management Zone | Horizon | N<20 | N<200 | Ne<50 | Ne<500 | Ne<50 | Ne<500 |
| I Great Plains | 30 yr | 39.6 (7.6) | 54.5 (9.9) | 52.6 (9.6) | 55.2 (9.9) | 0% | 0% |
| | 100 yr | 55.1 (9.9) | 74.5 (6.5) | 55.6 (9.8) | 92.6 (5.1) | 0% | 100% |
| II Wyoming Basin | 30 yr | 0.1 (0) | 14.2 (5.5) | 4.1 (1.6) | 21.4 (8.1) | 0% | 0% |
| | 100 yr | 21.8 (8.2) | 22.5 (8.2) | 22.2 (8.2) | 76.2 (8.0) | 0% | 78% |
| III Southern Great Basin | 30 yr | 0 (0) | 0 (0) | 0 (0) | 0.3 (0.2) | 0% | 0% |
| | 100 yr | 9.9 (6.0) | 10.4 (6.1) | 10.1 (6.0) | 25.3 (6.3) | 0% | 91% |
| IV Snake River Plain | 30 yr | 0.5 (0.6) | 2.6 (3.1) | 2.1 (2.6) | 4.5 (3.7) | 0% | 0% |
| | 100 yr | 10.1 (6.0) | 20.6 (6.4) | 6.5 (4.9) | 46.7 (7.3) | 0% | 100% |
| V Northern Great Basin | 30 yr | 9.9 (5.3) | 13.6 (6.7) | 12.6 (6.5) | 46.7 (7.3) | 0% | 2% |
| | 100 yr | 35.3 (8.1) | 90.2 (5.7) | 72.2 (6.2) | 92.3 (4.9) | 25% | 100% |
| VI Columbia Basin | 30 yr | 11.8 (6.1) | 85.2 (6.0) | 42 (6.1) | 100 (0) | 85% | 100% |
| | 100 yr | 77.7 (8.0) | 90.5 (5.3) | 80.2 (7.5) | 100 (0) | 100% | 100% |
| VII Colorado Plateau | | NA | NA | NA | NA | NA | NA |
| Range-wide Population | | | | | | 0% | 0% |

Table 8. Correlations in residuals among sage-grouse management zones from predictions of the overall best AICc Gompertz type model of density dependence in annual rates of change with 1-year time lag and declining trend in carrying capacity through time.

| | Great Plains | Wyoming Basin | Southern Great Basin | Snake River Plain | Northern Great Basin | Columbia Basin |
|---|---|---|---|---|---|---|
| Great Plains | 1 | 0.51 | 0.126 | 0.375 | 0.051 | 0.163 |
| Wyoming Basin | | 1 | 0.299 | 0.348 | 0.083 | 0.061 |
| Southern Great Basin | | | 1 | 0.604 | 0.573 | 0.219 |
| Snake River Plain | | | | 1 | 0.407 | 0.281 |
| Northern Great Basin | | | | | 1 | 0.278 |

Table 9. Dispersal rates among sage-grouse management zones representing the proportion of the population dispersing to another management zone each year.

| | Wyoming Basin | Southern Great Basin | Snake River Plain | Northern Great Basin |
|---|---|---|---|---|
| Great Plains | 0.050 | | | |
| Wyoming Basin | | 0.020 | 0.011 | |
| Southern Great Basin | | | 0.024 | 0.004 |
| Snake River Plain | | | | 0.035 |

Connections between management zones not presented are assumed to be zero.
Taken from Garton et al. 2011:367 Table 15.71.

Appendix 1. Top models of annual rates of change with estimates of carrying capacity in 2013, 2043 and 2113 for Populations.

| Populations | Best Models | a | $b_1 lnNt$ | $b_2 Nt$ | $b_2 lnN_{t-1}$ | $b_3 lnN_{t-2}$ | c(period) | d(year) | S | $r^2$ | $K_{2013}$ | $K_{2043}$ | $K_{2113}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| I Great Plains Management Zone | | | | | | | | | | | | | |
| Dakotas | Gompertz + Year | 35.8948 | -0.3942 | | | | | -0.0167 | 0.256 | 0.189 | 323 | 91 | 5 |
| **Northern Montana** | Gompertz t-1 + Period | 2.8591 | | | -0.3347 | | 0.3066 | | 0.1847 | 0.352 | 5127 | 5127 | 5127 |
| Powder River Basin | Gompertz t-1 + year | 67.1015 | | | -0.396 | | | -0.0318 | 0.2769 | 0.317 | 2436 | 219 | 1 |
| Yellowstone Watershed | Ricker + Year | 32.4125 | | -6E-05 | | | | -0.016 | 0.218 | 0.364 | 3393 | 0 | 0 |
| II Wyoming Basin Management Zone | | | | | | | | | | | | | |
| Jackson Hole | NA[+] | | | | | | | | | | | | |
| Wyoming Basin | Gompertz t-1 + year | 23.619 | | | -0.2946 | | | -0.0103 | 0.1485 | 0.246 | 17913 | 6275 | 543 |
| III Southern Great Basin Management Zone | | | | | | | | | | | | | |
| Mono Lake, Californai-Nevada | Gompertz | 3.1176 | -0.5521 | | | | | | 0.465 | 0.267 | 283 | 283 | 283 |
| South Mono Lake, California | Gompertz | 2.491 | -0.4528 | | | | | | 0.3431 | 0.228 | 245 | 245 | 245 |
| Northeast Interior Utah | NA[+] | | | | | | | | | | | | |
| Sanpete-Emery Counties, Utah | NA[+] | | | | | | | | | | | | |
| **South-Central Utah** | Gompertz | 2.2129 | -0.3196 | | | | | | 0.2779 | 0.186 | 1016 | 1016 | 1016 |
| Summit-Morgan Counties, Utah | NA[+] | | | | | | | | | | | | |
| Toole-Juab Counties, Utah | NA[+] | | | | | | | | | | | | |
| Southern Great Basin | Gompertz t-2 + Year | 28.088 | | | | -0.4317 | | -0.0123 | 0.1853 | 0.357 | 2229 | 948 | 129 |
| IV Snake River Plain Management Zone | | | | | | | | | | | | | |
| Baker, Oregon | NA[+] | | | | | | | | | | | | |
| Bannack, Montana | Gompertz + Period | 1.651 | -0.3144 | | | | 0.2848 | | 0.1959 | 0.172 | 191 | 191 | 191 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Red Rocks Lake, Montana | NA[+] | | | | | | | | | | |
| East Central Idaho | NA[+] | | | | | | | | | | |
| Snake-Salmon-Beaverhead, Idaho | Gompertz t-1 + Period | 3.0269 | | -0.3423 | 0.2949 | | 0.1794 | 0.371 | 6925 | 6925 | 6925 |
| Northern Great Basin | Gompertz t-1 + year | 49.0596 | | -0.5015 | | -0.0222 | 0.1251 | 0.514 | 6099 | 1616 | 73 |
| Weiser, Idaho | NA[+] | | | | | | | | | | |
| V Northern Great Basin Management Zone | | | | | | | | | | | |
| Central Oregon | Gompertz + Year, Period | 60.8892 | -0.5485 | | -0.1821 | -0.0286 | 0.1881 | 0.321 | 423 | 89 | 2 |
| Klamath-Oregon-California | NA[+] | | | | | | | | | | |
| Northwest-Interior Nevada | NA[+] | | | | | | | | | | |
| Western Great Basin | Gompertz t-1 + Year,Period | 2.5868 | | -0.3036 | 0.251 | | 0.2602 | 0.241 | 5016 | 5016 | 5016 |
| VI Columbia Basin Management Zone | | | | | | | | | | | |
| Moses-Coulee, Washington | Gompertz t-1 + year | 27.7956 | | -0.3647 | | -0.0129 | 0.2795 | 0.199 | 150 | 52 | 4 |
| Yakima, Washington | NA[+] | | | | | | | | | | |
| VII Colorado Plateau Management Zone | NA* | | | | | | | | | | |

*NA - Not Available because Colorado Parks and Wildlife Denied 4 requests to participate in this study.

NA[+] - Not Estimated because fewer than 26 leks counted

Appendix 2. Top models of annual rates of change with estimates of carrying capacity in 2013, 2043 and 2113 for SMZs.

Sage-Grouse

| Management Zone | Best Models | a | *lnNt* | $b_1Nt$ | $b_2lnN_{t-1}$ | c(period) | d(year) | S | $r^2$ | $K_{2013}$ | $K_{2043}$ | $K_{2113}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| I Great Plains | Ricker + Year | 30.2053 | . | -1.7E-05 | . | . | -0.015 | 0.2082 | 0.239 | 616 | 0 | 0 |
| | Gompertz t-1 + year | 31.6958 | . | . | -0.3949 | . | -0.014 | 0.2103 | 0.223 | 7317 | 2526 | 211 |
| II Wyoming Basin | Gompertz t-1 + year | 23.5212 | . | . | -0.2978 | . | -0.0102 | 0.1479 | 0.247 | 22825 | 8169 | 743 |
| III Southern Great Basin | Gompertz t-1 + year | 15.2114 | . | . | -0.3777 | . | -0.006 | 0.1299 | 0.339 | 4008 | 2488 | 818 |
| IV Snake River Plain | Gomperz t-1 + Year,Period | 25.4738 | . | . | -0.4124 | 0.1566 | -0.0107 | 0.1319 | 0.448 | 13919 | 6391 | 1039 |
| | Gompertz t-1 + year | 35.0669 | . | . | -0.407 | . | -0.0155 | 0.1367 | 0.393 | 13324 | 4250 | 296 |
| V Northern Great Basin | Gompertz t-1 + year | 27.4378 | . | . | -0.33 | . | -0.0123 | 0.1947 | 0.221 | 3344 | 1093 | 80 |
| | Gomperz t-1 + Year,Period | 40.9475 | . | . | -0.367 | -0.1634 | -0.0189 | 0.1926 | 0.256 | 2716 | 579 | 16 |
| VI Columbia Basin | Gompertz t-1 + year | 27.8921 | . | . | -0.3956 | . | -0.0128 | 0.209 | 0.208 | 216 | 82 | 8 |
| | Gompertz + Year | 26.9596 | -0.3979 | . | . | . | -0.0123 | 0.2102 | 0.199 | 252 | 100 | 11 |
| VII Colorado Plateau | NA* | | | | | | | | | | | |

*NA - Not Available because Colorado Parks and Wildlife denied 4 requests to participate in this study.

Figure 1. Greater sage-grouse populations and management zones in western North America.

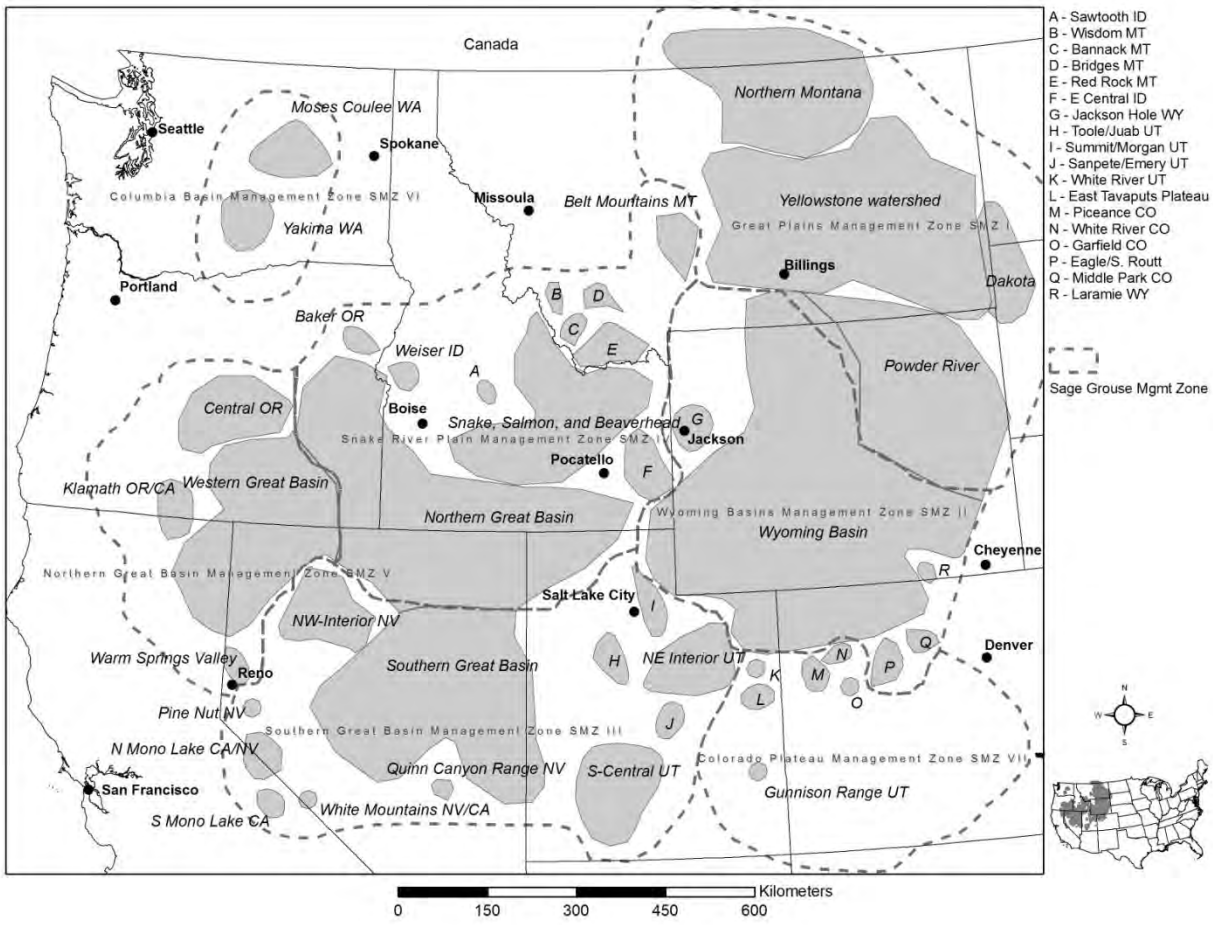
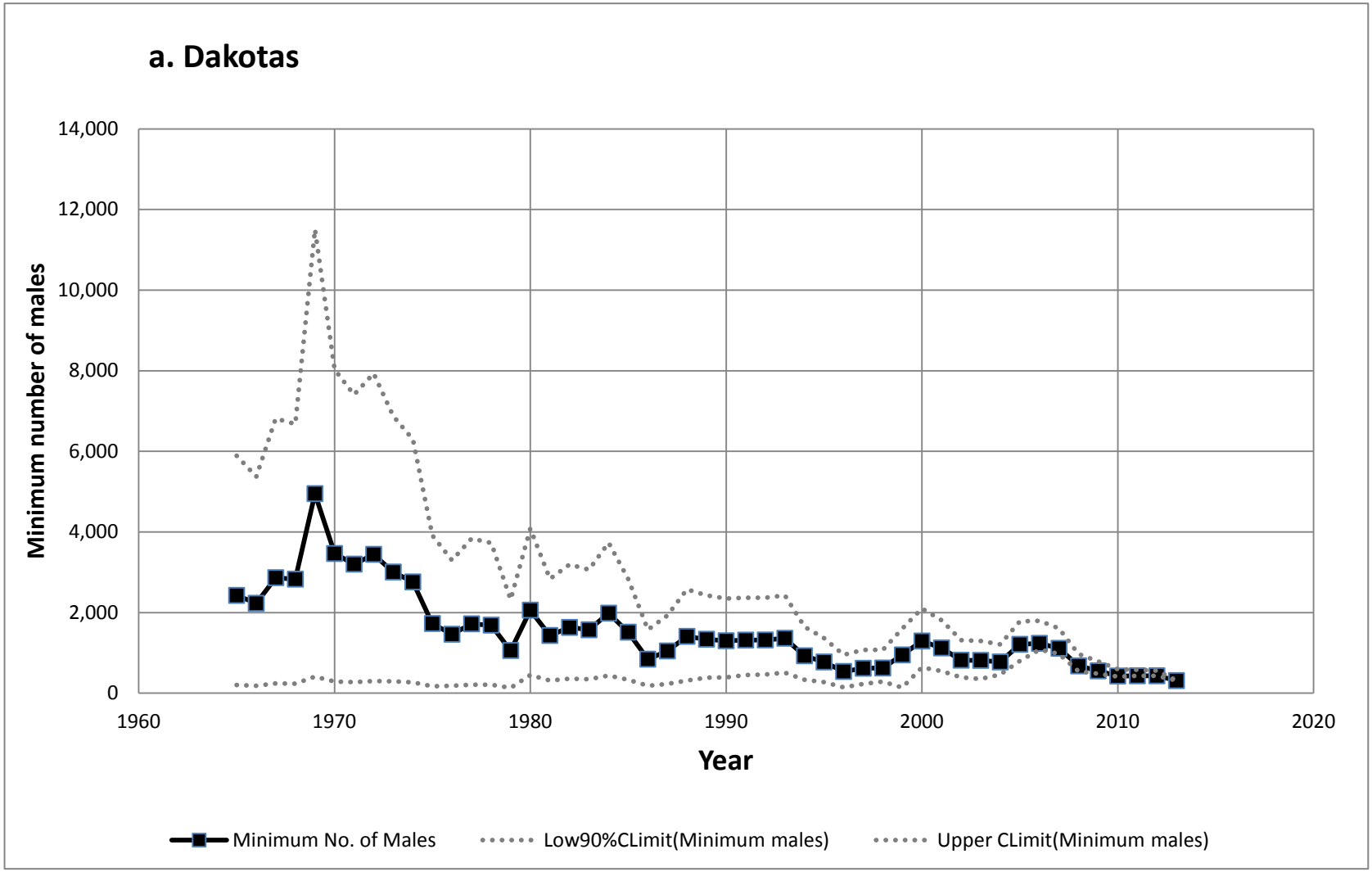
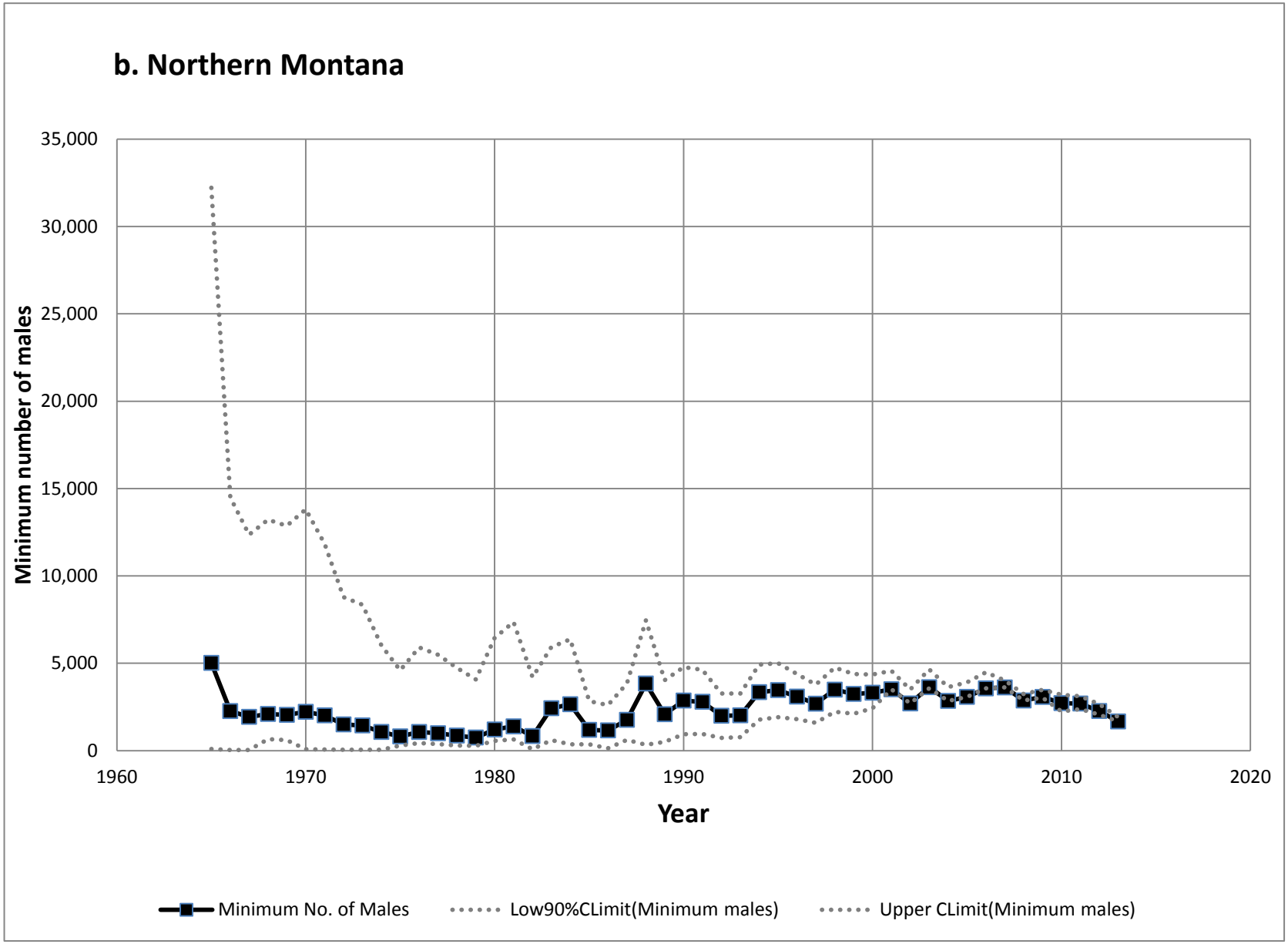
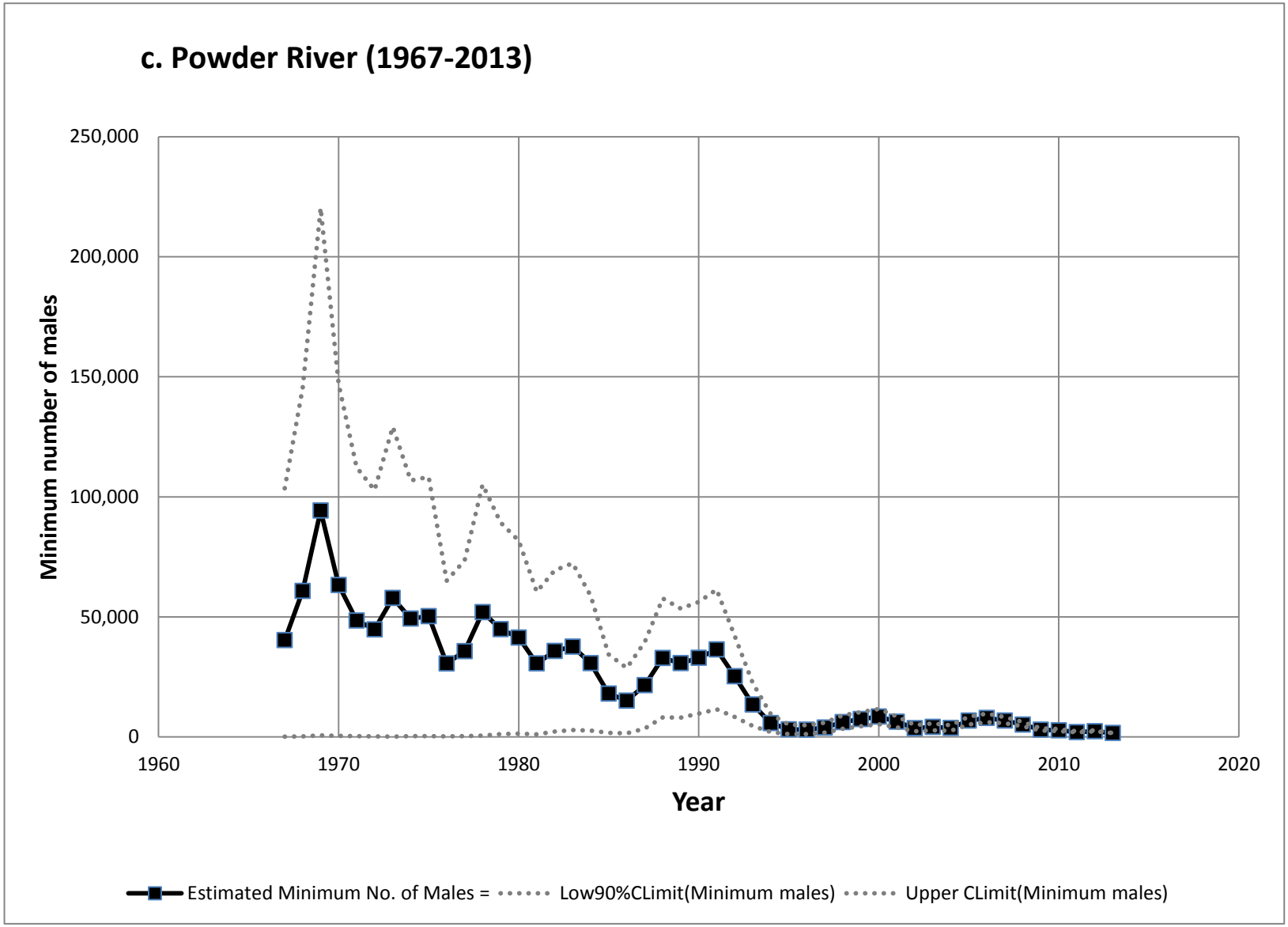
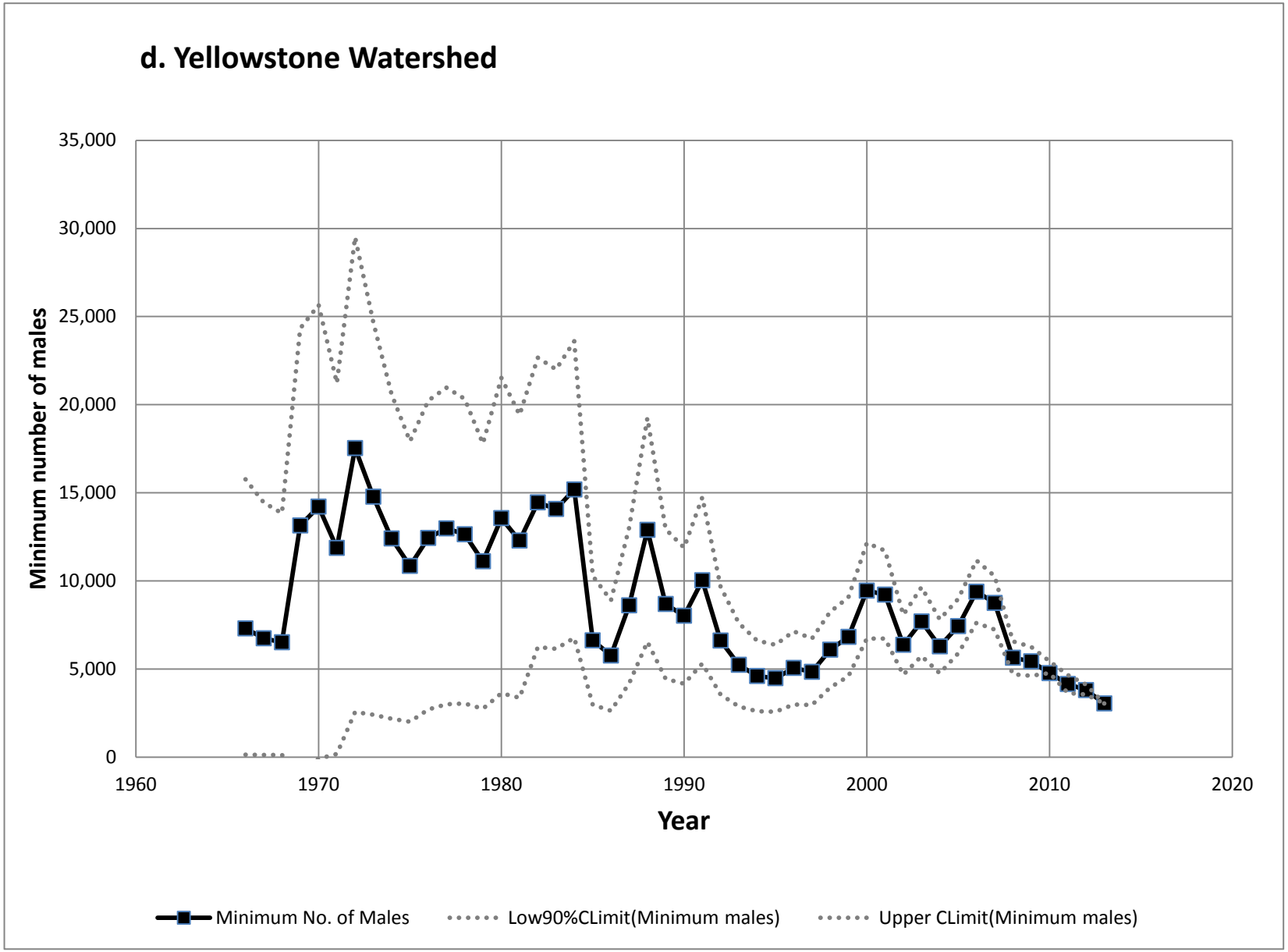


Figure 2. Population reconstructions for Great Plains populations and Management Zone I: a. Dakotas b. Northern Montana c. Powder River Basin d. Yellowstone Watershed e. Great Plains Management Zone I.


a. Dakotas
Minimum number of males
14,000
12,000
10,000
8,000
6,000
4,000
2,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Minimum No. of Males
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


b. Northern Montana
Minimum number of males
35,000
30,000
25,000
20,000
15,000
10,000
5,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Minimum No. of Males
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


c. Powder River (1967-2013)
250,000
200,000
150,000
100,000
50,000
0
Minimum number of males
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


d. Yellowstone Watershed
Minimum number of males
35,000
30,000
25,000
20,000
15,000
10,000
5,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Minimum No. of Males
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

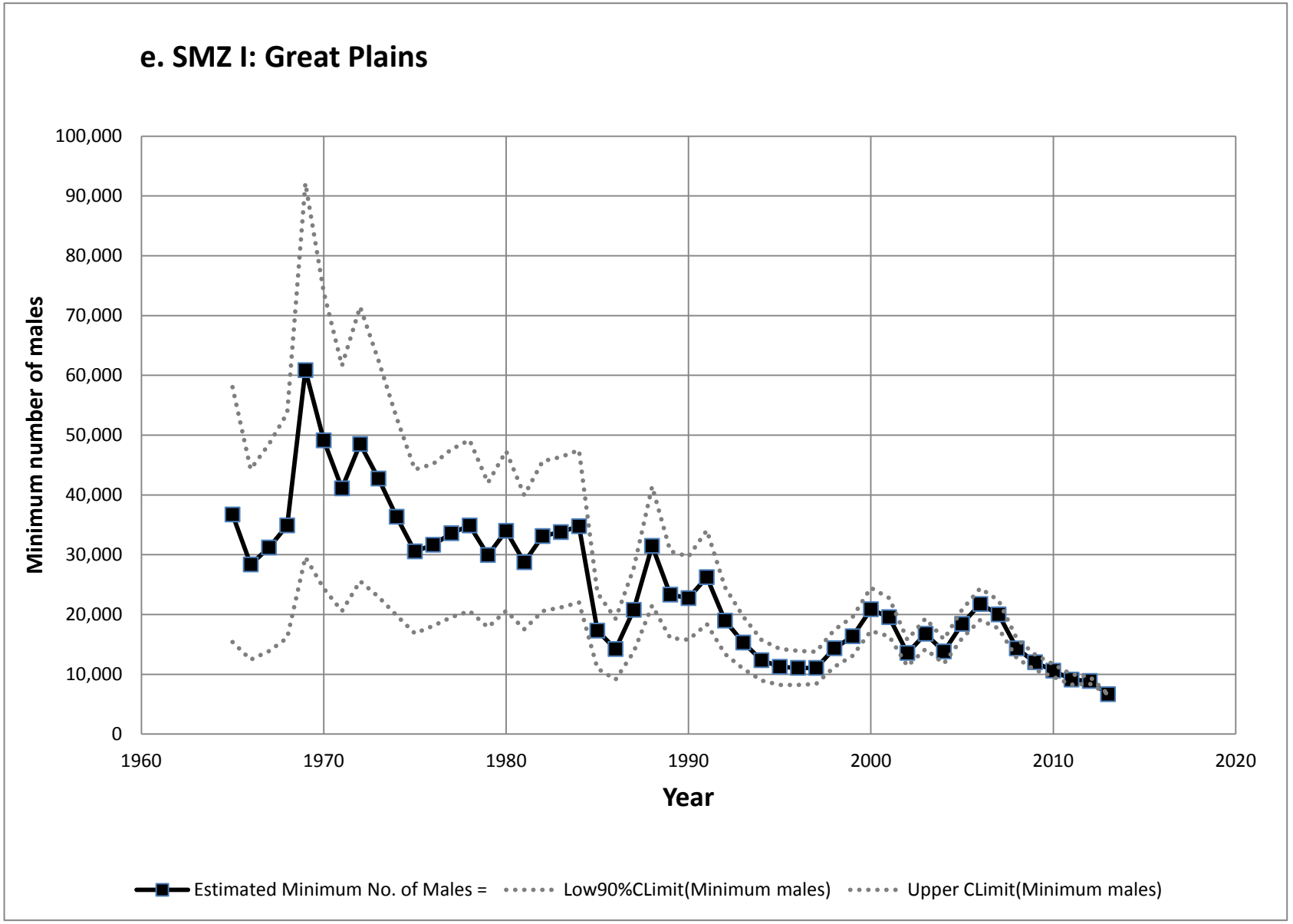
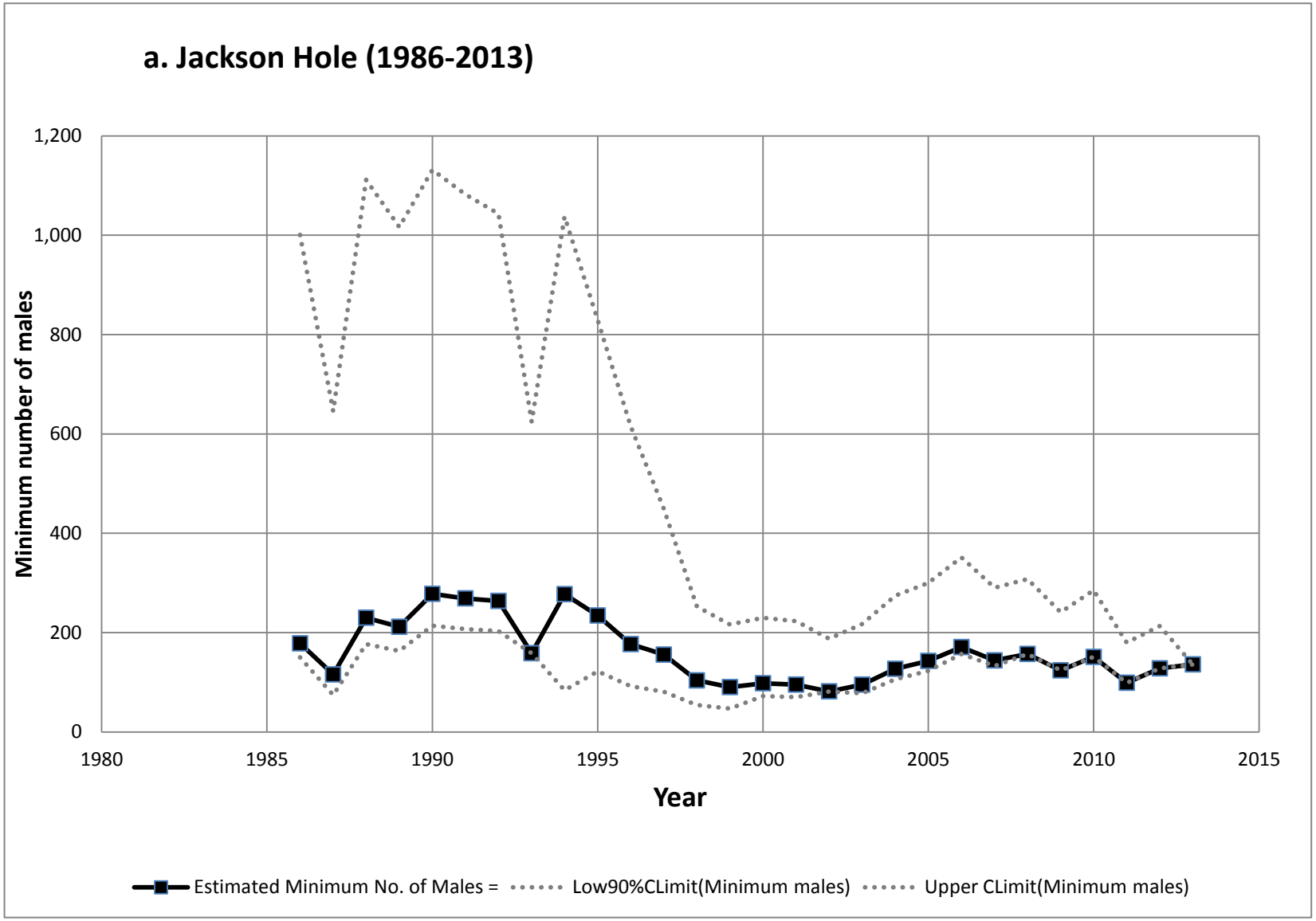
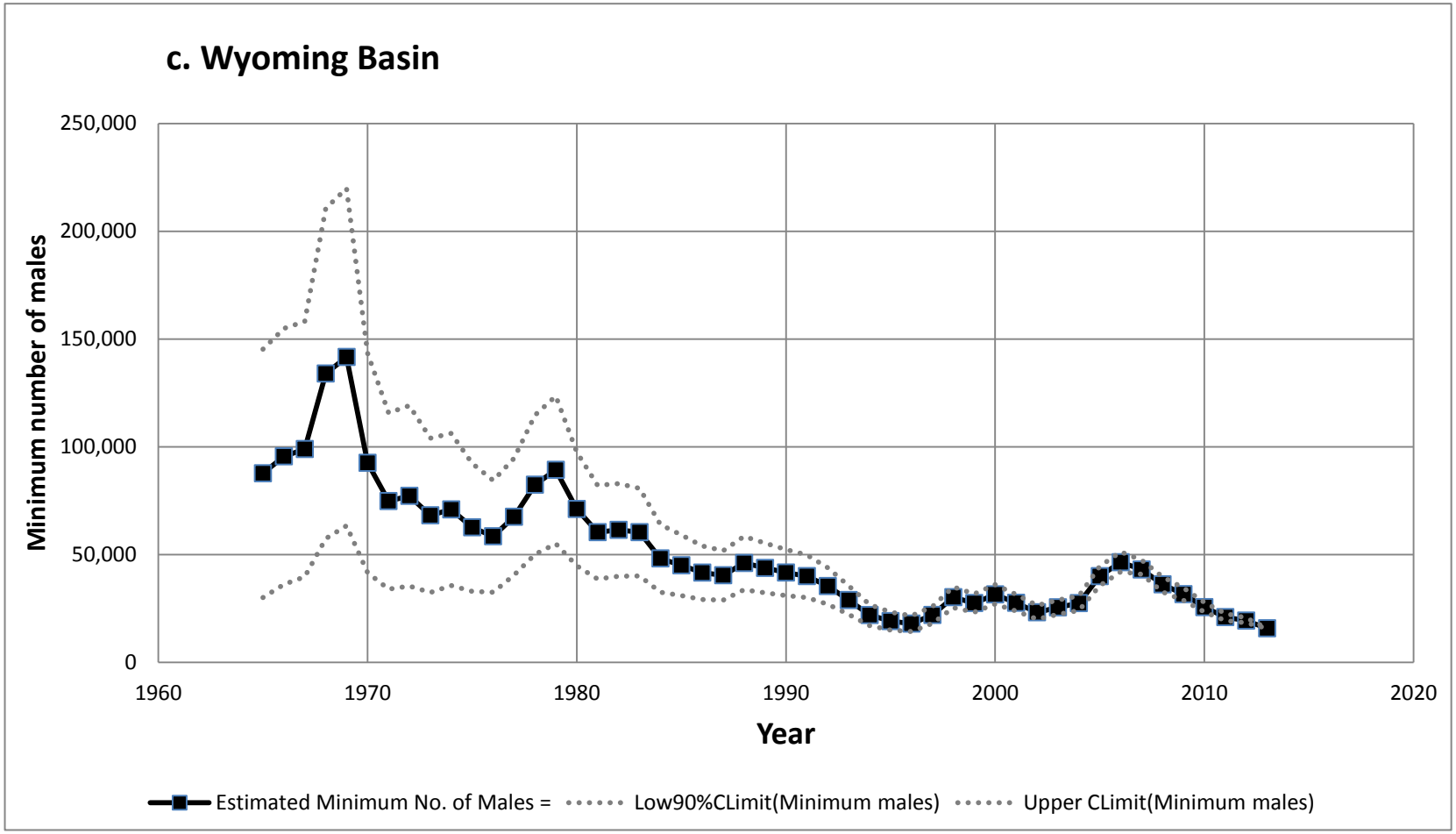

e. SMZ I: Great Plains
Minimum number of males
100,000
90,000
80,000
70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

Figure 3. Population reconstructions for Wyoming Basins populations and Management Zone II: a. Jackson Hole, Wyoming; b. Middle Park, Colorado; c. Wyoming Basins; d. Management Zone II.


a. Jackson Hole (1986-2013)
Minimum number of males
1,200
1,000
800
600
400
200
0
1980
1985
1990
1995
2000
2005
2010
2015
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

NO UPDATED COLORADO DATA YET


c. Wyoming Basin
Minimum number of males
250,000
200,000
150,000
100,000
50,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

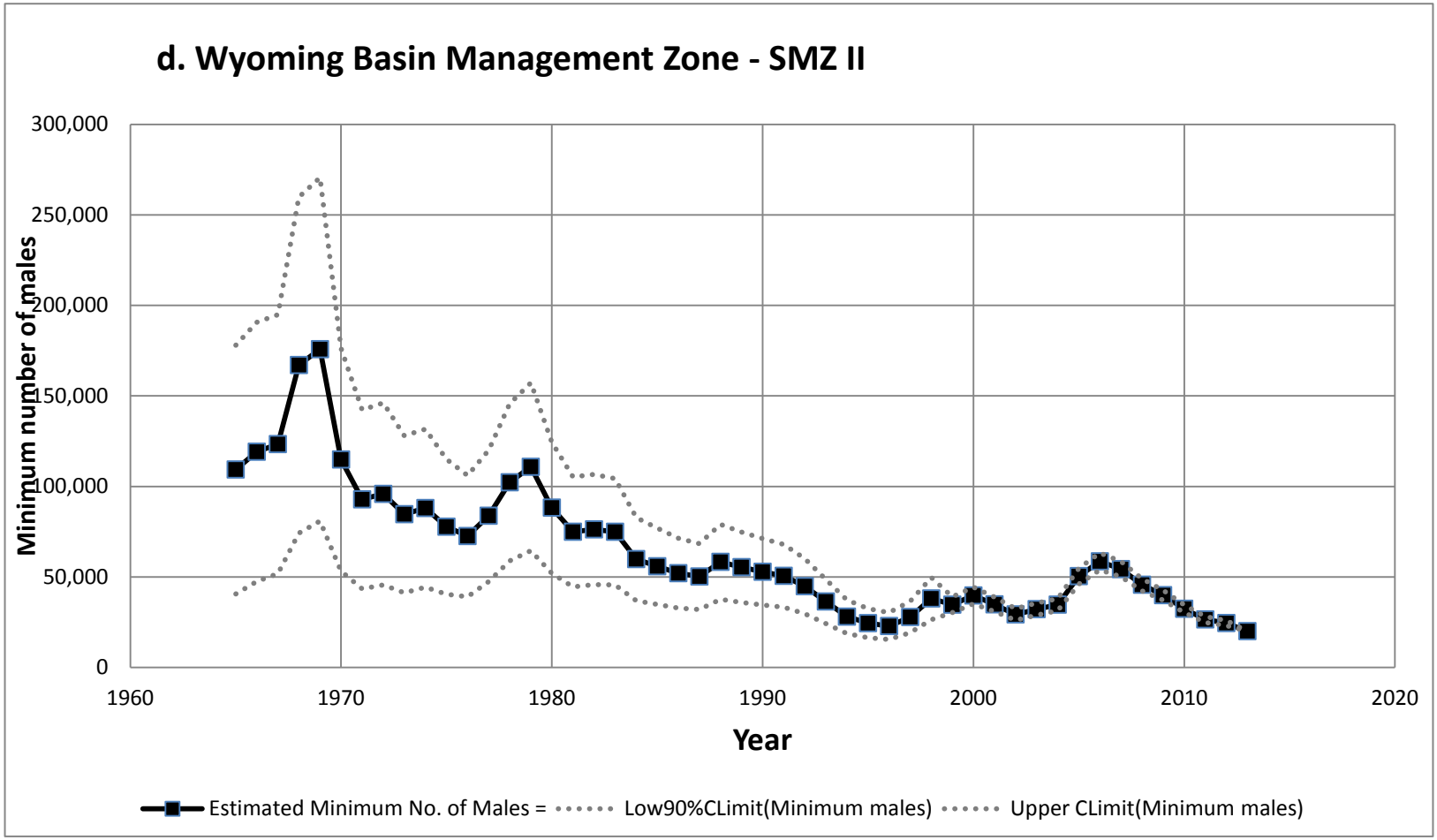
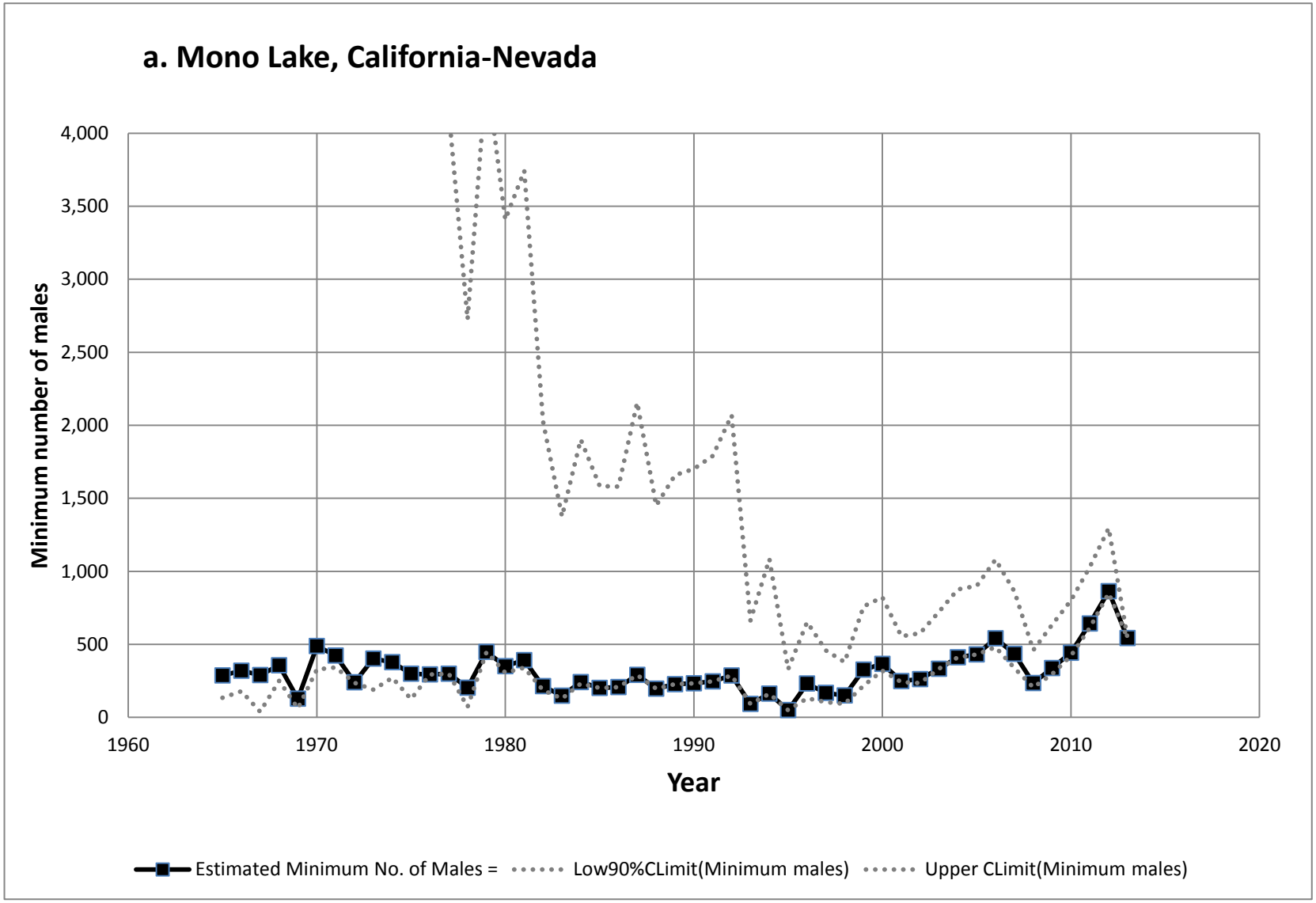
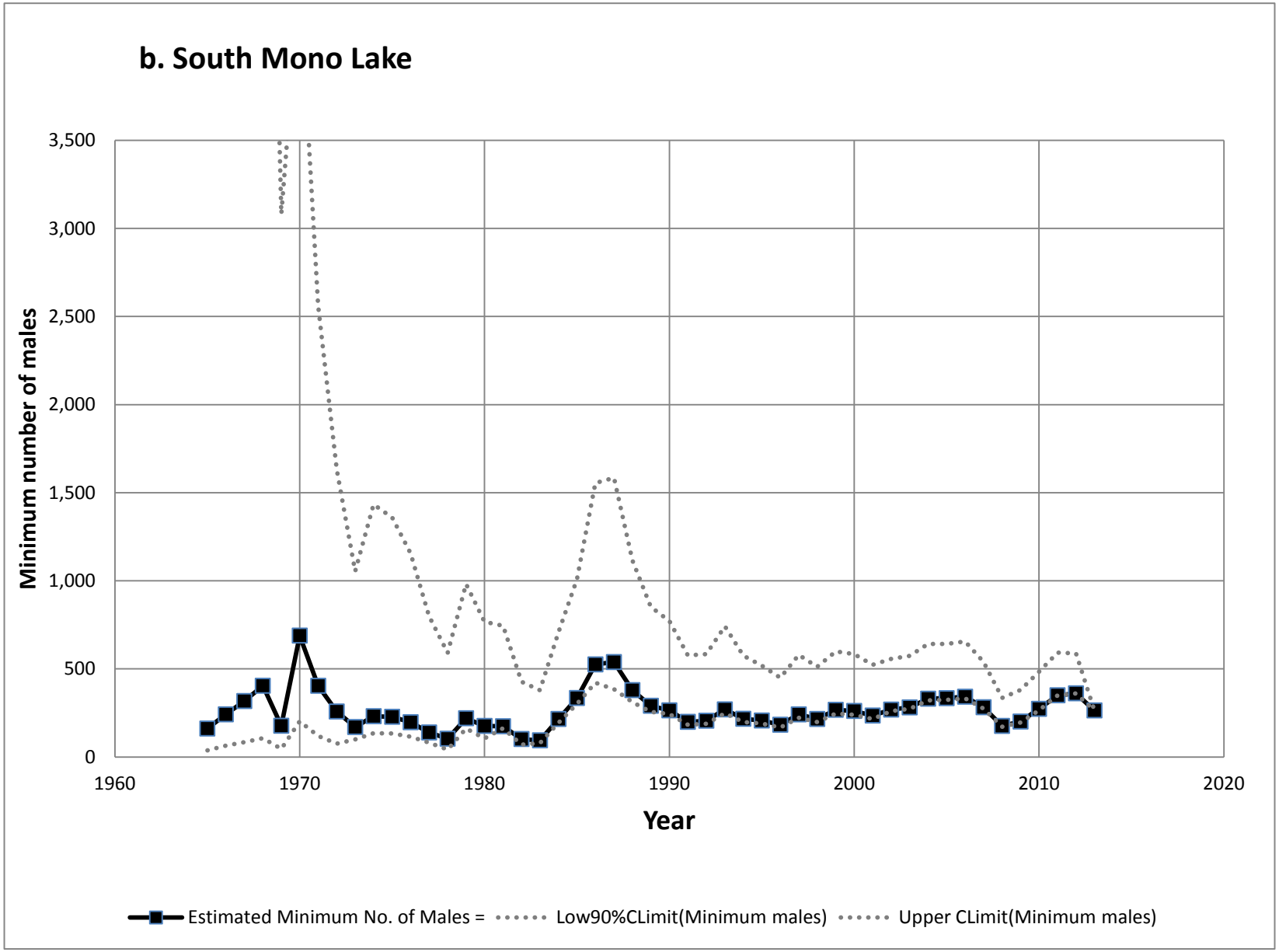
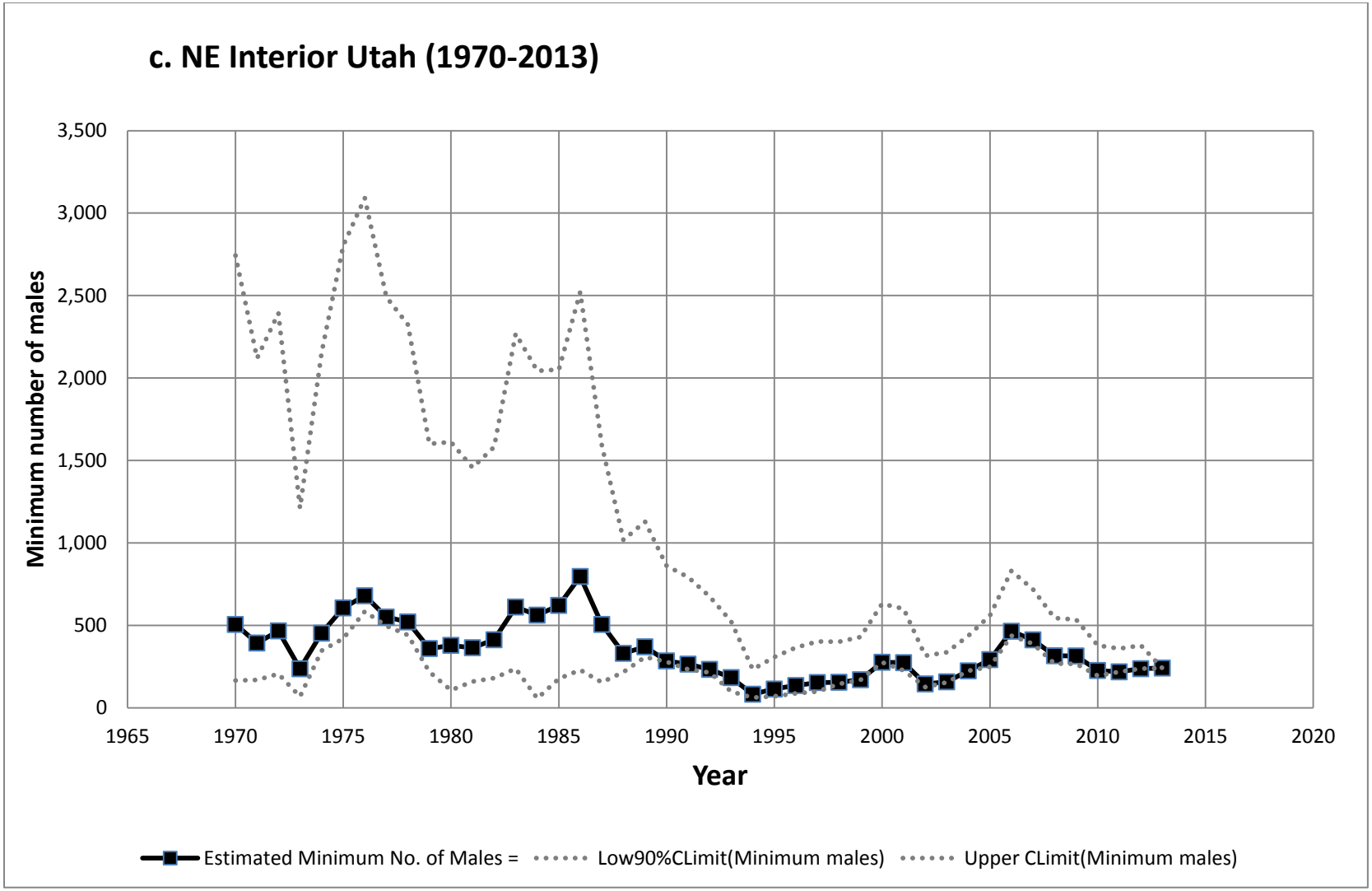
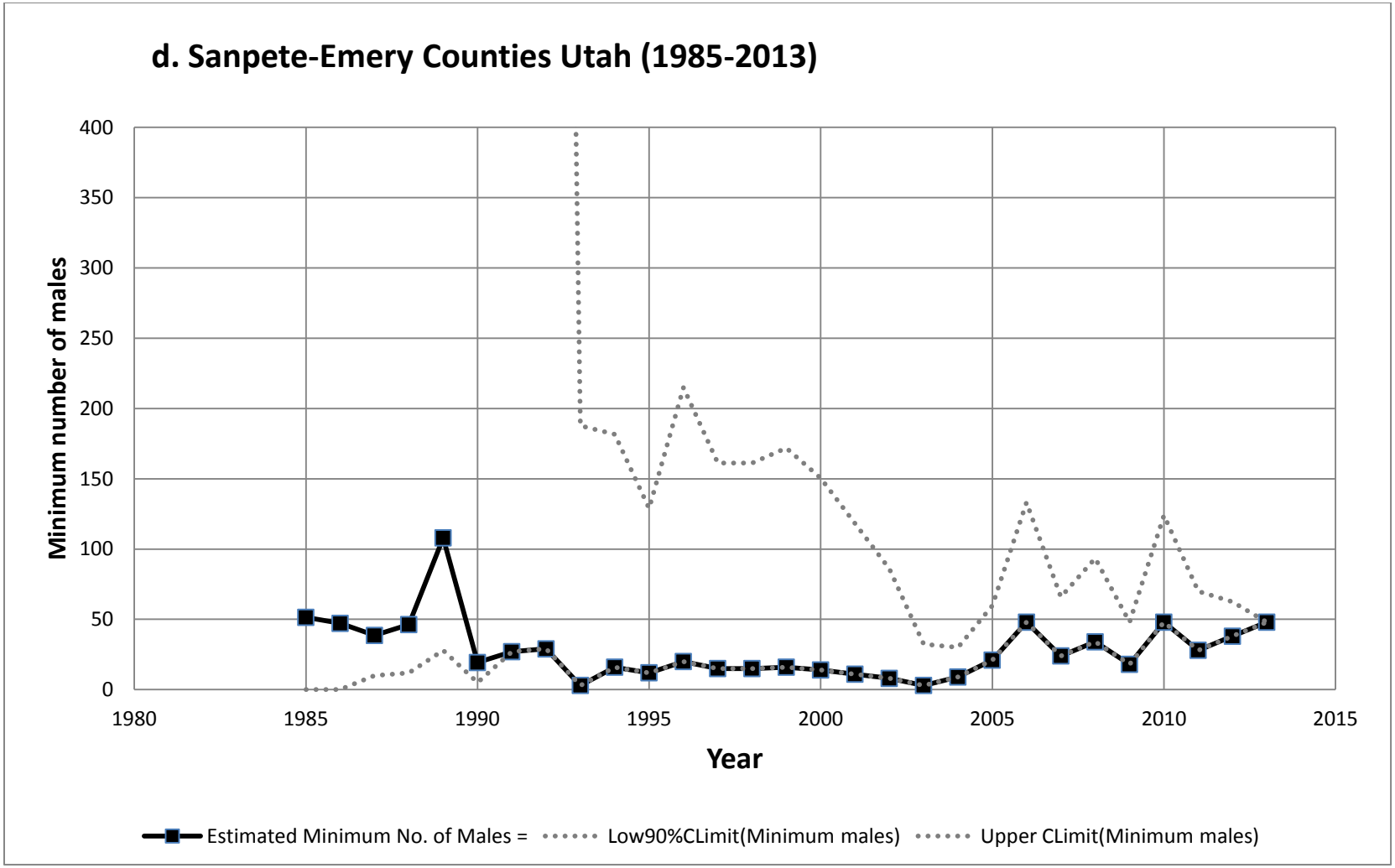

d. Wyoming Basin Management Zone - SMZ II
Minimum number of males
300,000
250,000
200,000
150,000
100,000
50,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

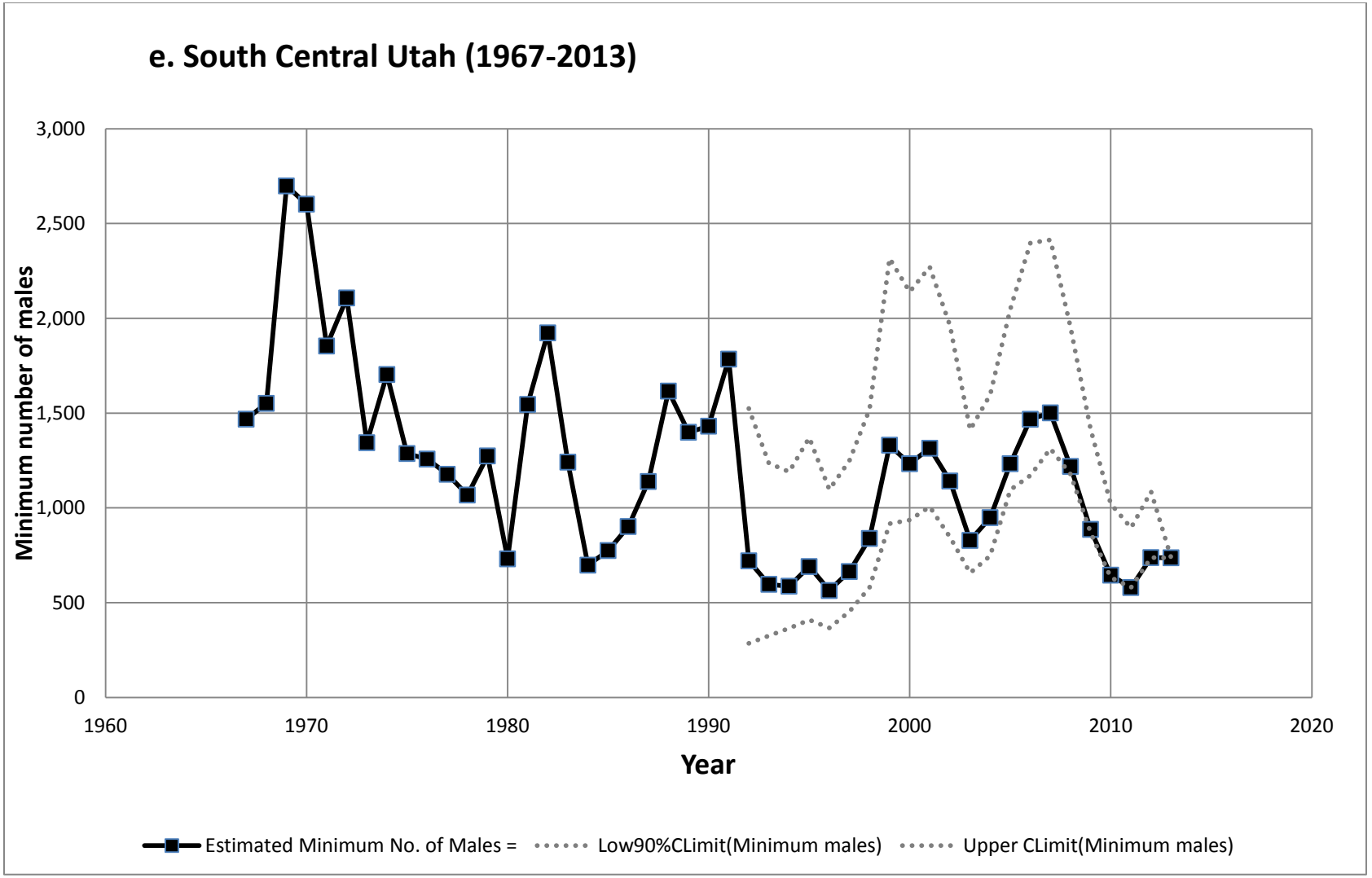
Figure 4. Population reconstructions for Southern Great Basin populations and Management Zone III: a. Mono Lake, California-Nevada; b. South Mono Lake; c. Northeast Interior, Utah; d. Sanpete-Emery; e. South-central Utah; f. Summit-Morgan, g. Toole-Juab Utah; h. Southern Great Basin; i. Management Zone III.

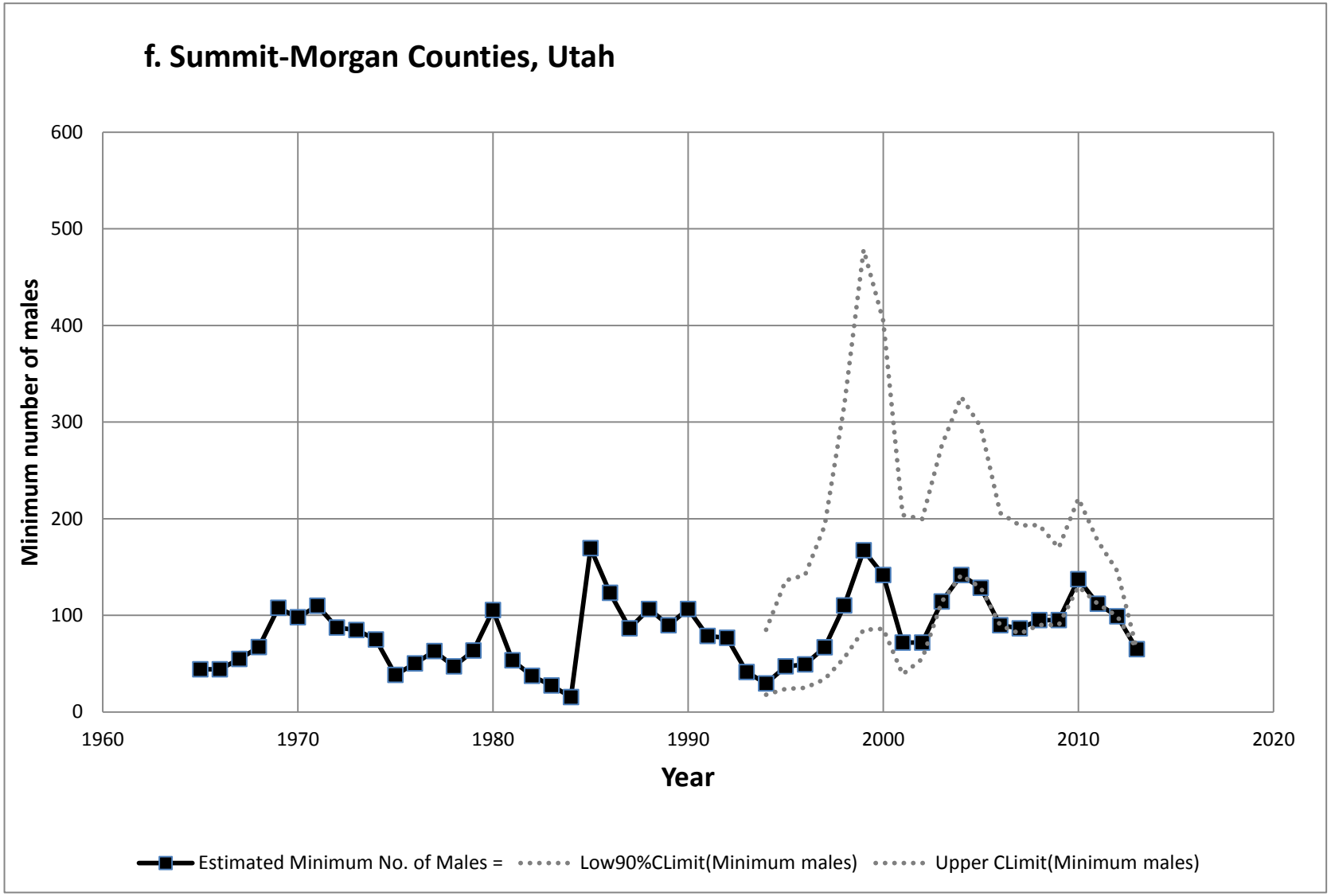

a. Mono Lake, California-Nevada
Minimum number of males
4,000
3,500
3,000
2,500
2,000
1,500
1,000
500
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

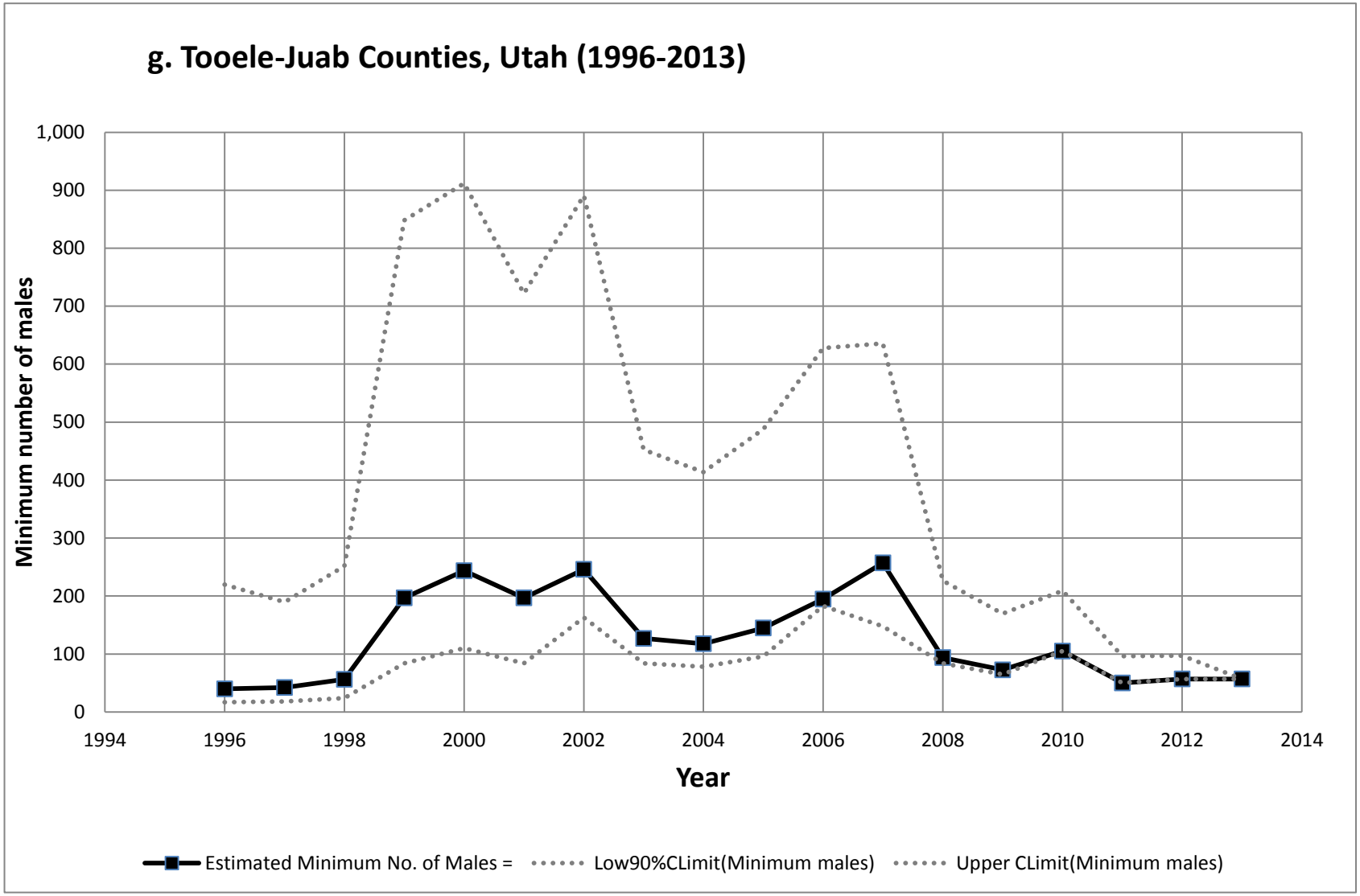

b. South Mono Lake
Minimum number of males
3,500
3,000
2,500
2,000
1,500
1,000
500
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

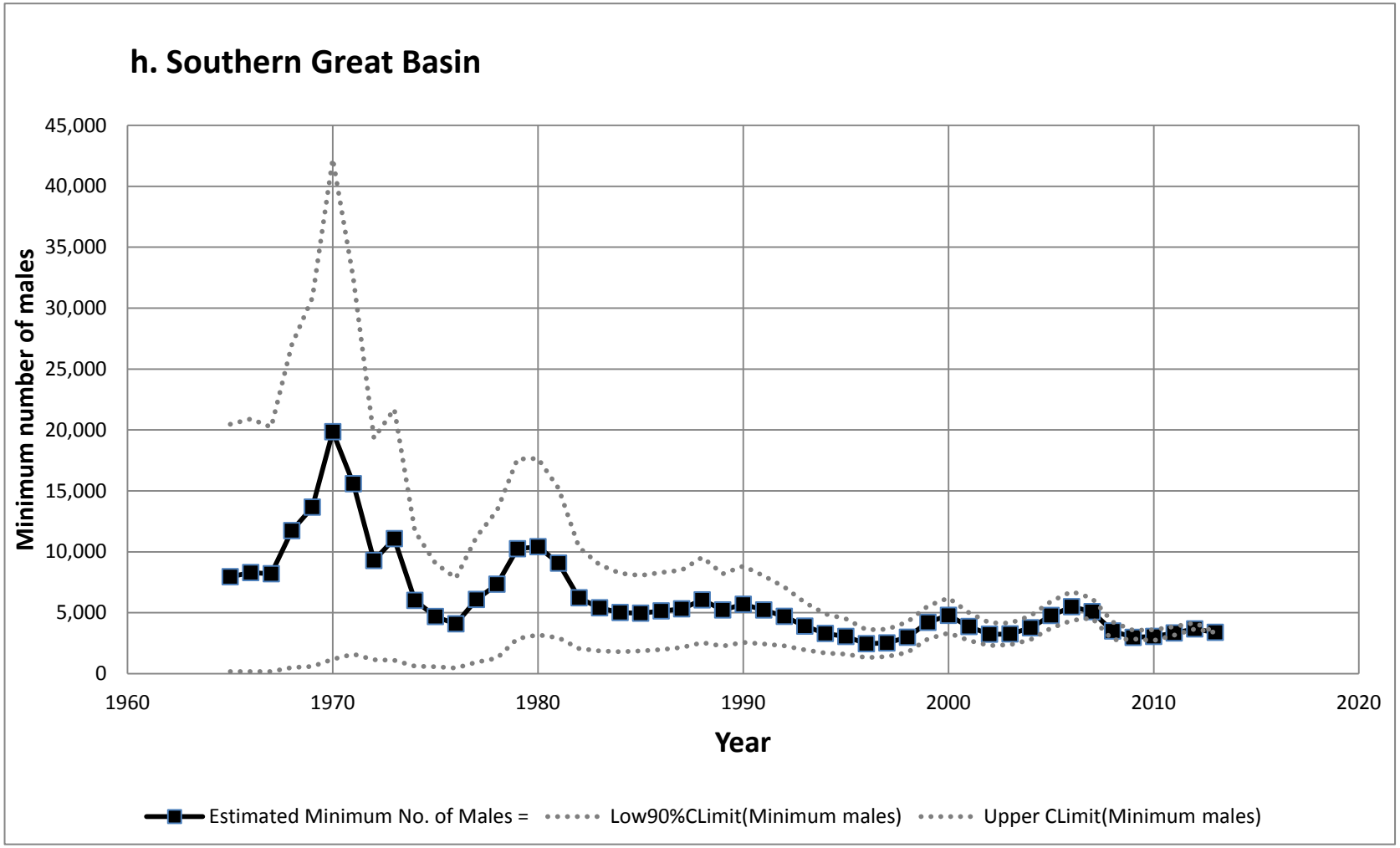

c. NE Interior Utah (1970-2013)
Minimum number of males
3,500
3,000
2,500
2,000
1,500
1,000
500
0
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
2015
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


d. Sanpete-Emery Counties Utah (1985-2013)
Minimum number of males
400
350
300
250
200
150
100
50
0
1980
1985
1990
1995
2000
2005
2010
2015
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


e. South Central Utah (1967-2013)
Minimum number of males
3,000
2,500
2,000
1,500
1,000
500
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


f. Summit-Morgan Counties, Utah
Minimum number of males
600
500
400
300
200
100
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


g. Tooele-Juab Counties, Utah (1996-2013)
Minimum number of males
1,000
900
800
700
600
500
400
300
200
100
0
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


h. Southern Great Basin
Minimum number of males
45,000
40,000
35,000
30,000
25,000
20,000
15,000
10,000
5,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

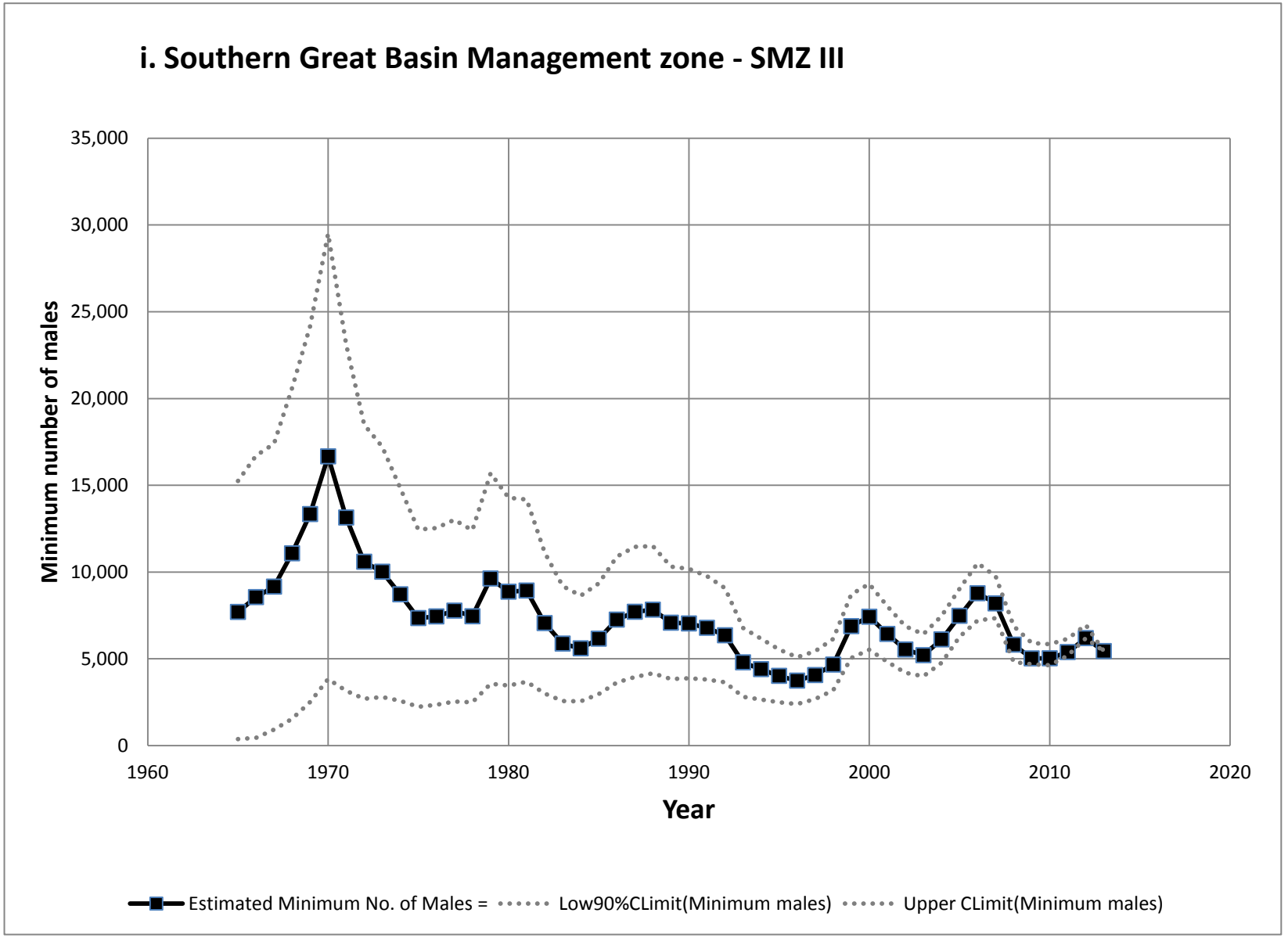
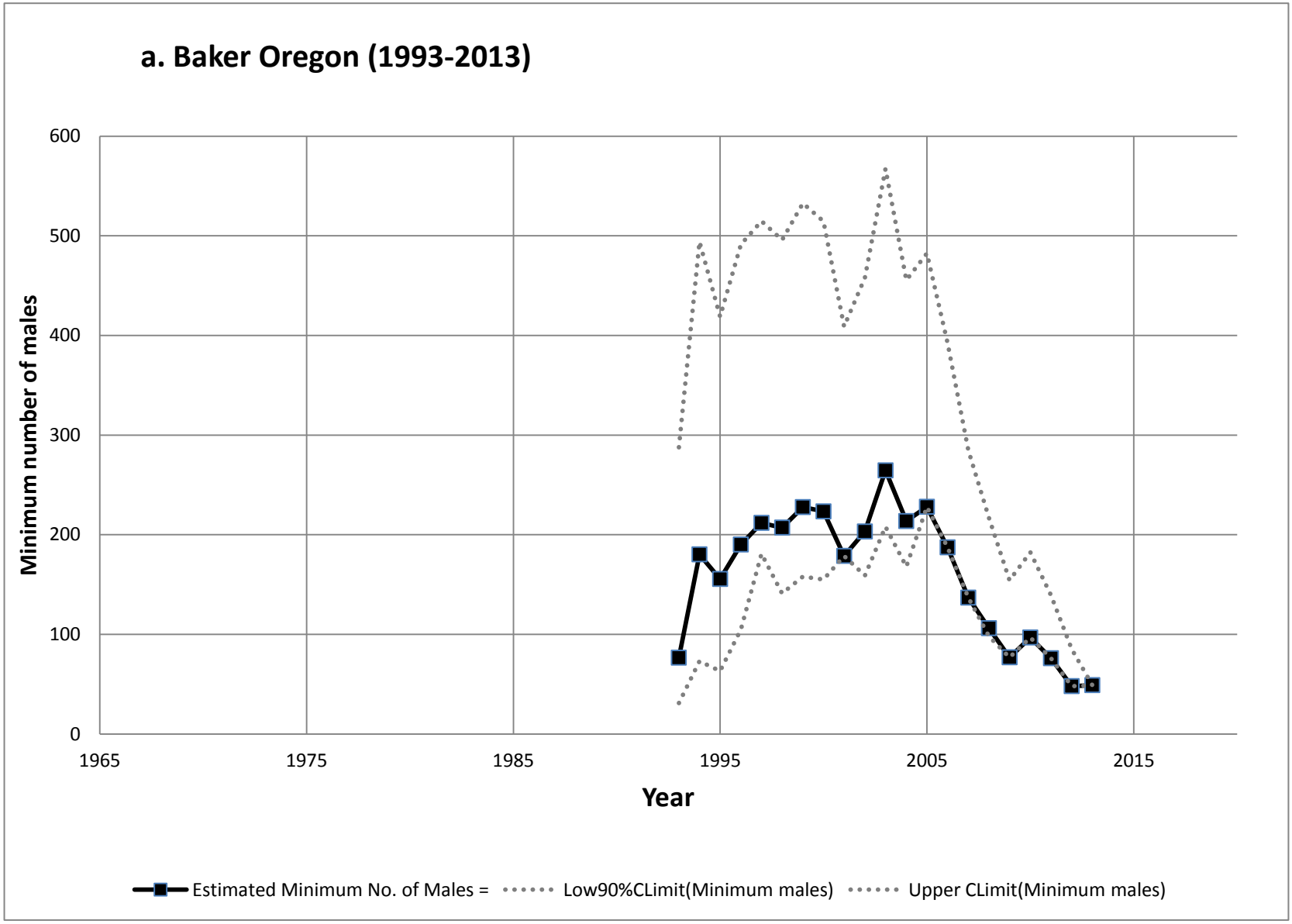
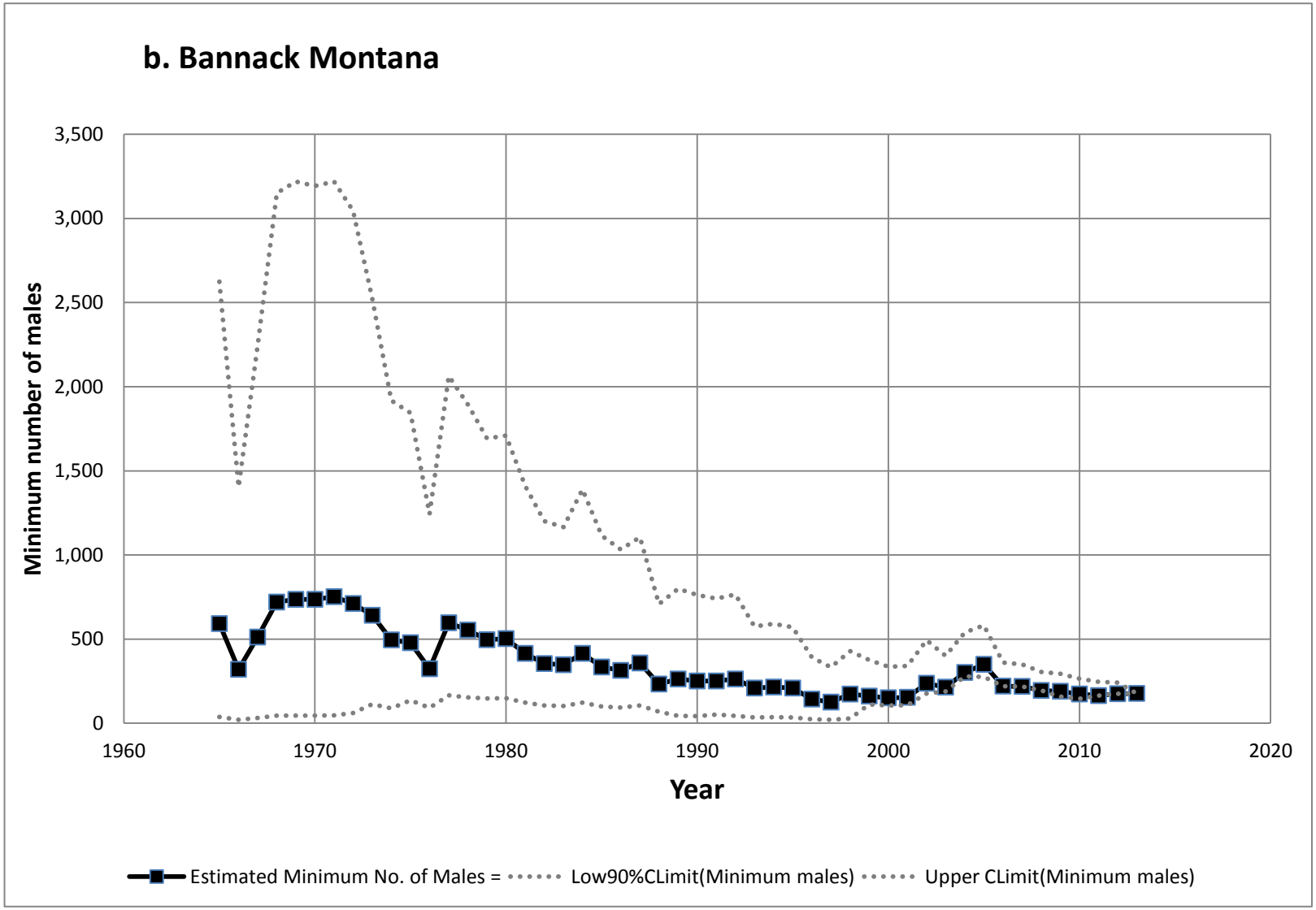
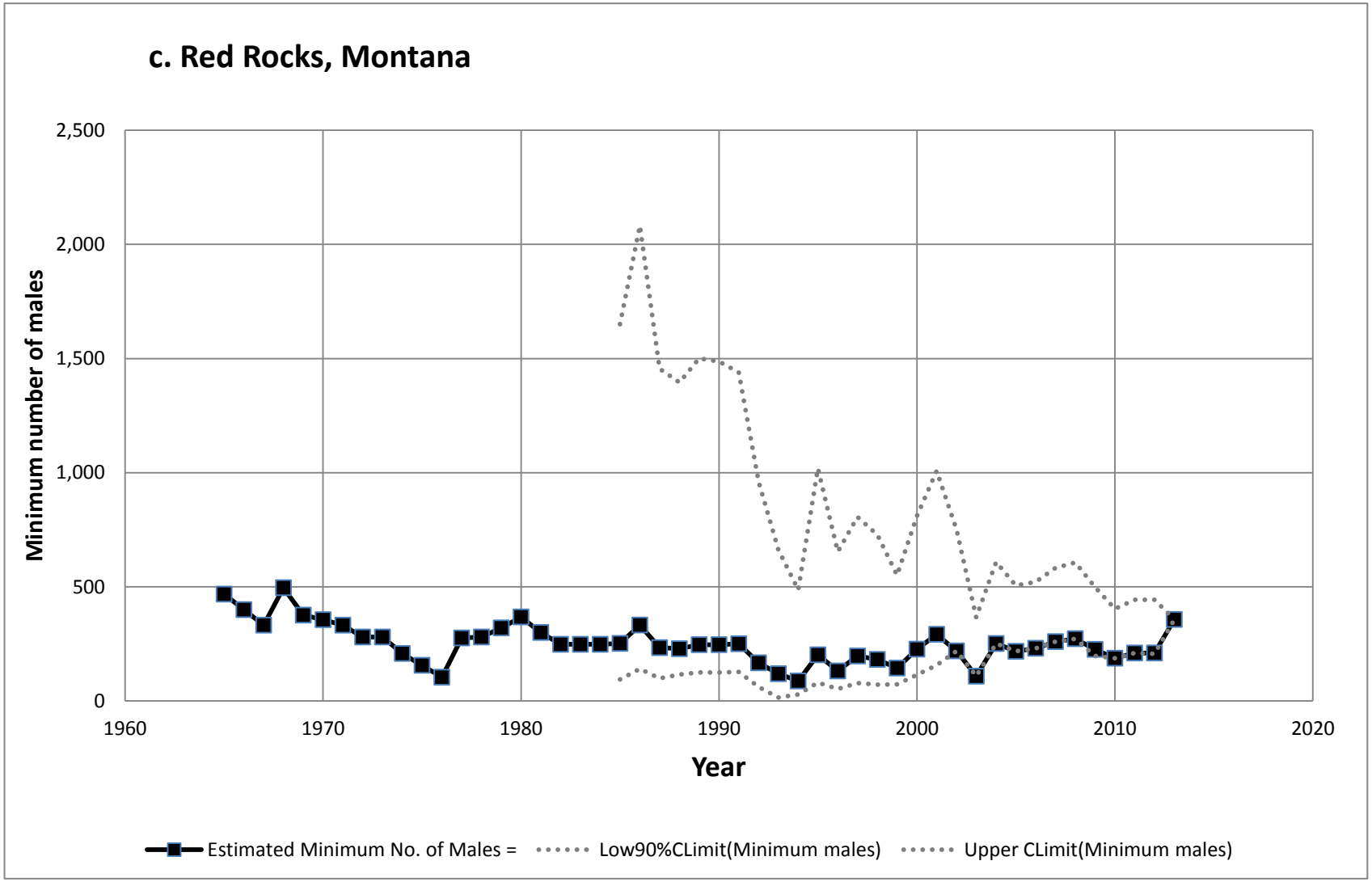
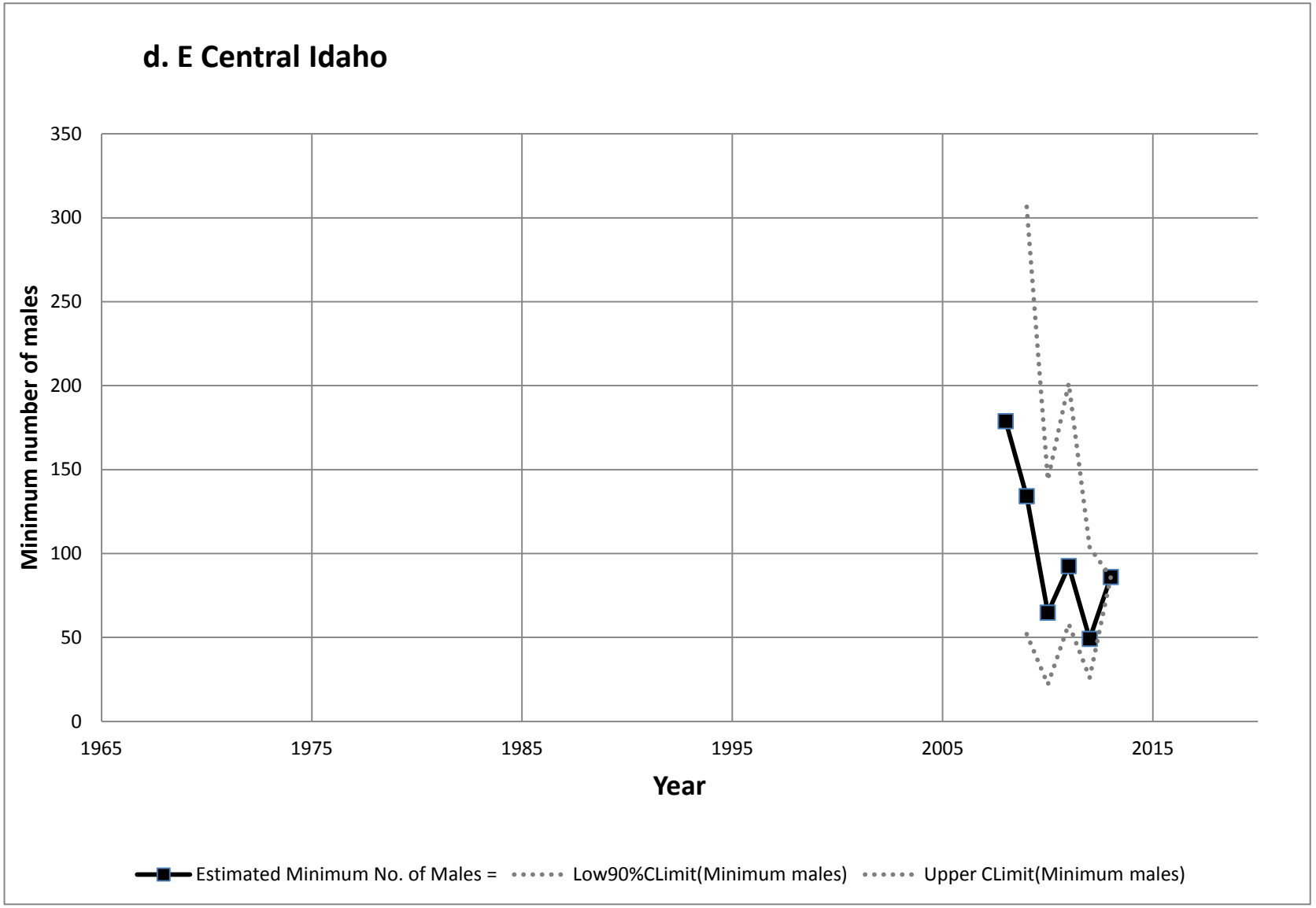

i. Southern Great Basin Management zone - SMZ III
Minimum number of males
35,000
30,000
25,000
20,000
15,000
10,000
5,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

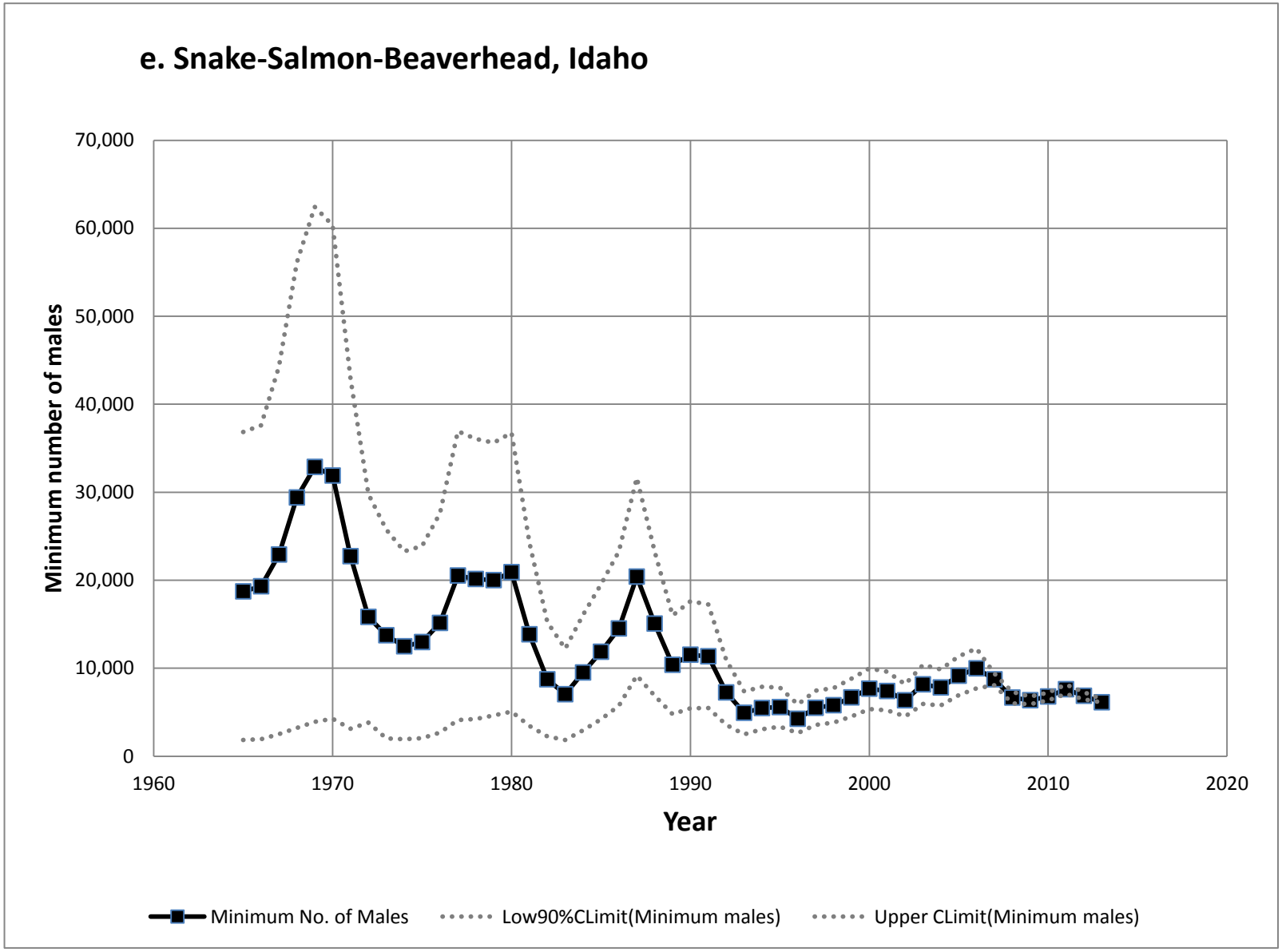
Figure 5. Population reconstructions for Snake River Plain populations and Management Zone IV: a. Baker, Oregon; b. Bannack, Montana; c. Red Rocks, Montana; d. East-central Idaho; e. Snake-Salmon-Beaverhead; f. Northern Great Basin; g. Weiser Idaho; h. Management Zone IV.

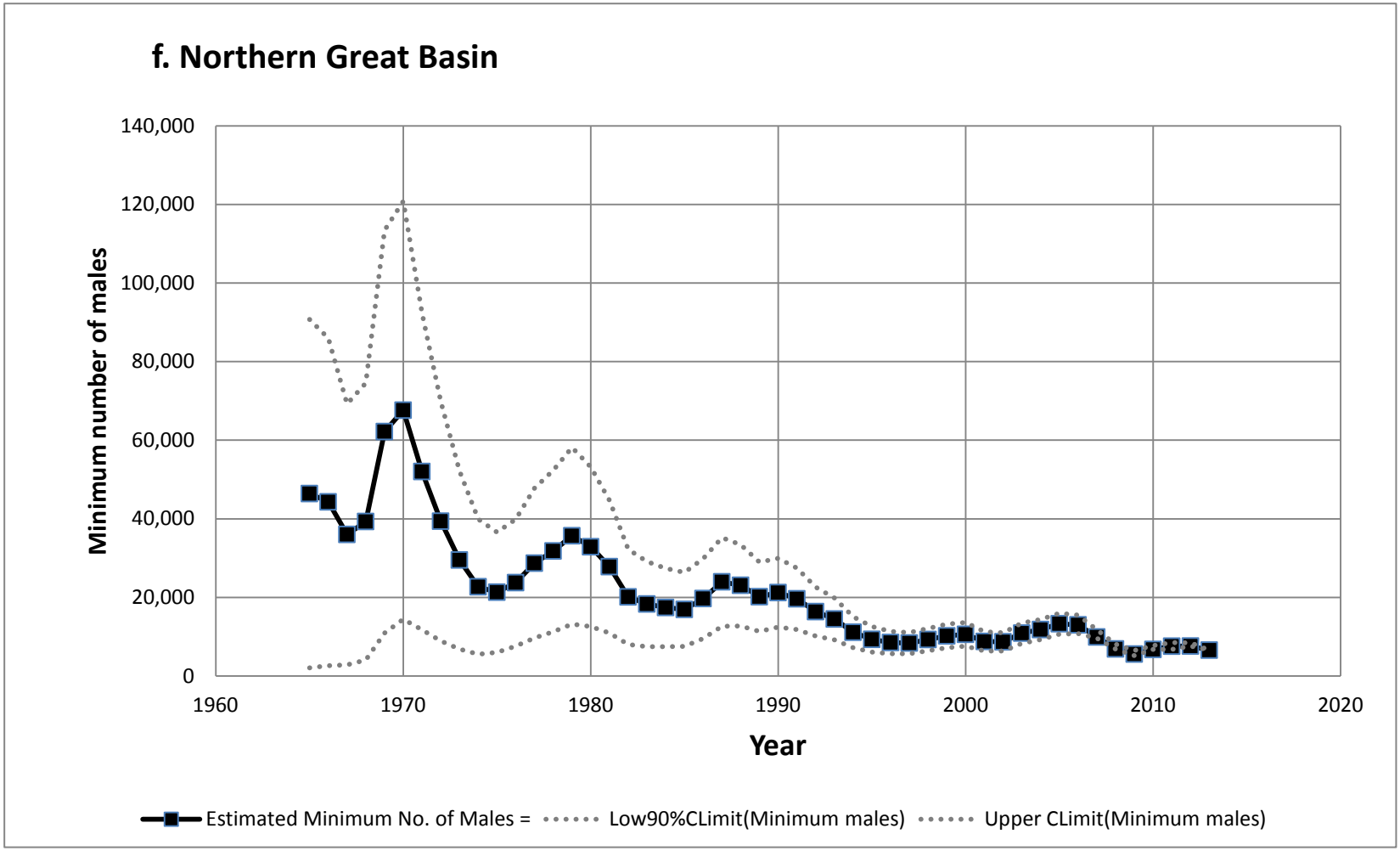

a. Baker Oregon (1993-2013)
Minimum number of males
600
500
400
300
200
100
0
1965
1975
1985
1995
2005
2015
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

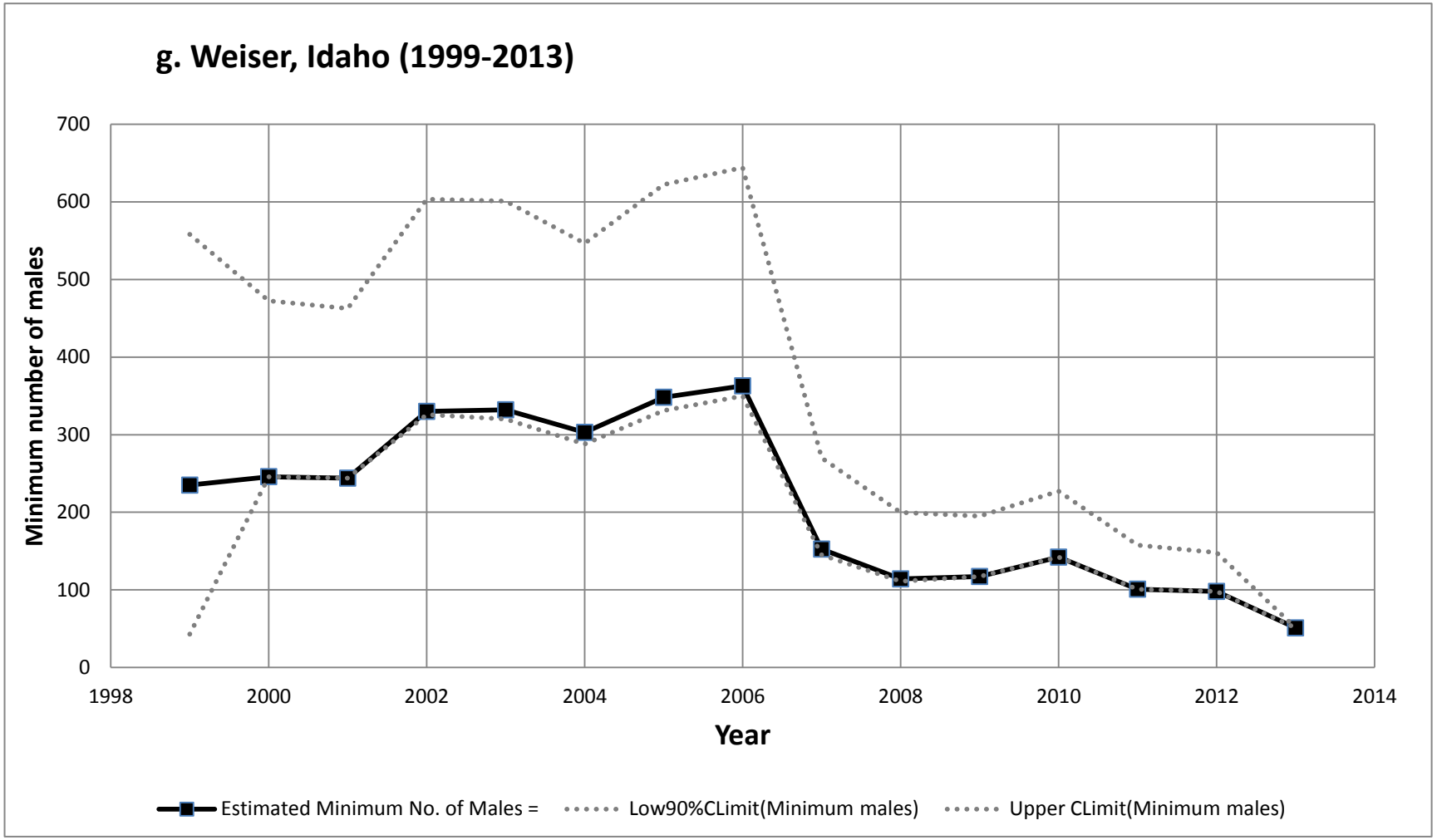

b. Bannack Montana
Minimum number of males
3,500
3,000
2,500
2,000
1,500
1,000
500
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


c. Red Rocks, Montana
Minimum number of males
2,500
2,000
1,500
1,000
500
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


d. E Central Idaho
Minimum number of males
350
300
250
200
150
100
50
0
1965
1975
1985
1995
2005
2015
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


e. Snake-Salmon-Beaverhead, Idaho
70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
Minimum number of males
1960
1970
1980
1990
2000
2010
2020
Year
Minimum No. of Males
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


f. Northern Great Basin
Minimum number of males
140,000
120,000
100,000
80,000
60,000
40,000
20,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


g. Weiser, Idaho (1999-2013)
Minimum number of males
700
600
500
400
300
200
100
0
1998
2000
2002
2004
2006
2008
2010
2012
2014
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

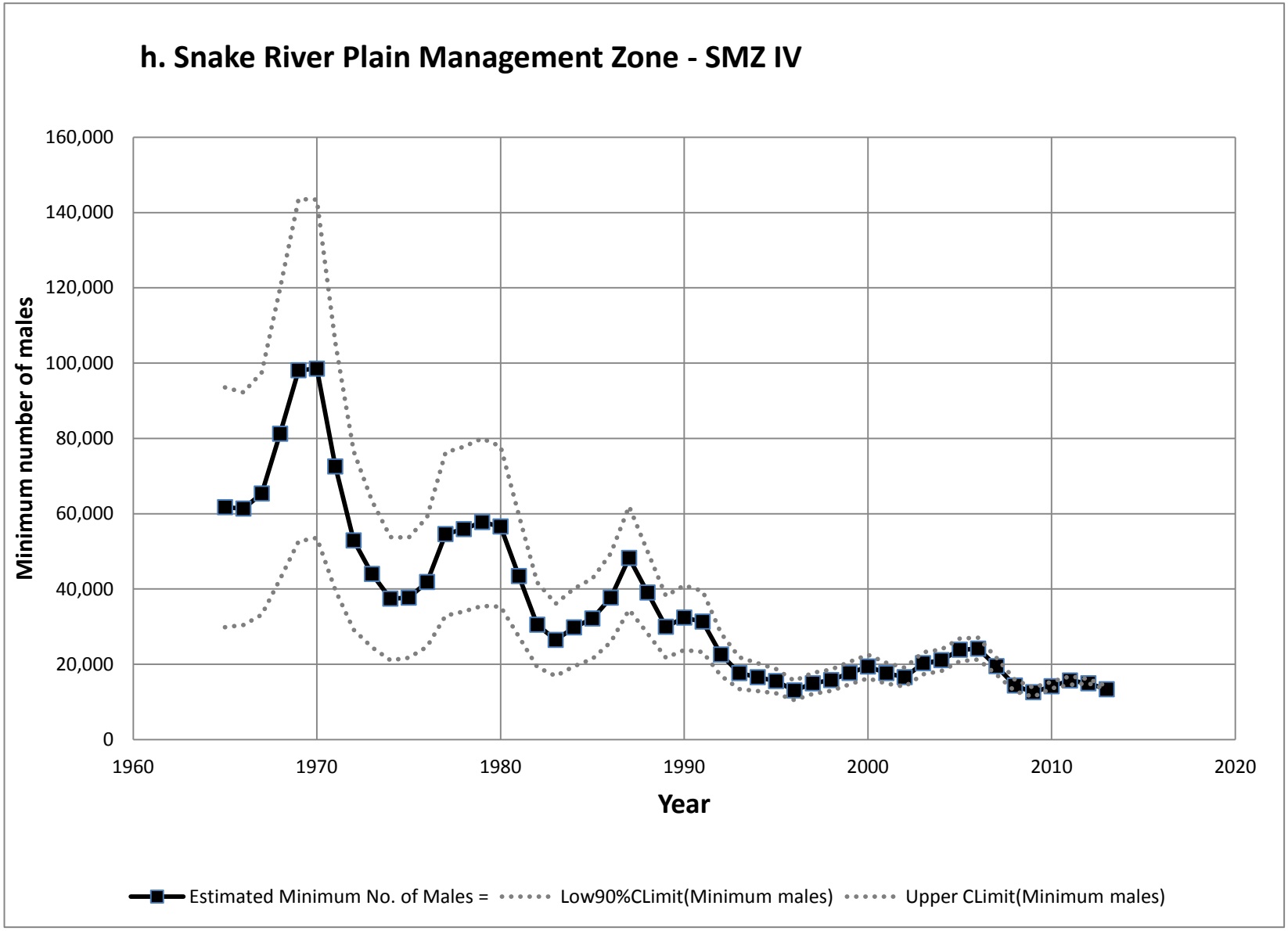
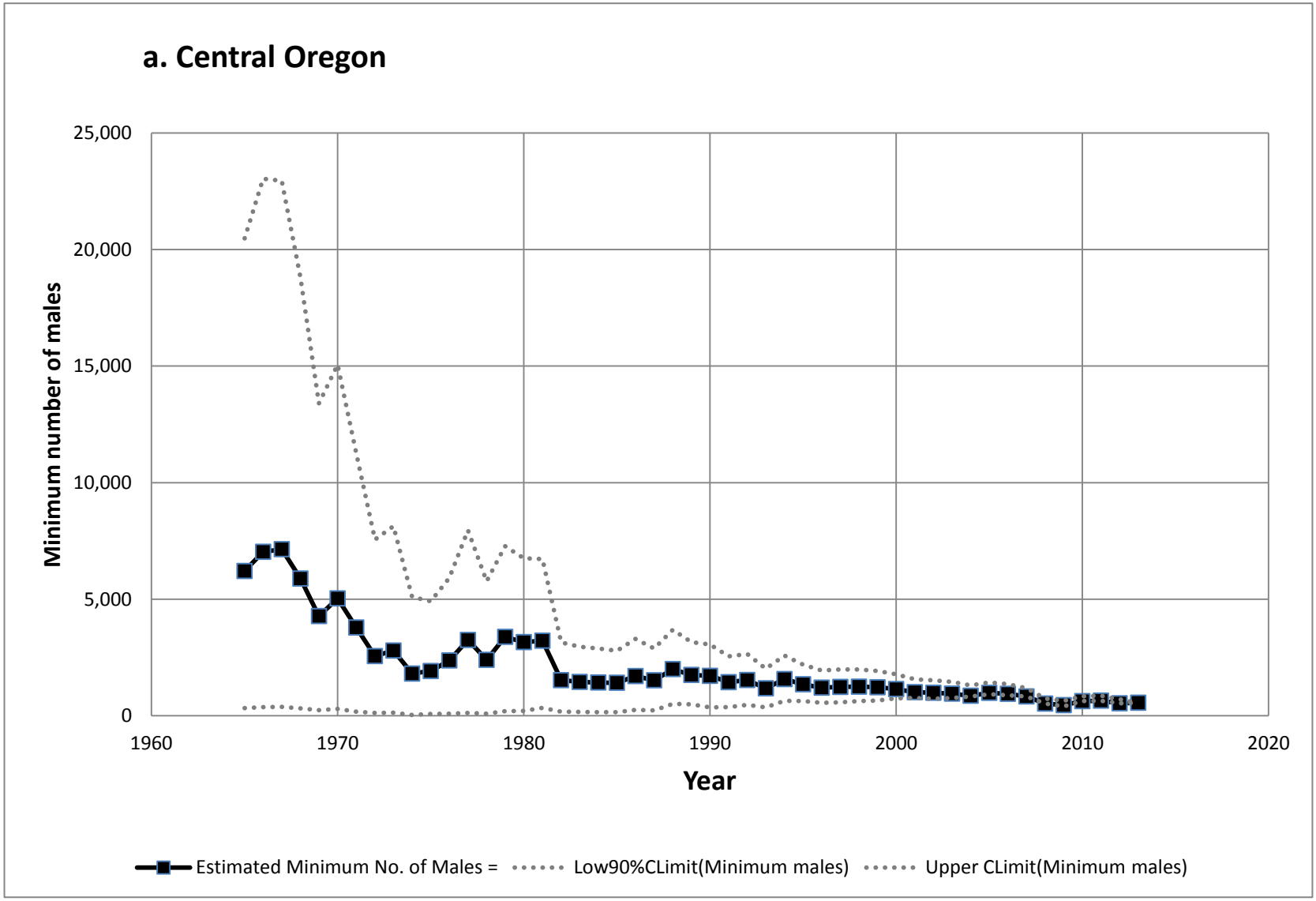
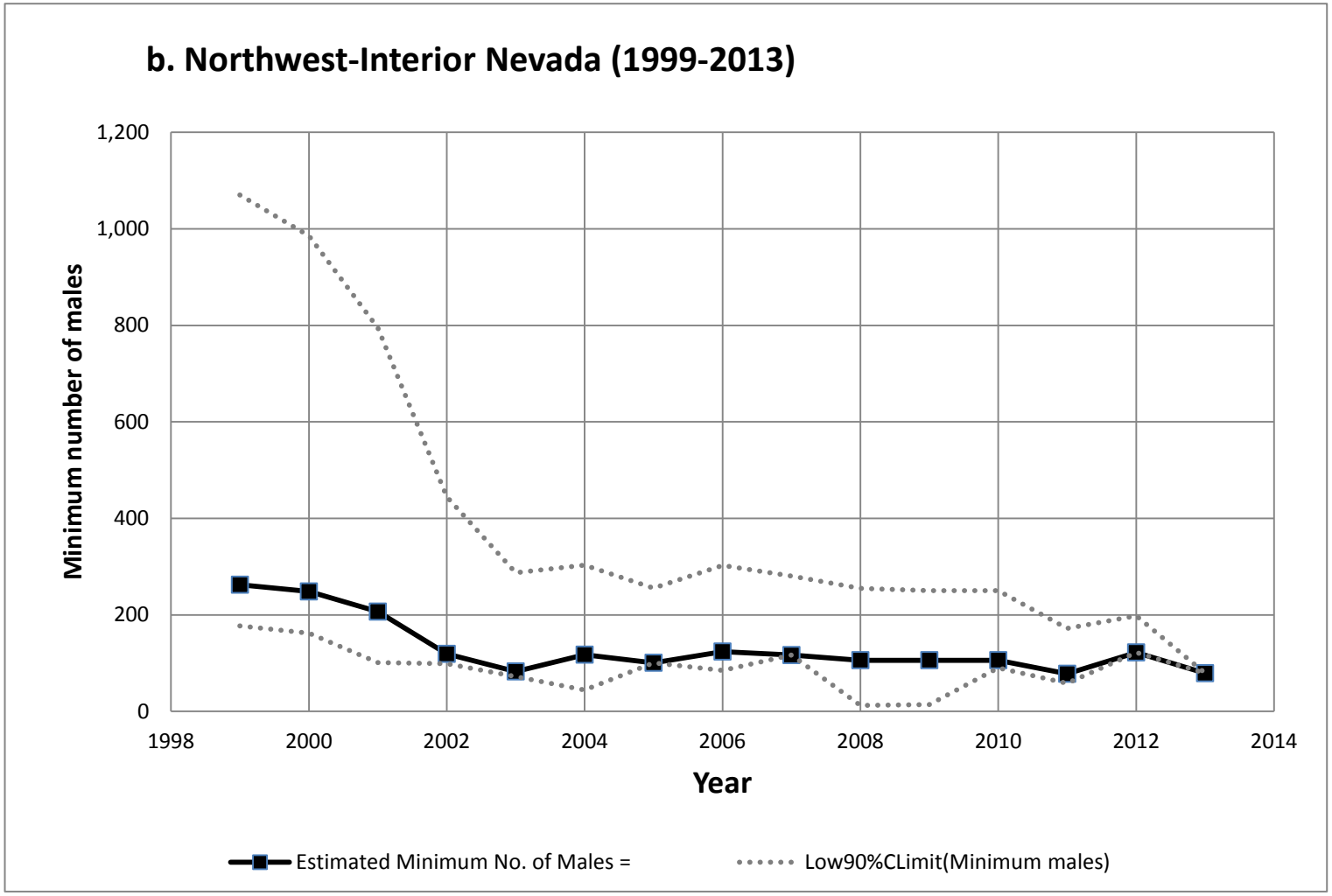
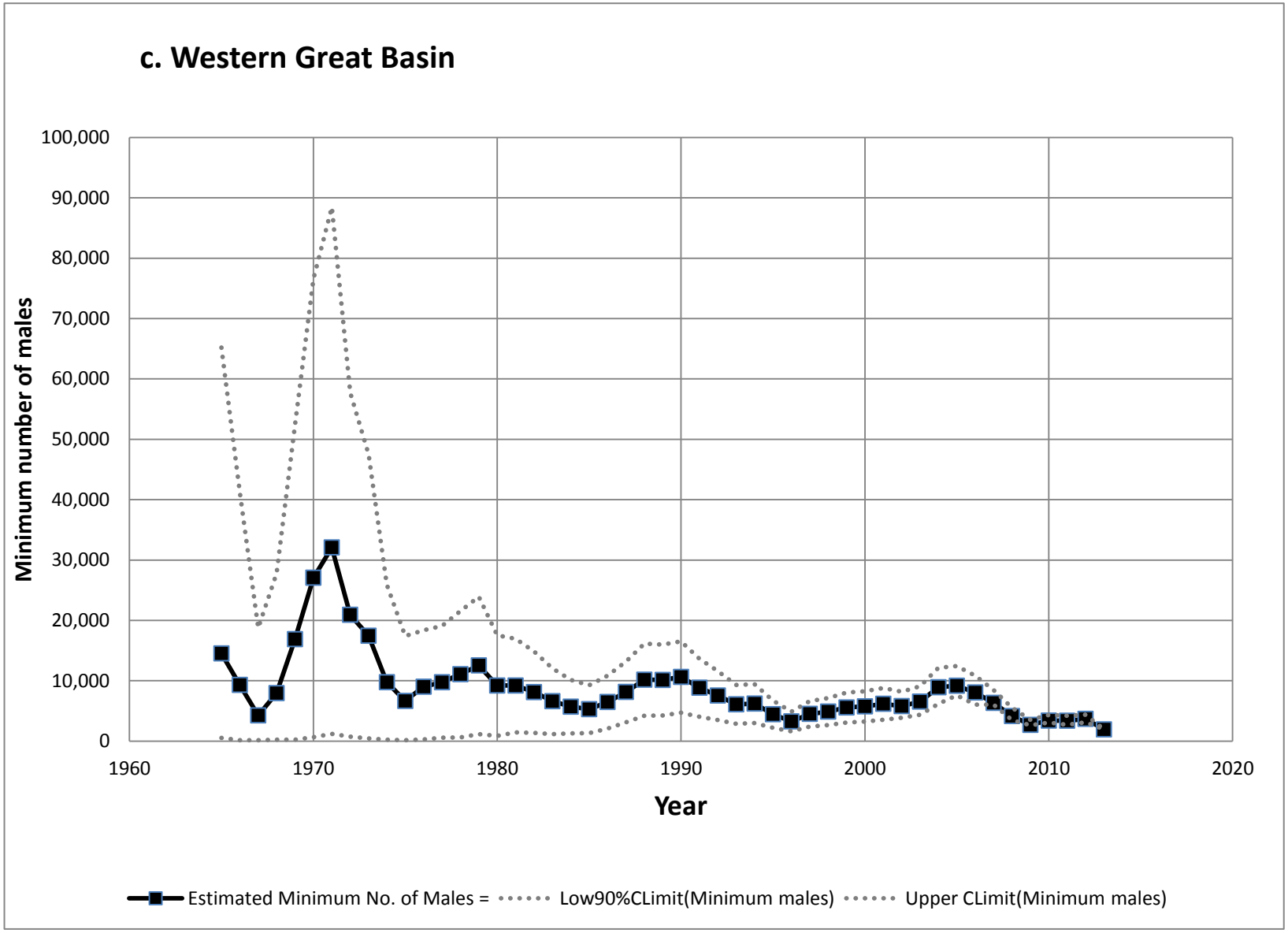

h. Snake River Plain Management Zone - SMZ IV
Minimum number of males
160,000
140,000
120,000
100,000
80,000
60,000
40,000
20,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

Figure 6. Population reconstructions for Northern Great Basin populations and Management Zone V: a. Central Oregon. b. Northwest-Interior Nevada; c. Western Great Basin Core; d. Management Zone V.


a. Central Oregon
25,000
20,000
15,000
10,000
5,000
0
Minimum number of males
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


b. Northwest-Interior Nevada (1999-2013)
Minimum number of males
1,200
1,000
800
600
400
200
0
1998
2000
2002
2004
2006
2008
2010
2012
2014
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)


c. Western Great Basin
Minimum number of males
100,000
90,000
80,000
70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

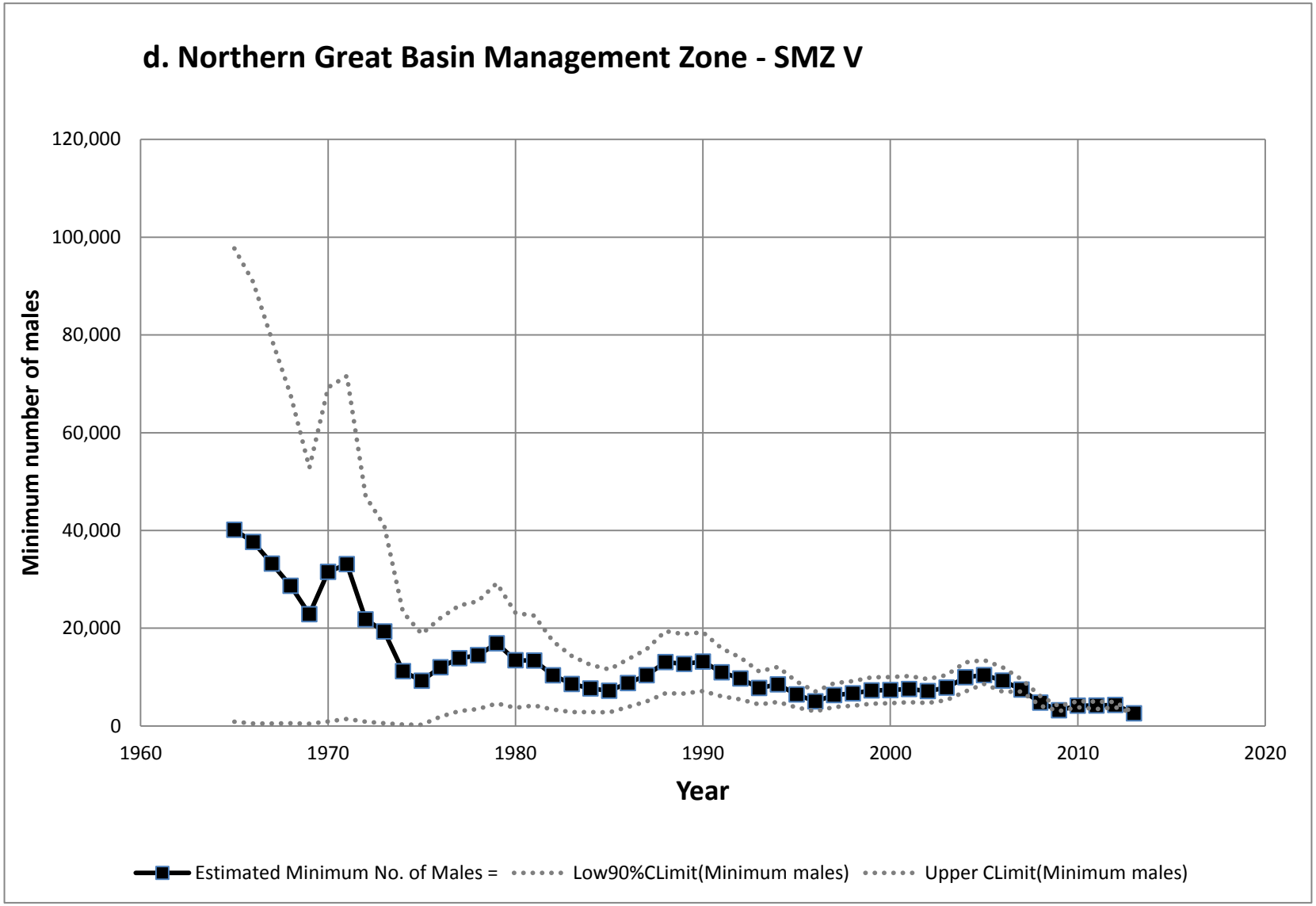
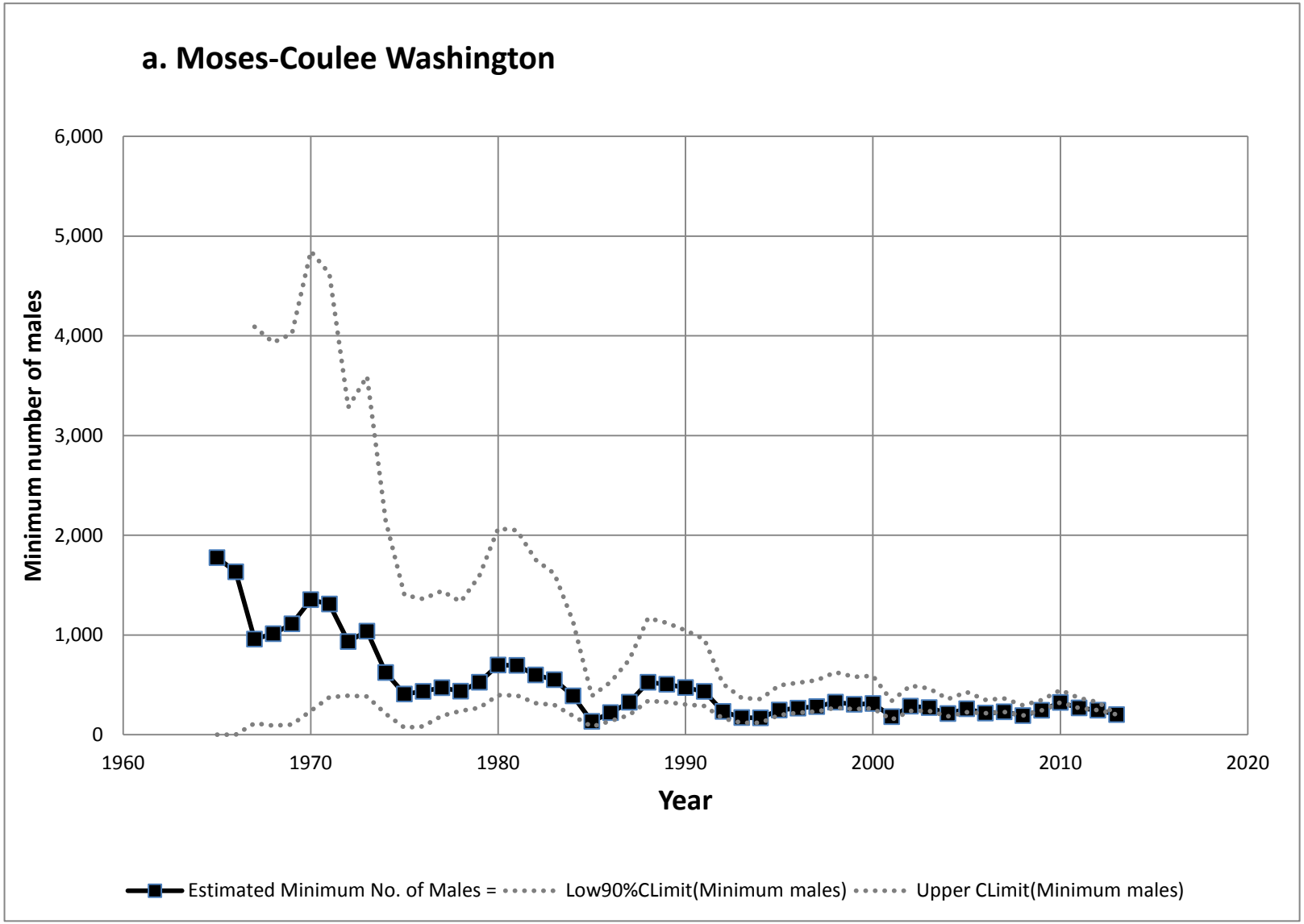
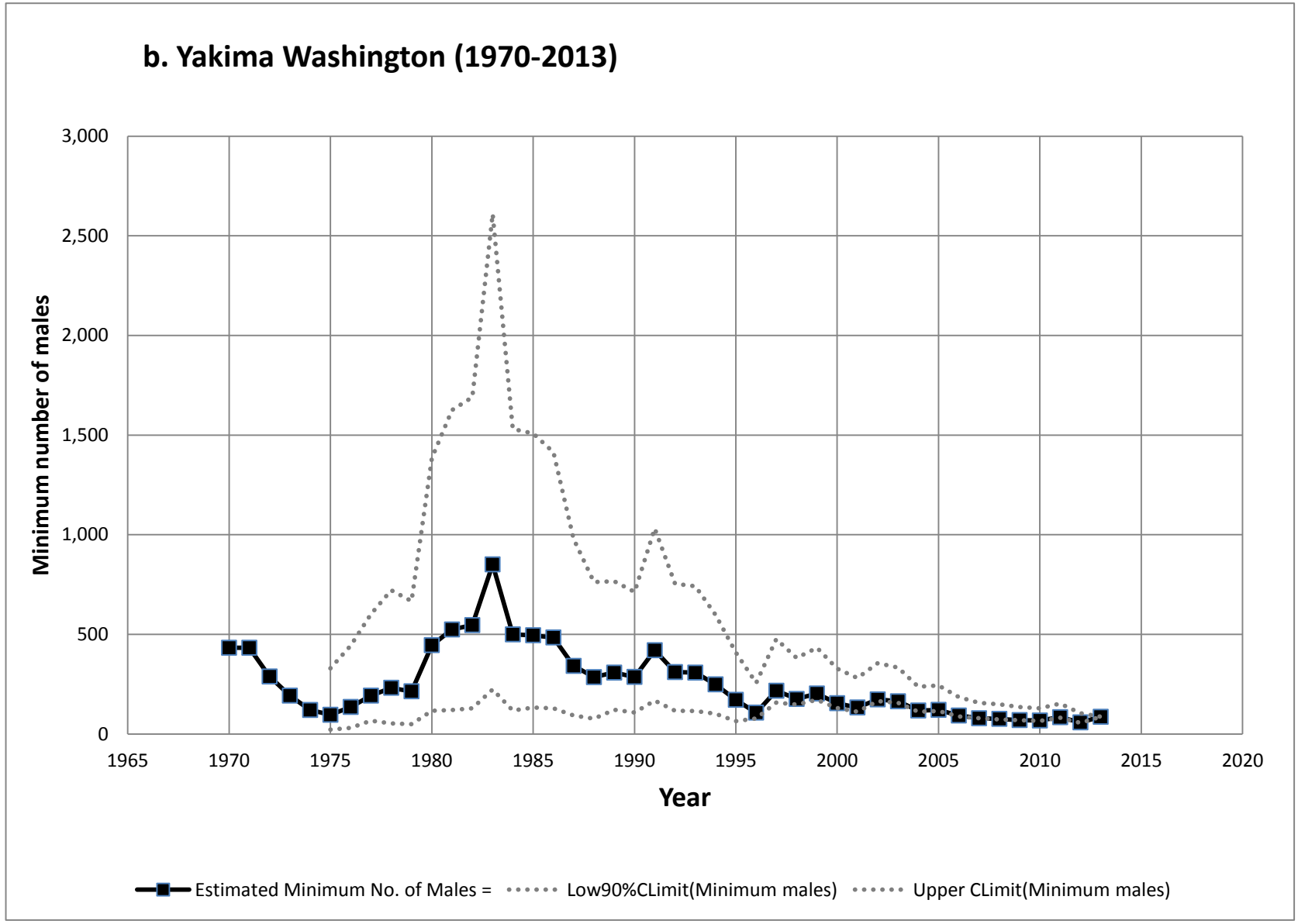

d. Northern Great Basin Management Zone - SMZ V
Minimum number of males
120,000
100,000
80,000
60,000
40,000
20,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

Figure 7. Population reconstructions for Columbia Basin populations and Management Zone VI: a. Moses-Coulee, Washington. b. Yakima, Washington. c. Management Zone VI.


a. Moses-Coulee Washington
Minimum number of males
6,000
5,000
4,000
3,000
2,000
1,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


b. Yakima Washington (1970-2013)
Minimum number of males
3,000
2,500
2,000
1,500
1,000
500
0
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
2015
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

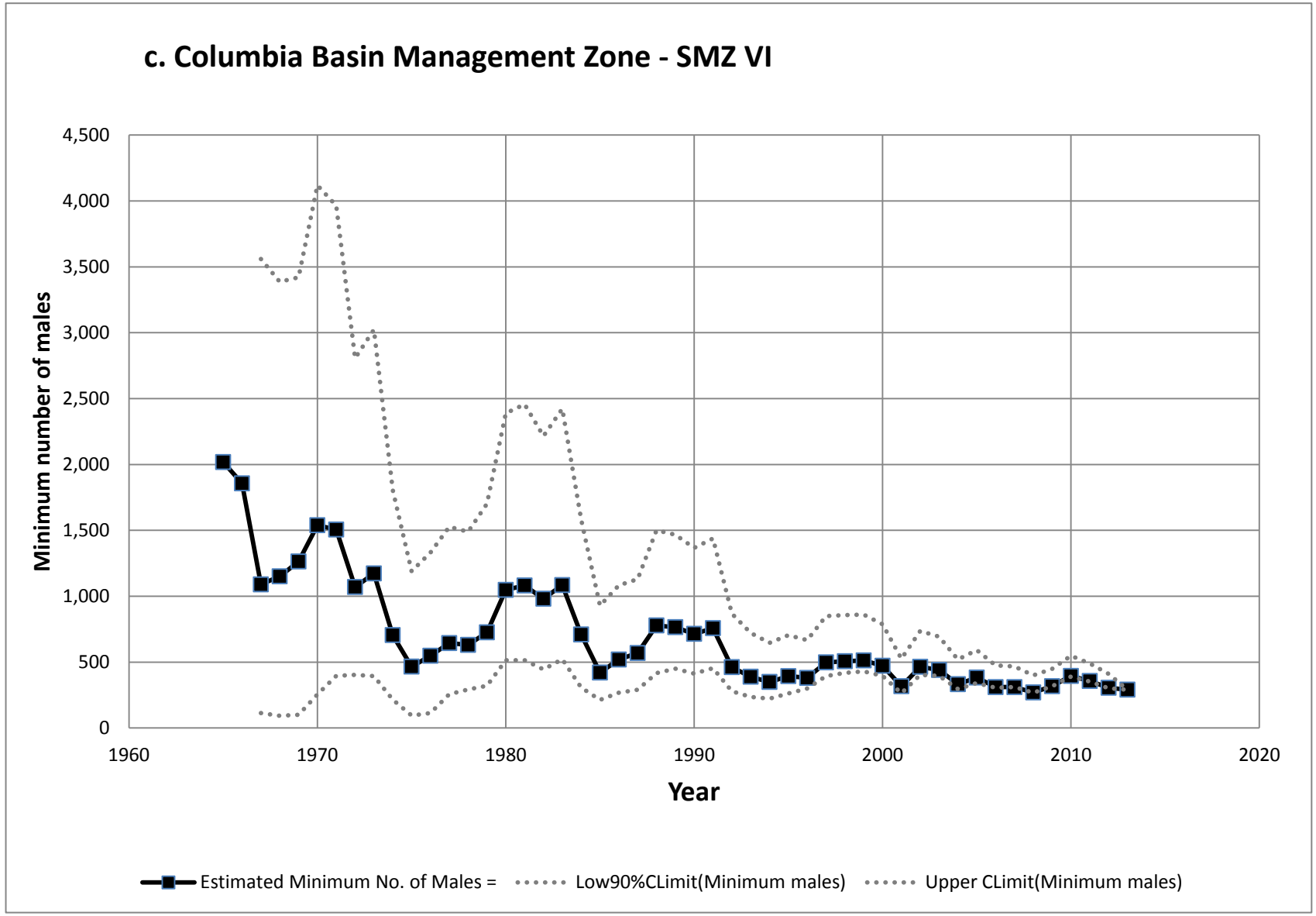

c. Columbia Basin Management Zone - SMZ VI
Minimum number of males
4,500
4,000
3,500
3,000
2,500
2,000
1,500
1,000
500
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

Figure 8. Estimated minimum number of males attending leks from population reconstructions for each management zone and range-wide population of Greater Sage-Grouse from combining total estimates across all Sage-Grouse Management Zones I-VI for period 2007 to 2013. SMZ I –Great Plains = navy blue; SMZII Wyoming Basin =red; SMZIII Southern Great Basin=chartreuse; SMZIV Snake River Plain = black; SMZ V Northern Great Basin = pink; SMZ VI Columbia Basin = light blue; Range-wide = purple.

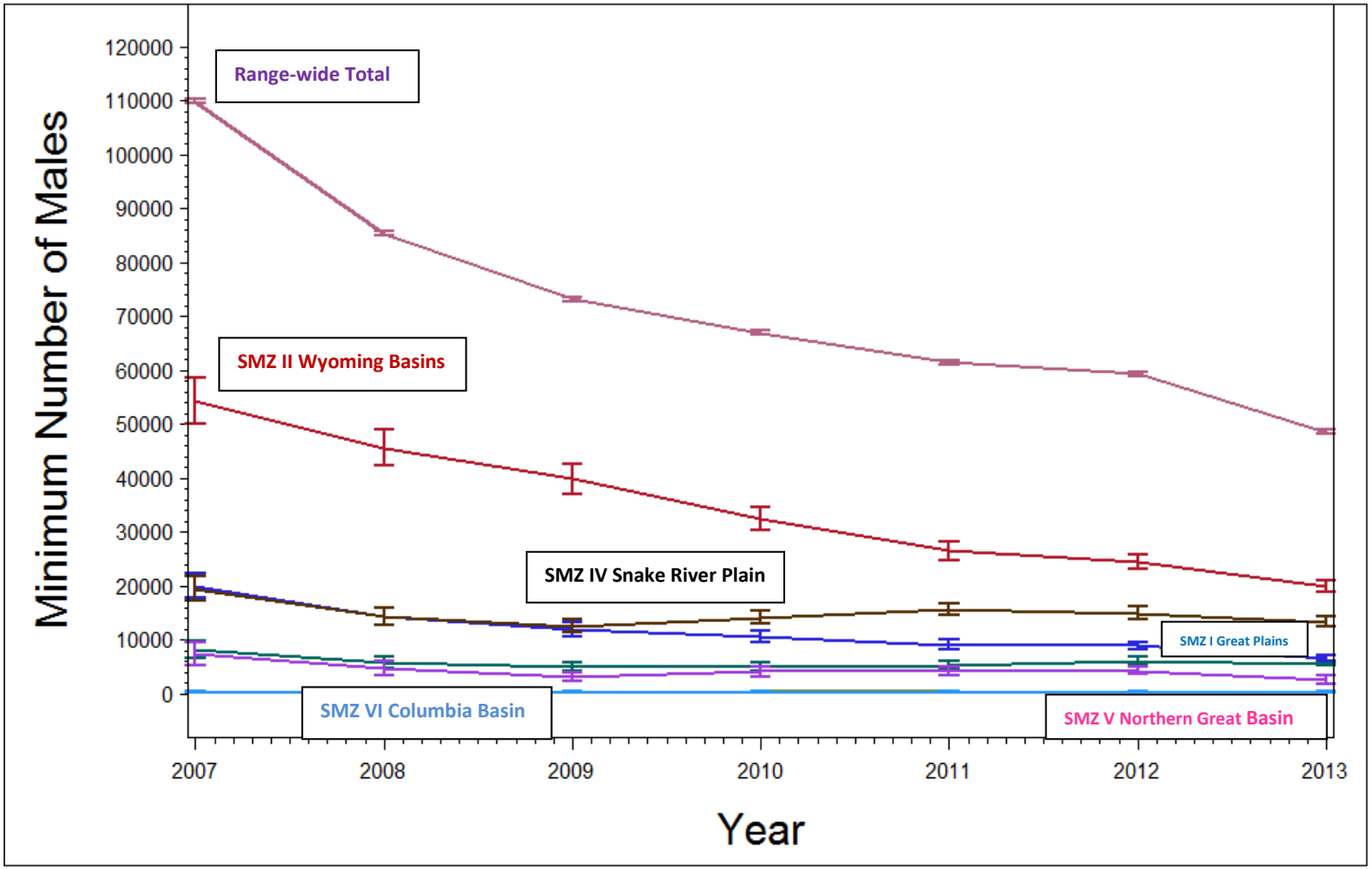


Figure 9. Population reconstruction for range-wide population of Greater Sage-Grouse from combining total estimates across all Sage-Grouse Management Zones I-VI.

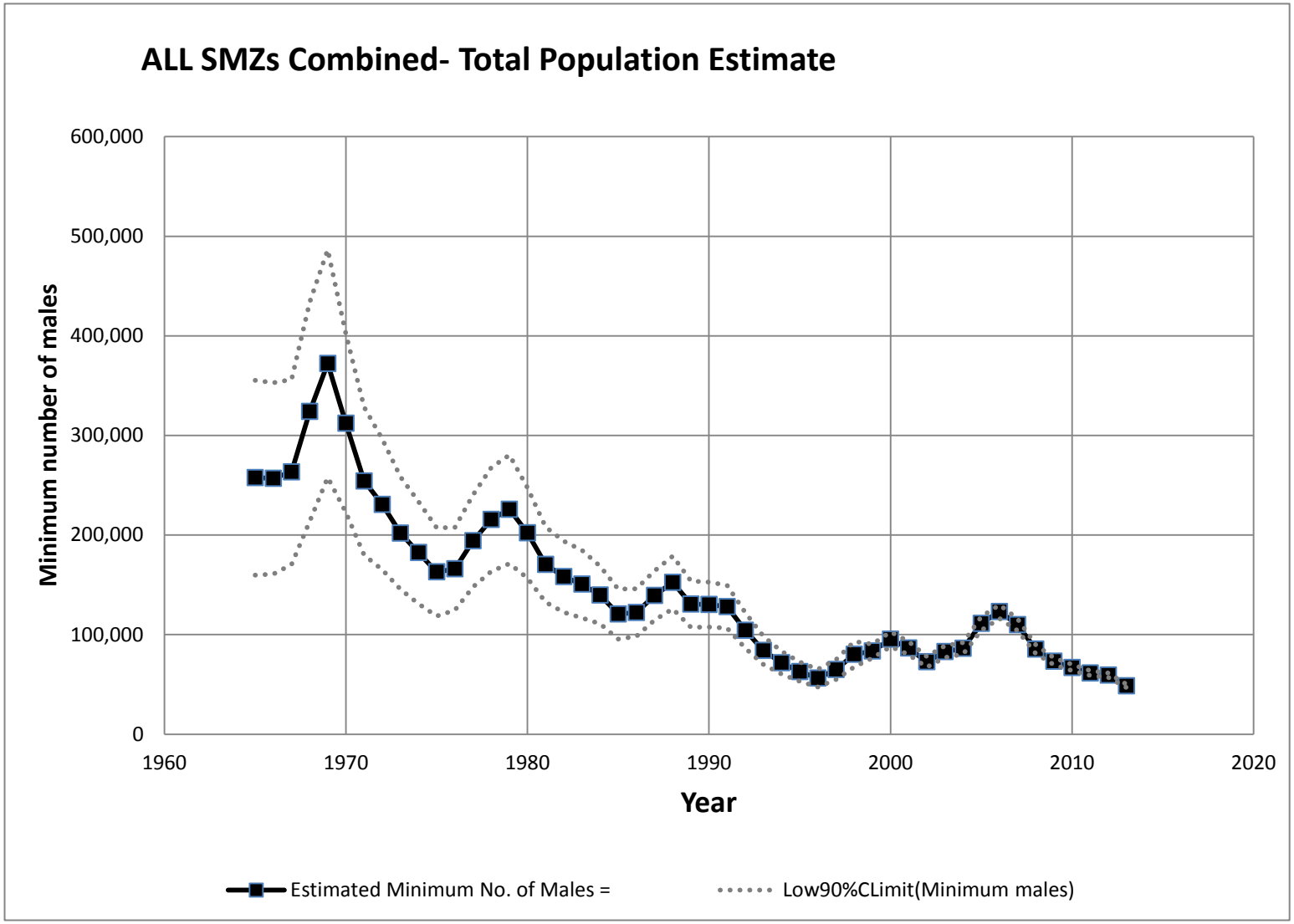
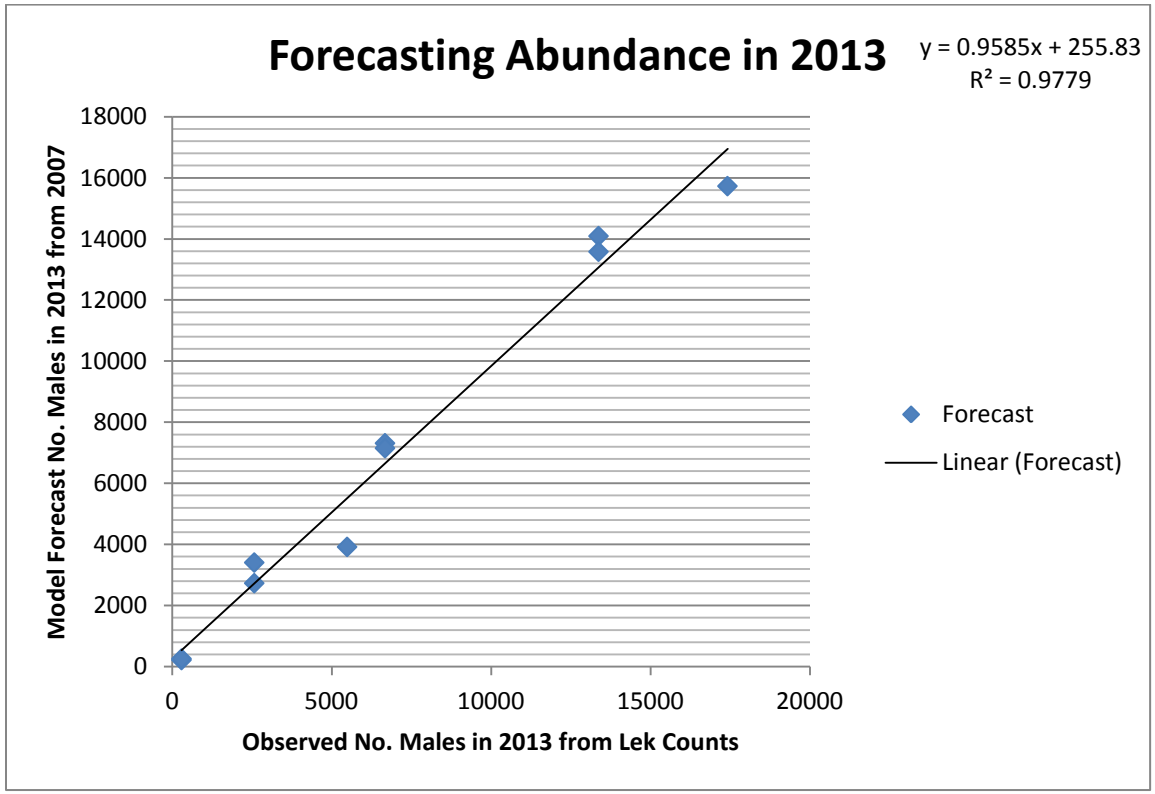


Figure 10. Validation of model predictions by comparing observed abundance in 2013 to forecasts of best models for 2013 estimated from mean rates of change forecast from 2007 to 2013. Note that predictions were tested from the 10 best models in Appendix 2 for all management zones except Colorado Plateau.



M. Scott, eds. Estimating numbers of terrestrial birds. Cooper Ornithol. Soc., Stud. Avian Biol. 6.
U.S. FISH AND WILDLIFE SERVICE. 1988. Nongame bird strategies. Off. Migr. Bird Manage., Washington, D.C. 23pp.
WILEY, J. W. 1979. The white-crowned pigeon in Puerto Rico: status, distribution and movements. J. Wildl. Manage. 43:402–413.
———, AND B. N. WILEY. 1979. The biology of the white-crowned pigeon. Wildl. Monogr. 64. 54pp.
WOOD, D. A. 1992. Official lists of endangered and potentially endangered fauna and flora in Florida. Florida Game and Freshwater Fish Comm., Tallahassee. 25pp.

*Received 5 October 1992.*
*Accepted 18 June 1993.*
*Associate Editor: Sauer.*

# VEGETATIONAL COVER AND PREDATION OF SAGE GROUSE NESTS IN OREGON

MICHAEL A. GREGG, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331-3803
JOHN A. CRAWFORD, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331-3803
MARTIN S. DRUT, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331-3803
ANITA K. DELONG, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331-3803

*Abstract:* Because of long-term declines in sage grouse (*Centrocercus urophasianus*) abundance and productivity in Oregon, we investigated the relationship between vegetational cover and nesting by sage grouse in 2 study areas. Medium height (40–80 cm) shrub cover was greater ($P < 0.001$) at nonpredated ($\bar{x} = 41\%$, $n = 18$) and predated ($\bar{x} = 29\%$, $n = 106$) nests than in areas immediately surrounding nests ($\bar{x} = 15$ and 10%, $n = 18$ and 106, nonpredated and predated, respectively) or random locations ($\bar{x} = 8\%$, $n = 499$). Tall (>18 cm), residual grass cover was greater ($P < 0.001$) at nonpredated nests ($\bar{x} = 18\%$) than in areas surrounding nonpredated nests ($\bar{x} = 6\%$) or random locations ($\bar{x} = 3\%$). There was no difference ($P > 0.05$) in grass cover among predated nests, nest areas, and random sites. However, nonpredated nests had greater ($P < 0.001$) cover of tall, residual grasses ($\bar{x} = 18\%$) and medium height shrubs ($\bar{x} = 41\%$) than predated nests ($\bar{x} = 5$ and 29% for grasses and shrubs, respectively). Removal of tall grass cover and medium height shrub cover may negatively influence sage grouse productivity.

***J. WILDL. MANAGE. 58(1):162–166***

**Key words:** *Centrocercus urophasianus*, habitat, nesting, Oregon, predation, reproduction, sage grouse, selection.

Sage grouse populations declined in several western states from the 1950s through the 1980s (Crawford and Lutz 1985, Klebenow 1985). In Oregon, the decrease in abundance of sage grouse was attributed to impaired productivity (Crawford and Lutz 1985). Reduced productivity may result from several factors, including excessive nest predation (Autenrieth 1981:39). Batterson and Morse (1948) and Nelson (1955) identified predation as the primary factor directly influencing sage grouse nesting success in Oregon. Although predators may be the immediate cause of nest loss, the amount and composition of vegetational cover at nests may influence predation (Bowman and Harris 1980, Redmond et al. 1982). We hypothesized that predation of sage grouse nests in Oregon was related to amount and composition of vegetational structural components surrounding nests. Our objective was to identify vegetational characteristics at nonpredated and predated sage grouse nest sites in comparison with randomly selected locations in 2 areas of southeastern Oregon.

Funds were provided by the Bureau of Land Management through a research contract administered by the Oregon Department of Fish and Wildlife. Logistical support was supplied by the U.S. Fish and Wildlife Service. We acknowledge J. K. Barnett and W. H. Pyle for assistance in data collection. We thank C. E. Braun, J. W. Connelly, R. L. Eng, D. A. Klebenow, K. P. Reese, and T. Rich for reviewing early drafts of this manuscript. This is Technical Paper 9839 of the Oregon Agricultural Experiment Station. Publication of this paper was sup-

ported, in part, by the Thomas G. Scott Achievement Fund.

## STUDY AREAS

We conducted the study in 2 areas of southeastern Oregon: Hart Mountain National Antelope Refuge (Lake County) and Jackass Creek (Harney County). Topography of both areas consisted of flat sagebrush plains interrupted by rolling hills, ridges, and draws. Elevations ranged from 1,500 to 2,450 m at Hart Mountain and from 1,200 to 1,700 m at Jackass Creek. Mean maximum temperature (Mar–Aug) was 21 C at Hart Mountain and 24 C at Jackass Creek. Annual precipitation averaged 29 cm in both areas.

Vegetation at Hart Mountain and Jackass Creek consisted of low sagebrush (*Artemisia arbuscula*), big sagebrush (*A. tridentata*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and western juniper (*Juniperus occidentalis*). Stands of aspen (*Populus tremuloides*), curl-leaf mountain-mahogany (*Cercocarpus ledifolius*), and bitter-brush (*Purshia tridentata*) occurred only at Hart Mountain. Common annual and perennial forbs included mountain-dandelion (*Agoseris* spp.), hawksbeard (*Crepis* spp.), milk-vetch (*Astragalus* spp.), lupine (*Lupinus* spp.), and phlox (*Phlox* spp.). Grasses consisted mainly of bluegrass (*Poa* spp.), bluebunch wheatgrass (*Agropyron spicatum*), needlegrass (*Stipa* spp.), fescue (*Festuca* spp.), giant wildrye (*Elymus cinereus*), and bottlebrush squirreltail (*Sitanion hystrix*) (plant nomenclature from Hitchcock and Cronquist [1987]).

## METHODS

From summer 1988 through spring 1991, we captured (Giesen et al. 1982) female sage grouse during July–August near watering areas and during March–April on and near leks. We fitted each hen with an aluminum leg band and a poncho-mounted, solar-powered radio transmitter with a nickel-cadmium battery (Amstrup 1980). The radio package (radio and poncho) weighed approximately 25 g. Juvenile females captured during summer were not marked with radios. We monitored radio-marked hens 3 times weekly throughout the nesting season with a hand-held antenna and portable receiver. When monitoring indicated a hen initiated a nest, visual confirmation was made without intentionally flushing the hen. Subsequently, we monitored hens remotely to avoid disturbance. When monitoring indicated a hen had ceased nesting efforts, we determined nest fate. We classified nests as nonpredated if $\geq 1$ egg hatched or if incubation exceeded 30 days. Predated nests were identified by the presence of firmly attached shell membranes in broken eggs or by missing eggs.

We measured vegetation in a 78-$m^2$ area (circular area with a radius of 5 m) at nonpredated nest sites after completion of incubation and at predated nest sites on predicted hatch dates. We measured vegetation at randomly selected locations during early May. We located random sites with a random numbers table, which was used to determine starting points, compass bearing, and distance traveled. The number of random locations sampled in each study area was determined by canopy cover of sagebrush and sample size requirements (Snedecor and Cochran 1967:516). We measured canopy cover (%) of shrubs by line-intercept (Canfield 1941) along 2 10-m perpendicular transects intersecting at the nest or random location. The position of the first transect was determined from a randomly selected compass bearing. We placed each intercepted shrub into 1 of 3 height classes: short (<40 cm), medium (40–80 cm), or tall (>80 cm). We based height classes on results of previous studies (Nelson 1955, Wallestad and Pyrah 1974, Autenrieth 1981:17, Wakkinen 1990). Canopy cover of shrubs was recorded separately for each height class. We estimated cover (%) of forbs and grasses in 5 20- × 50-cm plots spaced equidistantly along each transect (Daubenmire 1959). We measured maximum droop height (excluding flowering stalks) of grasses at the nest bush and at random locations throughout each study area and classified grass genera as short (<18 cm) or tall (>18 cm), following results of Wakkinen (1990). We identified shrubs to species and forbs and grasses to genus.

To determine the relationship between vegetational features and predation of sage grouse nests, we apportioned the 78-$m^2$ area in which vegetational measurements were taken at each nest into 2 components: a 3-$m^2$ area at the nest and a 75-$m^2$ area immediately surrounding the nest. We used a factorial analysis of variance (ANOVA) and Student-Newman-Keuls multiple range tests adjusted for unequal sample sizes (Zar 1974:154) to compare vegetational characteristics among plot types (nonpredated nest and nest area, predated nest and nest area, and random location). Study area and year were additional factors in the ANOVA model to account for variation associated with spatial and tem-

poral differences. The only interactions were those for plot type by study area for forb ($P = 0.009$) and tall grass ($P < 0.001$) cover. However, individual ANOVAs coupled with Student-Newman-Keuls multiple range tests for these 2 variables by study area revealed identical patterns of mean separation, which indicated that these vegetational characteristics were not confounded by study area. Consequently, we assumed plot type was independent of study area. We detected no other interactions for any vegetational characteristic. Pearson correlation coefficients were used to test for intercorrelation among variables. All data were normally distributed, and we considered results significant if $P \leq 0.05$.

## RESULTS

During 3 years, we located 124 sage grouse nests (57 at Hart Mountain and 67 at Jackass Creek); 18 of these were nonpredated (11 and 7 at Hart Mountain and Jackass Creek, respectively). Sage grouse nested in big sagebrush, low sagebrush, and mixed sagebrush (mosaic of big and low sagebrush) stands. Of 18 nonpredated nests, 13 were in big sagebrush stands, whereas only 3 and 2 nonpredated nests were in low and mixed sagebrush stands, respectively. Ninety-four percent of all nests from radio-marked hens were under sagebrush. Other vegetation used for nesting included rabbitbrush ($n = 5$), bitterbrush ($n = 1$), and giant wildrye ($n = 1$). Sagebrush collectively represented 87% of the shrub component in both study areas. Other shrubs included bitter-brush (6%), rabbitbrush (4%), horsebrush (*Tetradymia* spp.) (1%), and mountain snowberry (*Symphoricarpos oreophilus*) (1%). Tall grass genera included giant wildrye, wheatgrass, fescue, and needlegrass. Short grass genera consisted of bottlebrush squirreltail, junegrass (*Koleria cristata*), brome (*Bromus* spp.), and bluegrass.

Cover of tall grasses was greater ($P < 0.001$) at nonpredated nests than at predated nests or random locations (Table 1). No differences in grass cover were detected between predated nests and random sites. Except for one case, tall grasses at nonpredated nests were composed of residual cover.

For all nests, shrub cover of medium height was greater ($P < 0.001$) at nests than in the immediate area surrounding nests or random locations (Table 1). However, cover of medium height shrubs was greater ($P < 0.001$) at nonpredated nests than at predated nests. Furthermore, the immediate area surrounding nonpredated nest sites had greater ($P < 0.001$) cover of medium height shrubs than random locations. Shrub cover of short height was greater ($P = 0.02$) at predated nests than at random locations. Amount of tall grass was not correlated with short ($r = -0.06$) or medium ($r = 0.12$) shrub cover.

## DISCUSSION

We found a relationship between vegetational cover and predation of sage grouse nests. Nonpredated nests had greater cover of tall, residual grasses and medium height shrubs than predated nests. No previous research demonstrated the value of residual grass cover at sage grouse nests, although its importance was suggested by Pyrah (1971) and Wakkinen (1990). Wakkinen (1990) reported data about grass height and nest fate but found no relationships. Our data, however, indicated that tall, residual grass cover may enhance sage grouse nest success. Grass cover was identified as an important nesting habitat component for other galliformes, including California quail (*Callipepla californica*) (Leopold 1977: 168), Attwater prairie-chickens (*Tympanuchus cupido attwateri*) (Lehman 1941:14), and plains sharp-tailed grouse (*T. phasianellus jamesi*) (Hillman and Jackson 1973:24). Lehman (1941: 14) noted that all prairie-chicken nests he located were in residual grass cover. The presence of tall, residual grass cover influenced nest site selection and nest predation rates of gray partridge (*Perdix perdix*) in Great Britain (Rands 1982).

We also demonstrated the importance of medium height shrub cover to successful nesting sage grouse. Wallestad and Pyrah (1974) found that successful nests had greater sagebrush cover than unsuccessful nests. Contrastingly, Autenrieth (1981:20) and Wakkinen (1990) found no relationship between canopy cover of sagebrush and nest fate. Hulet et al. (1986) reported that successful nests were located in areas of less shrub cover and shorter height sagebrush than nests that were predated.

Tall, dense, vegetational cover may provide scent, visual, and physical barriers between predators and nests of ground-nesting birds (Bowman and Harris 1980, Redmond et al. 1982, Sugden and Beyersergen 1987, Crabtree et al. 1989). Greater amounts of tall grasses and medium height shrubs at successful sage grouse

Table 1. Vegetational characteristics (% cover) at nonpredated and predated nests and areas immediately surrounding nests of radio-marked sage grouse, and random locations in southeastern Oregon, 1989–91.

| | Nonpredated ($n$ = 18) | | | | Predated ($n$ = 106) | | | | Random ($n$ = 499) | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Nest[a] | | Nest area[b] | | Nest | | Nest area | | | |
| Characteristic | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE |
| Grass cover | | | | | | | | | | |
| Short, <18 cm | 6A[c] | 1.1 | 7A | 1.2 | 6A | 0.7 | 8A | 0.5 | 8A | 0.3 |
| Tall, >18 cm | 18A | 5.5 | 6B | 2.0 | 5B | 1.2 | 3B | 0.6 | 3B | 0.2 |
| Forb cover | 8A | 1.2 | 10A | 1.4 | 9A | 0.9 | 9A | 0.5 | 9A | 0.3 |
| Shrub cover | | | | | | | | | | |
| Short, <40 cm | 14AB | 3.9 | 15AB | 2.7 | 19B | 1.9 | 17AB | 1.0 | 14A | 0.4 |
| Medium, 40–80 cm | 41A | 5.2 | 15B | 3.3 | 29C | 2.1 | 10BD | 1.0 | 8D | 0.4 |
| Tall, >80 cm | 1A | 0.7 | 1A | 0.7 | 4A | 1.2 | 1A | 0.3 | 3A | 0.3 |

[a] 3-m$^2$ area at nest.
[b] 75-m$^2$ area immediately surrounding nest.
[c] Means with same letter within rows were not different $P \geq 0.05$.

nests likely provided the lateral and overhead concealment needed for security from predators. Nests lacking adequate cover were more likely to be predated. Our results confirmed the hypothesis of a relationship between vegetational cover and predation, but further investigation, in the form of controlled experimental tests, is needed to elucidate this principle.

## MANAGEMENT IMPLICATIONS

Land management practices that decrease tall grass and medium height shrub cover at potential nest sites may be detrimental to sage grouse populations because of increased nest predation. Livestock grazing remains the most common and widespread use of rangelands in Oregon and is the principal land management practice and proximate factor that affects grass cover and height (Rickard et al. 1975). Grazing of tall grasses to <18 cm would decrease their value for nest concealment. Land management practices that affect medium height shrub cover include eradication of sagebrush for agricultural production, increased livestock forage, urban development, and mining activities (Klebenow 1972, 1985; Braun et al. 1977). Habitats that support the amount and type of grass cover needed for successful sage grouse nesting typically contain 8–12% shrub cover in Wyoming big sagebrush (*A. t. wyomingensis*) stands and 15–20% shrub cover in mountain (*A. t. vaseyana*) or basin (*A. t. tridentata*) big sagebrush stands (Winward 1991). Management activities should allow for maintenance of tall, residual grasses or, where necessary, restoration of grass cover within these stands.

## LITERATURE CITED

AMSTRUP, S. C. 1980. A radio-collar for game birds. J. Wildl. Manage. 44:214–217.

AUTENRIETH, R. E. 1981. Sage grouse management in Idaho. Idaho Dep. Fish and Game, Boise. Wildl. Bull. 9. 238pp.

BATTERSON, W. M., AND W. B. MORSE. 1948. Oregon sage grouse. Oregon State Game Comm., Portland. Fauna Ser. 1. 29pp.

BOWMAN, G. B., AND L. D. HARRIS. 1980. Effect of spatial heterogeneity on ground-nest depredation. Ecol. Monogr. 38:269–308.

BRAUN, C. E., T. BRITT, AND R. O. WALLESTAD. 1977. Guidelines for maintenance of sage grouse habitats. Wildl. Soc. Bull. 5:99–106.

CANFIELD, R. H. 1941. Application of the line interception method in sampling of range vegetation. J. For. 39:386–394.

CRABTREE, R. L., L. S. BROOME, AND M. L. WOLFE. 1989. Effects of habitat characteristics on gadwall nest predators and nest-site selection. J. Wildl. Manage. 53:129–137.

CRAWFORD, J. A., AND R. S. LUTZ. 1985. Sage grouse population trends in Oregon, 1941–1983. Murrelet 66:69–74.

DAUBENMIRE, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Sci. 33: 224–227.

GIESEN, K. M., T. J. SCHOENBERG, AND C. E. BRAUN. 1982. Methods for trapping sage grouse in Colorado. Wildl. Soc. Bull. 10:224–231.

HILLMAN, C. N., AND W. W. JACKSON. 1973. The sharp-tailed grouse in South Dakota. South Dakota Dep. Game, Fish, and Parks, Pierre. Tech. Bull. 3. 64pp.

HITCHCOCK, C. L., AND A. CRONQUIST. 1987. Flora of the Pacific Northwest. Sixth ed. Univ. Washington Press, Seattle. 730pp.

HULET, B. V., J. T. FLINDERS, J. S. GREEN, AND R. B. MURRAY. 1986. Seasonal movements and habitat selection of sage grouse in southern Idaho. Pages 168–175 *in* E. D. McArthur and B. L. Welch, eds. Proc. symposium of the biology of

*Artemisia* and *Chrysothamnus*. USDA For. Serv. Gen. Tech. Rep. INT-200. 398pp.

KLEBENOW, D. A. 1972. The habitat requirements of sage grouse and the role of fire in management. Proc. Tall Timbers Tire Ecol. Conf. 12:305–315.

———. 1985. Habitat management for sage grouse in Nevada. World Pheasant Assoc. J. 10:34–46.

LEHMAN, V. W. 1941. Attwater's prairie chicken: its life history and management. U.S. Fish and Wildl. Serv. North Am. Fauna 57. 63pp.

LEOPOLD, A. S. 1977. The California quail. Univ. California Press, Berkeley. 281pp.

NELSON, O. C. 1955. A field study of the sage grouse in southeastern Oregon with special reference to reproduction and survival. M.S. Thesis, Oregon State Univ., Corvallis. 113pp.

PYRAH, D. B. 1971. Sage grouse habitat research in central Montana. Proc. West. Assoc. State Game and Fish Comm. 51:293–300.

RANDS, M. R. 1982. The influence of habitat on the population ecology of partridge. Ph.D. Thesis, Univ. Oxford, U.K. 350pp.

REDMOND, G. W., D. M. KEPPIE, AND P. W. HERZOG. 1982. Vegetative structure, concealment, and success at nests of two races of spruce grouse. Can. J. Zool. 60:670–675.

RICKARD, W. H., D. W. URESK, AND J. F. CLINE. 1975. Impact of cattle grazing on three perennial grasses in south-central Washington. J. Range Manage. 28:108–112.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. Sixth ed. Iowa State Univ. Press, Ames. 507pp.

SUGDEN, L. G., AND G. W. BEYERSERGEN. 1987. Effect of nesting cover and density on American crow predation on simulated duck nests. J. Wildl. Manage. 51:481–485.

WAKKINEN, W. L. 1990. Nest site characteristics and spring-summer movements of migratory sage grouse in southeastern Idaho. M.S. Thesis, Univ. Idaho, Moscow. 57pp.

WALLESTAD, R. O., AND D. B. PYRAH. 1974. Movement and nesting of sage grouse hens in central Montana. J. Wildl. Manage. 38:630–633.

WINWARD, A. H. 1991. A renewed commitment to management of sagebrush grasslands. Pages 2–7 *in* Management in the sagebrush steppe. Agric. Exp. Stn. Spec. Rep. 880. Oregon State Univ., Corvallis. 48pp.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J. 620pp.

*Received 29 July 1992.*
*Accepted 20 April 1993.*
*Associate Editor: Morrison.*

# A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats

**Christian A. Hagen, John W. Connelly & Michael A. Schroeder**

Hagen, C.A., Connelly, J.W. & Schroeder, M.A. 2007: A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. - Wildl. Biol. 13 (Suppl. 1): 42-50.

The distribution and range of the greater sage-grouse *Centrocercus urophasianus* have been reduced by 56% since the European settlement of western North America. Although there is an unprecedented effort to conserve the species, there is still considerable debate about the vegetation composition and structure required for nesting and brood-rearing habitat. We conducted a meta-analysis of vegetation characteristics recorded in studies at nest sites (N = 24) and brood habitats (N = 8) to determine if there was an overall effect (Hedge's d) of habitat selection and to estimate average canopy cover of sagebrush *Artemisia* spp., grass and forbs, and also height of grass at nest sites and brood-rearing areas. We estimated effect sizes from the difference between use (nests and brood areas) and random sampling points for each study, and derived an overall effect size across all studies. Sagebrush cover ($d_{++}$ = 0.39; 95% C.I.: 0.19-0.54) and grass height ($d_{++}$ = 0.28; 95% C.I.: 0.13-0.42) were greater at nest sites than at random locations. Vegetation at brood areas had less sagebrush cover ($d_{++}$ = -0.17; 95% C.I.: -0.44 - +0.18), significantly taller grasses ($d_{++}$ = 0.31; 95% C.I.: 0.14-0.45), greater forb ($d_{++}$ = 0.48; 95% C.I.: 0.30-0.67) and grass cover ($d_{++}$ = 0.17; 95% C.I.: 0.08-0.27) than at random locations. These patterns were especially evident when we examined early (< 6 weeks post hatching) and late brood-rearing habitats separately. The overall estimates of nest and brood area vegetation variables were consistent with those provided in published guidelines for the management of greater sage-grouse.

*Key words: Artemisia spp., breeding habitat, effect size, greater sage-grouse, Hedges' d, meta-analysis, sagebrush*

*Christian A. Hagen, Oregon Department of Fish and Wildlife, 61374 Parrell Rd, Bend, Oregon 97701, USA - e-mail: christian.a.hagen@state.or.us*
*John W. Connelly, Idaho Department of Fish and Game, Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, USA - e-mail: jcsagegrouse@aol.com*
*Michael A. Schroeder, Washington Department of Fish and Wildlife, P.O. Box 1077, Bridgeport, Washington 98813, USA - e-mail: schromas@dfw.wa.gov*

*Corresponding author: Christian A. Hagen*

The distribution and range of greater sage-grouse *Centrocercus urophasianus* have been reduced by 56% since the European settlement of western North America (Connelly & Braun 1997, Schroeder et al. 2004). Although loss and fragmentation of sagebrush *Artemisia* spp. habitats have been cited as the primary causes for the decline of the species, degradation of existing habitat also has been con-

sidered an important factor (Braun 1998). Guidelines for protection and management of nesting and brood-rearing habitat have been provided to land managers (Connelly et al. 2000). In general, a range of 15-25% sagebrush, > 10% forb, > 15 % grass canopy cover and, a herbaceous height of 18 cm are needed for breeding habitats of greater sage-grouse.

Techniques used to measure vegetation characteristics have not always been consistent (Wamboldt et al. 2006). Additionally, some researchers and managers have questioned the applicability of management guidelines (Connelly et al. 2000) across the range of the greater sage-grouse, as well as the techniques used to derive the earlier estimates of vegetative cover and height (Bates et al. 2004, Schultz 2004). In particular, subsequent debate over the quantitative properties of the recommended vegetative characteristics required for greater sage-grouse has become a hindrance to implementing conservation actions. To address these concerns and examine the relevance of management guidelines additional analyses are needed. One potential analytical method that was not used when producing the earlier guidelines (Braun et al. 1977, Connelly et al. 2000) was the research synthesis or meta-analysis, which allows an evaluation of the generality of a given effect as a result of combining parameter estimates (effect sizes) from a set of studies (Hall et al. 1994). The use of meta-analysis can advance our knowledge and understanding of observed findings, and contribute to the advancement of more theoretical issues (Hedges & Olkin 1985).

Schultz (2004) analysed the data set in Connelly et al. (2000) and used the analysis to critique the published guidelines. However, since these articles were published, more data have become available. Because the interpretation of earlier research is a fundamental tool in the development of appropriate guidelines to management, we employed meta-analytic techniques to the research summarized by Connelly et al. (2000) as well as research conducted more recently. The purpose of our meta-analysis was to estimate the effect of habitat selection of breeding habitats (i.e. nesting and brood rearing) of greater sage-grouse. To this end we compared vegetation characteristics at use sites to random points, to evaluate the similarity of effect sizes across studies, and to determine if the overall effect size for each vegetation characteristic is statistically or biologically meaningful.

## Methods

### Literature review and data selection

We reviewed peer-refereed articles and graduate research theses (N = 15) and non-refereed agency reports (N = 4) that pertained to greater sage-grouse habitat use during the nesting and brood-rearing periods (Tables 1 and 2). Because studies reported significant differences in vegetation between years (Fischer 1994, Apa 1998, Sveum et al. 1998, Holloran 1999) or study areas (Gregg 1991, Drut 1992, Slater 2003) we estimated effect size for each significant unit. We included estimates from studies that reported actual cover values (e.g. 32.3%) and excluded values from one study (Klott et al. 1993) that used ranked cover values (e.g. 1-5 from Daubenmire (1959) readings). In some studies, a limited number of vegetative characteristics were recorded, thus sample sizes in Tables 1 and 2 vary for each estimate of effect size. We examined the relationship of sagebrush cover, grass cover, forb cover and grass height at nest sites and brood-use sites compared to their respective random points. These variables were consistently reported across studies and provided the largest sample sizes for our comparisons. Several articles reported only shrub cover (e.g. Drut 1992, Gregg 1993, Fischer 1994, Hanf et al. 1994, Sveum et al. 1998), which may have included a mix of sagebrush and other shrubs. Because of limited sample sizes, we estimated effect sizes and parameter estimates for sagebrush only and shrub cover (i.e. sagebrush and other shrub cover) and present results for each. Canopy cover was sometimes estimated with line-intercept or quadrats. However, because we used a standardized metric in our meta-analysis, we could compare studies that used these different methodologies (Hedges & Olkin 1985, Gurevitch & Hedges 1999). Because brood survival rates and habitat use differ between 0-6 weeks post hatching and > 6 weeks post hatching (Holloran 1999, Lyon 2000), we estimated effect sizes for brood-use by early and late periods for studies that differentiated between them. We estimated a pooled effect size for studies that did not differentiate between early and late brood-rearing periods.

### Data analysis

A general equation for an effect size is the treatment mean minus control mean divided by the pooled variance (Hedges 1982). The effect size for each study serves as a dependent variable that can be modeled as a function of discrete or continuous explanatory

Table 1. Studies and vegetation data used in meta-analyses of greater sage-grouse nesting habitats throughout North America. Sagebrush (shrub), grass and forb canopy cover (in %) and grass height (in cm) were vegetation variables considered in the analyses. Vegetation community was described in each study as silver sagebrush (SS), mountain big sagebrush (MT) or Wyoming big sagebrush (WY). ND means that no data were available or had been reported in a manner that was usable in the meta-analysis.

| | | Nest site vegetation | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Study | Vegetation community | N | Shrub cover | SD | Grass cover | SD | Forb cover | SD | Grass height | SD |
| Aldridge 2005 | SS | 93 | 25.46 | 18.52 | 19.56 | 16.59 | 3.82 | 5.30 | 33.94 | 20.25 |
| Aldridge & Brigham 2002 | SS | 29 | 31.90 | 21.92 | 31.90 | 21.33 | 8.10 | 6.03 | 30.90 | 19.28 |
| Apa 1998 (1989) | MT | 11 | 22.00 | 12.60 | 16.20 | 9.95 | 11.50 | 5.64 | 23.00 | 4.97 |
| Apa 1998 (1990) | MT | 10 | 18.80 | 6.32 | 17.00 | 6.01 | 9.00 | 5.06 | 32.40 | 6.01 |
| Apa 1998 (1991) | MT | 18 | 16.70 | 7.64 | 13.50 | 5.09 | 8.60 | 12.73 | 41.90 | 7.64 |
| Fischer 1994 (Postburn) | WY | 67 | 17.90 | 38.08 | 29.30 | 10.64 | 4.30 | 4.09 | 22.10 | 7.37 |
| Fischer 1994 (Preburn) | WY | 71 | 29.00 | 1.20 | 7.20 | 25.85 | ND | ND | 19.80 | 6.74 |
| Gregg 1991(Jackass Creek) | WY | 51 | 56.00 | 22.00 | 11.10 | 10.00 | 12.80 | 11.00 | ND | ND |
| Gregg 1991 (Hart Mountain) | MT | 47 | 51.00 | 15.00 | 18.00 | 20.00 | 6.50 | 5.00 | ND | ND |
| Hanf et al. 1994 | WY | 20 | 44.00 | 8.90 | 15.00 | 8.94 | 5.00 | 8.94 | 22.00 | 13.42 |
| Hausleitner 2003 | MT | 93 | 26.90 | 13.50 | 3.70 | 3.86 | 6.90 | 7.71 | 13.80 | 6.75 |
| Heath et al. 1998 | WY | 42 | 19.00 | 12.90 | 8.20 | 4.73 | 2.04 | 2.33 | 16.60 | 3.56 |
| Holloran 1999 (1997) | WY | 32 | 24.90 | 11.80 | 5.50 | 3.53 | 6.70 | 3.64 | 20.80 | 4.25 |
| Holloran 1999 (1998) | WY | 45 | 25.20 | 9.72 | 4.10 | 1.74 | 7.80 | 3.65 | 17.10 | 2.73 |
| Klott et al. 1993 | WY | 8 | 24.47 | 15.75 | ND | ND | ND | ND | 16.69 | 8.70 |
| Lyon 2000 | WY | 50 | 25.60 | 991 | 10.60 | 11.70 | 8.20 | 9.21 | 21.30 | 4.25 |
| Popham & Gutiérrez 2003 | WY | 40 | 14.50 | 18.97 | 12.50 | 15.81 | ND | ND | 23.10 | 18.97 |
| Schroeder 1995 | WY | 78 | 17.24 | 9.76 | 51.03 | 15.94 | 20.64 | 13.35 | 107.88 | 28.62 |
| Slater 2003 (Collett Creek) | WY | 64 | 22.24 | 11.68 | 6.23 | 3.36 | 7.96 | 6.88 | 18.21 | 3.04 |
| Slater 2003 (Salt Creek) | WY | 21 | 24.80 | 8.29 | 3.26 | 2.84 | 1.33 | 1.47 | 16.23 | 3.16 |
| Sveum et al. 1998 (1992) | WY | 21 | 51.00 | 27.50 | 26.00 | 20.62 | 12.00 | 13.75 | ND | ND |
| Sveum et al. 1998 (1993) | WY | 45 | 59.00 | 26.83 | 27.00 | 20.12 | 21.00 | 20.12 | ND | ND |
| Wakkinen 1990 | WY | 49 | 21.50 | 41.08 | 6.50 | 24.65 | ND | ND | 18.20 | 7.00 |
| Wik 2002 | WY | 38 | 21.00 | 8.63 | 58.00 | 17.88 | ND | ND | 25.00 | 7.40 |

variables or used to estimate a cumulative effect size. The effect size magnitude can be ranked small (0.2), medium (0.5) or large (0.8) standard deviations from a null effect size of zero, as a general rule (Cohen 1969).

We used Hedges' d (Hedges 1982) to estimate effect sizes for sagebrush cover, grass height, grass cover and forb cover for each study because it is conducive to estimating an effect between paired treatments. With E as the treatment group and C as the control, Hedges' d was calculated as:

$$d = \frac{\bar{X}^E - \bar{X}^c}{S} J$$

where S is the pooled standard deviation and the variance ($v = \sqrt{S}$) of Hedges' d is:

$$v = \frac{N^c + N^E}{N^c N^E} + \frac{d^2}{2(N^c + N^E)}$$

and J is the correction for small sample sizes:

$$J = 1 - \frac{3}{4(N^c + N^E - 2) - 1}$$

We estimated cumulative effect size $d_{++}$ as:

$$d_{++} = \frac{\sum_{i=1}^{n} w_i d_i}{\sum_{i=1}^{n} w_i}$$

where the weight $w_i$ for study i is the reciprocal of the variance ($w_i = 1/v$). We used random sites as the 'control' group and use (nests or brood) sites as the 'treatment' group; thus, a positive estimate of d indicates that the variable was greater at use sites than at random points. Confidence limits (95% C.I.) were

Table 2. Studies and vegetation data used in the meta-analyses of greater sage-grouse brood-rearing habitats throughout North America. Sagebrush (shrub), grass and forb canopy cover (in %) and grass height (in cm) were vegetation variables considered in the analyses. Dominant vegetation community was described in each study as silver sagebrush (SS), mountain big sagebrush (MT) and Wyoming big sagebrush (WY). ND means that no data were available or had been reported in a manner that was usable in the meta-analysis.

| | Brood-rearing area vegetation | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Brood period/study | Vegetation community | N | Shrub cover | SD | Grass cover | SD | Forb cover | SD | Grass height | SD |
| Early | | | | | | | | | | |
| Drut 1992 (Hart Mt) | MT | 87 | 23.00 | 8.00 | 15.00 | 7.00 | 11.00 | 7.00 | ND | ND |
| Drut 1992 (Jackass) | WY | 84 | 26.00 | 8.00 | 9.00 | 5.00 | 13.00 | 6.00 | ND | ND |
| Hausleitner 2003 | MT | 31 | 12.70 | 10.02 | 5.80 | 2.78 | 7.50 | 3.90 | 21.70 | 5.57 |
| Heath et al. 1998 | WY | 16 | 14.40 | 8.80 | 12.50 | 13.20 | 2.80 | 2.80 | 16.10 | 4.80 |
| Holloran 1999 | WY | 67 | 15.83 | 8.67 | 5.89 | 5.74 | 9.25 | 4.93 | 18.59 | 4.94 |
| Lyon 2000 | WY | 23 | 21.50 | 7.35 | 14.20 | 18.10 | 8.30 | 9.91 | 23.30 | 4.90 |
| Sveum 1995 | WY | 53 | 11.00 | 7.28 | 17.00 | 21.84 | 22.00 | 14.56 | ND | ND |
| Late | | | | | | | | | | |
| Drut 1992 (Hart Mt) | MT | 38 | 24.00 | 9.50 | 16.00 | 7.00 | 20.00 | 8.00 | ND | ND |
| Drut 1992 (Jackass) | WY | 38 | 29.00 | 15.00 | 8.00 | 5.00 | 8.00 | 6.00 | ND | ND |
| Hausleitner 2003 | MT | 28 | 8.40 | 7.41 | 9.10 | 9.52 | 8.90 | 5.29 | 20.00 | 5.82 |
| Heath et al. 1998 | WY | 22 | 11.10 | 10.79 | 15.60 | 19.23 | 10.10 | 11.73 | 15.60 | 6.10 |
| Holloran 1999 | WY | 59 | 17.40 | 12.10 | 5.26 | 2.83 | 9.01 | 5.17 | 16.53 | 4.35 |
| Sveum 1995 | WY | 19 | 7.00 | 8.72 | 18.00 | 13.08 | 23.00 | 13.08 | ND | ND |
| Both | | | | | | | | | | |
| Aldridge 2005 | SS | 139 | 8.85 | 7.90 | 21.20 | 13.56 | 8.88 | 9.08 | 8.85 | 7.90 |
| Aldridge & Brigham 2002 | SS | 91 | 20.90 | 15.55 | 34.20 | 19.56 | 10.90 | 11.45 | 20.90 | 15.55 |
| Apa 1998 | MT | 49 | 14.10 | 11.90 | 10.00 | 9.80 | 8.00 | 11.20 | 14.10 | 11.90 |
| Klott et al. 1993 | WY | 13 | 16.76 | 5.72 | ND | ND | ND | ND | 10.60 | 11.51 |
| Hausleitner 2003 | MT | 92 | 10.60 | 11.51 | 6.50 | 5.75 | 8.00 | 6.71 | 16.48 | 4.21 |
| Slater 2003 | WY | 13 | 13.50 | 13.41 | 6.81 | 5.77 | 5.45 | 6.20 | 13.50 | 13.41 |
| Wik 2002 | WY | 46 | 15.00 | 10.17 | 50.00 | 14.24 | 16.00 | 10.17 | 20.00 | 6.78 |

estimated for d, and we used bias-corrected bootstrap sampling to estimate confidence limits for $d_{++}$, to account for replicate years or areas within studies. We evaluated the plausibility of using additional explanatory variables to explain the observed differences in effect sizes across studies. The $Q_T$ statistic is based on the total sum of squares and specifically tests for equal effect sizes across studies. If $Q_T$ is greater than would be expected at random ($\chi^2$-distribution), then additional variables (e.g. nest success rates) might help explain the observed variation in the data. We assumed that random variation occurred across nesting studies and estimated effect sizes using random effects models (Hedges 1982). However, we used mixed models to identify if there was a common effect size across brood-rearing periods (categorical data) for each cover type. The basic assumption for this analysis is that random variation occurs among effect sizes within a brood period, but may differ between periods (Gurevitch & Hedges 1999). Here the statistic $Q_B$ can be used to assess the amount of variation accounted for between groups. If $Q_B$ is significantly large, it suggests that effect sizes are larger between groups than expected from random. Applications of mixed-model meta-analysis are uncommon in ecological studies, but likely are the most appropriate for such data sets (Gurevitch & Hedges 1999). All meta-analytic calculations were conducted in MetaWin 2.0 (Rosenberg et al. 2000).

The quality of a research synthesis hinges on the quality of the publications available to analyse, as well as on studies not published because of a lack of significant results (Rosenberg 2005). This is referred to as publication bias and can overestimate the effect size if a large number of non-significant studies are not published or accessible. One of the simplest methods to evaluate the potential impact of publication bias is the calculation of a fail-safe number ($N_+$). A fail-safe number indicates the number of non-significant, unpublished (or missing) studies that would need to be added to a meta-analysis to reduce an overall statistically significant observed result to non-significance (Rosenberg 2005). We estimated fail-safe numbers for each significant effect size using Fail-Safe Number Calculator (Rosenberg 2005), and considered an effect size robust if $N_+ > 5N + 10$, where N is the observed number of studies used to estimate the effect size.

To add biological relevance to the meta-analysis, we used a weighted general linear model (PROC GLM; SAS Institute 2000) and estimated the mean and 95% C.I. for sagebrush cover, grass cover, forb cover and grass height at nest and brood-use sites.

## Results

### Effect sizes

Greater sage-grouse females selected nest sites with generally more sagebrush cover ($d_{++}$ = 0.39; 95% C.I.: 0.19-0.54) and taller grass height ($d_{++}$ = 0.28; 95% C.I.: 0.15-0.41) than random sites (Fig. 1). Grass ($d_{++}$ = 0.13; 95% C.I.: -0.03 - +0.25) and forb cover ($d_{++}$ = 0.15; 95% C.I.: -0.06 - +0.37) were greater at nest sites, but neither effect was significantly large. An examination of $Q_T$ indicated that d was homogenous ($P > 0.2$) among studies for each variable and that additional information would not explain the observed effect sizes (Table 3). Shrub cover had a larger effect size than sagebrush only ($d_{++}$ = 0.74; 95% C.I.: 0.39-1.13).

Vegetation at brood areas combined among all periods had greater forb cover ($d_{++}$ = 0.46; 95% C.I.: 0.30-0.66), grass cover ($d_{++}$ = 0.19; 95% C.I.: 0.09-0.30), significantly taller grasses ($d_{++}$ = 0.29; 95% C.I.: 0.13-0.42), and less sagebrush cover ($d_{++}$ = -0.17; 95% C.I.: -0.44 - +0.18) than random locations (see Fig. 1). However, females exhibited some variation in habitat selection for sagebrush between these periods ($Q_B$ = 6.12, df = 2, P = 0.046). Generally, early brood-use areas were comprised of greater forb cover ($d_{++}$ = 0.57; 95% C.I.: 0.23-0.80), grass cover ($d_{++}$ = 0.27; 95% C.I.: 0.11-0.50), and taller grass ($d_{++}$ = 0.39; 95% C.I.: 0.26-0.60), but less sagebrush cover ($d_{++}$ = -0.46; 95% C.I.: -0.75 - -0.19) than random sites. Effect size for shrub cover changed moderately when using all studies ($d_{++}$ = -0.61; 95% C.I.: -0.95 - -0.31). During late brood rearing, forb cover ($d_{++}$ = 0.55; 95% C.I.: 0.23-0.79) and grass cover ($d_{++}$ = 0.16; 95% C.I.: 0.05-0.30) were greater at use sites, but sagebrush cover ($d_{++}$ = -0.08; 95% C.I.: -0.48 - +0.12) and shrub cover ($d_{++}$ = -0.04; 95% C.I.: -0.31 - +0.15) were similar between use and random sites. For studies that pooled estimates across both periods, forb cover was greater ($d_{++}$ = 0.27; 95% C.I.: 0.04-0.54) and grass height taller ($d_{++}$ = 0.34; 95% C.I.: 0.20-0.48) than at random sites. Sagebrush cover ($d_{++}$ = 0.15; 95% C.I.: -0.36 - +0.77) and grass cover ($d_{++}$ = 0.11; 95% C.I.: -0.01 - +0.32) were greater at brood use areas but neither of these factors was significant. Examination of $Q_T$ values indicated that effect sizes were homogenous ($P > 0.25$) except for shrub cover, and additional explanatory variables would not explain variation in effect sizes across all studies (see Table 3). The test of heterogeneity is conservative with small sample sizes and therefore interpreted in an appropriately conservative manner.

### Publication bias

We conducted fail-safe calculations for 12 effect sizes that were significant (see Table 3). The effect size of disproportional use of sagebrush and grass height was robust for nest sites as was forb cover at early and late brood-rearing areas (see Table 3). Grass cover and height effect sizes for brood-rearing areas were not

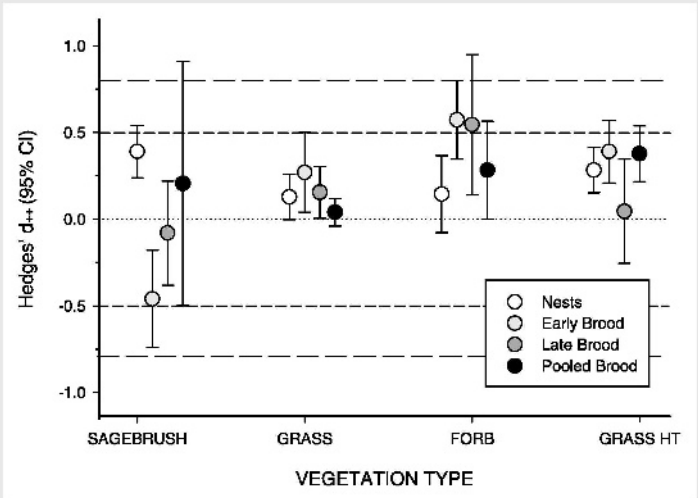



Figure 1. Cumulative effect sizes ($d_{++}$) by vegetation types and across nesting and brood-rearing habitats. Long-dashed lines indicate large ($d > 0.8$), small-dashed lines indicate medium ($0.8 \geq d > 0.5$), and dotted line indicates small ($0 < d < 0.5$) effects. Significant positive and negative effects indicate selection for or against a vegetation type, respectively. Estimates with 95% C.I. including 0, indicate no effect of habitat selection.

Table 3. Estimates of vegetation characteristics at greater sage-grouse use sites from 19 studies across the species range, and diagnostic statistics ($Q_T$, $N_+$) for meta-analysis. Means and confidence intervals were derived from a weighted mean linear model where the inverse of the variance was the weighting factor. The 'early' period was defined as brood habitat used < 6 weeks post hatching, the 'late' period as > 6 weeks post hatching, and 'both' were studies that pooled estimates across both periods. An asterisk (*) indicates that a fail-safe number ($N_+$) is robust (> 5N + 10). The fail-safe number is equivalent to the number of studies of null effect and mean weight necessary to reduce the observed significance level to $\alpha = 0.05$.

| | | | Parameter estimates | | Diagnostics | | | |
|---|---|---|---|---|---|---|---|---|
| Cover type | Period | N | $\bar{x}$ | 95% C.I. | $Q_T$ | df | P | Fail safe ($N_+$) |
| Forb (%) | Nest | 19 | 4.02 | 2.05-5.99 | 21.3 | 18 | 0.27 | NA |
| | Early | 7 | 6.74 | 3.91-9.56 | 4.5 | 6 | 0.61 | 94* |
| | Late | 6 | 10.78 | 6.50-15.06 | 5.3 | 5 | 0.38 | 49* |
| | Both | 6 | 8.51 | 2.92-14.10 | 4.4 | 5 | 0.50 | 13 |
| Grass (%) | Nest | 23 | 6.75 | 4.53-8.98 | 25.9 | 22 | 0.26 | NA |
| | Early | 7 | 7.56 | 4.35-10.76 | 7.5 | 6 | 0.28 | 14 |
| | Late | 6 | 7.57 | 4.17-10.98 | 3.6 | 5 | 0.61 | 1 |
| | Both | 6 | 11.44 | 5.79-17.10 | 5.4 | 5 | 0.38 | NA |
| Sagebrush (%) | Nest | 19 | 21.51 | 19.91-23.93 | 13.7 | 16 | 0.62 | 270* |
| | Early | 4 | 16.84 | 9.59-24.08 | 3.2 | 3 | 0.37 | 14 |
| | Late | 3 | 10.92 | 1.67-20.16 | 1.9 | 2 | 0.38 | NA |
| | Both | 7 | 14.15 | 8.39-19.92 | 5.1 | 6 | 0.53 | NA |
| Shrub cover (%) | Nest | 24 | 25.13 | 20.35-29.91 | 35.3 | 23 | 0.05 | 1133* |
| | Early | 7 | 18.07 | 13.31-22.83 | 5.3 | 6 | 0.50 | 204* |
| | Late | 6 | 13.71 | 7.53-19.88 | 5.3 | 5 | 0.38 | NA |
| Grass height (cm) | Nest | 20 | 19.77 | 17.36-22.18 | 16.6 | 19 | 0.61 | 193* |
| | Early | 4 | 19.78 | 15.91-23.65 | 2.8 | 3 | 0.41 | 5 |
| | Late | 3 | 17.24 | 12.58-21.90 | 1.6 | 2 | 0.45 | NA |
| | Both | 7 | 19.16 | 15.17-23.15 | 7.5 | 6 | 0.28 | 40 |

robust for missing studies. However, these were relatively small effect sizes (see Fig. 1). The effect size of sagebrush cover at brood-rearing areas was robust.

### Parameter estimates

Sagebrush canopy cover was apparently greater at nest sites (21.5%) than at brood areas (< 16.9%; see Table 3). Combined forb (4.1%) and grass cover (6.5%) was less at nest sites than at brood areas (forb > 6.7%, grass > 7.6%). However, grass height was comparable (~19 cm) in nest and brood areas. During brood rearing, sagebrush cover decreased from early to late periods, forb cover increased, whereas grass cover and height did not change appreciably (see Table 3).

## Discussion

Our study provides the first quantitative assessment of available data for greater sage-grouse habitat selection during the nesting and brood-rearing periods. We found a general effect for habitat selection across the range of these studies, as evidenced by low levels of variation in effect sizes across studies and regions. Many of our estimated effect sizes were robust to the potential impacts of publication bias, lending considerable support to the generality of our findings. There was a medium to large effect (d = 0.37-0.74) of selection for vegetation characteristics, with greater sagebrush cover for nest concealment and forb cover for females with broods. There were smaller effects (d ~ 0.2) for selection of grass height and cover by nesting and brood-rearing females. The variation of effect sizes in sagebrush cover was more substantial between brood periods, signifying a seasonal shift in habitat use.

### Effect sizes

Because random variation was as expected, we can infer that greater sage-grouse females were selecting for similar nesting vegetation (greater sagebrush cover, grass cover and/or taller grasses) throughout the geographic range of these studies. This quantitative assessment supports earlier qualitative reviews of sage-grouse habitat requirements during the nesting period (Braun et al. 1977, Connelly et al. 2000) that suggested the importance of sagebrush and grass cover as well as grass height. Our study also indicated the importance of reporting sagebrush cover separately from other shrub species as there was a moderate

change in effect size and increase in variance of effect size, when comparing studies reporting sagebrush versus shrub cover. Although the measurement of grass height has only recently been standardized (Connelly et al. 2003), we identified an overall selection for taller grasses at nest sites. Additionally, the relatively small selection effect of greater grass cover may have been confounded with grass height. Many short stature grasses may have been included in the estimates of grass cover, and may contribute to the relatively small effect size of grass cover at use sites.

Brood females selected early and late habitats with less sagebrush cover and greater herbaceous cover (grass and forbs) than random sites. This generalized effect for greater herbaceous cover during brood rearing is likely a result of mesic plant communities with an abundance of invertebrates and foods that are critical to the growth and development of chicks (Johnson & Boyce 1991, Drut et al. 1994). Alternatively, this effect may have been correlated with broods seeking habitats with less shrub cover and greater understory in more xeric sites. Taller grasses were selected more so during early brood rearing than during late brood rearing. The proximity of early brood rearing to nesting sites may have contributed to this result, or because females were selecting sites with less sagebrush cover, the use of taller grasses may have provided greater vertical screening and protection. However, as broods mature tall stature grasses appeared to become less important, as did sagebrush cover. For studies that pooled vegetation measurements across both brood periods the effect sizes were generally small and may have been confounded by potential effects between early and late broods. Sagebrush cover was greater at brood use sites for pooled studies and was likely due to selection for silver sagebrush *A. cana* sites in Alberta where the extent of sagebrush could be a limiting factor (Aldridge & Brigham 2002, Aldridge 2005).

## Publication bias

Generally, our findings were robust to publication bias with respect to vegetation needs for each life stage. Our evaluation of potential impacts of publication bias indicated that habitat usage by greater sage-grouse at nest sites was robust for sagebrush cover and grass height, each effect requiring two to several hundred studies of 'no effect' to nullify our results. Similarly, our estimated effects of less shrub cover and greater forb cover during brood rearing were robust to publication bias. The effects of grass cover were relatively small and more susceptible to non-significant or missing studies. These findings may help guide future work to identify vegetation characteristics that should be evaluated more carefully and perhaps reduce some of this ambiguity (e.g. grass cover).

## Parameter estimates

The weighted average of cover and height values were within the range specified by the greater sage-grouse management guidelines for breeding habitats (Connelly et al. 2000). Our analysis indicated that the range (95% C.I.s) of vegetation measurements encompassed those in the guidelines published by Connelly et al. (2000), recommending 15-25% sagebrush cover, $>$ 10% forb cover, $>$ 15% grass cover and $\geq$ 18-cm grass height (see Table 3). Estimates of sagebrush were not markedly different when we included studies that reported only shrub cover. Despite criticisms of the established guidelines (Bates et al. 2004, Schultz 2004), our quantitative analysis that includes new data published after 2000 strongly suggests that these values for describing breeding habitats are reasonable. Because these measurements are generally recorded over relatively small scales ($<$ 30 m), identifying the appropriate proportions of these vegetative characteristics in a larger landscape is paramount (Bates et al. 2004).

## Conclusions and recommendations

The magnitude of effects sizes combined with the parameter estimates in our meta-analyses demonstrated a shift in habitat selection by females between nesting and brood-rearing periods, primarily a shift in sagebrush and forb canopy cover. However, most studies have not quantified the spatial distribution or juxtaposition of these vegetative communities. Understanding the optimum mix and spatial arrangement of these communities and their effects on demographic rates in a landscape could substantially enhance management of the greater sage-grouse. More importantly, studies of breeding habitats need to begin to examine the relationship between vegetative communities, landscape metrics (e.g. habitat patch size, fragmentation and distance to roads) and demographic rates. Similarly, as more studies begin to compare vegetation and other differences between successful and unsuccessful nests, a meta-analysis could prove useful in identifying a general effect for factors contributing to nest success.

*Acknowledgements* - many biologists and ecologists from state and federal natural resources agencies provided useful

insight and encouraged us to write this paper. We appreciate their support. We thank the Oregon Department of Fish and Wildlife, Idaho Department of Fish and Game, and Washington Department of Fish and Wildlife for supporting our efforts in this work. This is a contribution from Idaho Federal Aid in Wildlife Restoration Project W-160-R and Washington Federal Aid in Wildlife Restoration. M.J. Holloran, L. Ellison and three anonymous reviewers provided comments that greatly enhanced the quality of this manuscript.

## References

Aldridge, C.L. 2005: Identifying habitats for persistence of greater sage-grouse (Centrocercus urophasianus) in Alberta, Canada. - PhD thesis, University of Alberta, Edmonton, Canada, 250 pp.

Aldridge, C.L. & Brigham, R.M. 2002: Sage-grouse nesting and brood habitat use in southern Canada. - Journal of Wildlife Management 66: 433-444.

Apa, A.D. 1998: Habitat use and movements of sympatric sage and Columbian sharp-tailed grouse in southeastern Idaho. - PhD thesis, University of Idaho, Moscow, USA, 199 pp.

Bates, J., Davies, K. & Miller, R. 2004: Ecology of the Wyoming big sagebrush alliance in the northern Great Basin: 2004 Progress Report. - Eastern Oregon Agricultural Research Center, Burns, Oregon, USA, 65 pp.

Braun, C.E. 1998: Sage grouse declines in western North America: what are the problems? - Transactions of Western Association of Fish and Wildlife Agencies 78: 139-156.

Braun, C.E., Britt, T. & Wallestad, R.O. 1977: Guidelines for maintenance of sage grouse habitats. - Wildlife Society Bulletin 5: 99-106.

Cohen, J. 1969: Statistical power analysis for the behavioral sciences. - Erlbaum, Hillsdale, New Jersey, USA, 567 pp.

Connelly, J.W. & Braun, C.E. 1997: Long-term changes in sage grouse Centrocercus urophasianus populations in western North America. - Wildlife Biology 3: 229-234.

Connelly, J.W., Schroeder, M.A., Sands, A.R. & Braun, C.E. 2000: Guidelines to manage sage grouse populations and their habitats. - Wildlife Society Bulletin 28: 967-985.

Connelly, J.W., Reese, K.P. & Schroeder, M.A. 2003: Monitoring of greater sage-grouse habitats and populations. - College of Natural Resources Experiment Station Bulletin 80, University of Idaho, Moscow, USA, 50 pp.

Daubenmire, R. 1959: A canopy-coverage method of vegetational analysis. - Northwest Science 33: 43-64.

Drut, M.S. 1992: Habitat use and selection by sage grouse broods in southeastern Oregon. - M.Sc. thesis, Oregon State University, Corvallis, USA, 44 pp.

Drut, M.S., Crawford, J.A. & Gregg, M.A. 1994: Brood habitat use by sage grouse in Oregon. - Great Basin Naturalist 54: 170-176.

Fischer, R.A. 1994: The effects of prescribed fire on the ecology of migratory sage grouse in southeastern Idaho. - PhD thesis, University of Idaho, Moscow, USA, 150 pp.

Gregg, M.A. 1991: Use and selection of nesting habitat by sage grouse in Oregon. - M.Sc. thesis, Oregon State University, Corvallis, USA, 46 pp.

Gurevitch, J. & Hedges, L.V. 1999: Statistical issues in ecological meta-analyses. - Ecology 80: 1142-1149.

Hall, J.A., Rosenthal, R., Tickle-Degnen, L. & Mosteller, F. 1994: Hypotheses and problems in research synthesis. - In: Cooper, H. & Hedges, L.V. (Eds.); The Handbook of research synthesis. Russell Sage Foundation, New York, USA, pp. 17-28.

Hanf, J.M., Schmidt, P.A. & Groshens, E.B. 1994: Sage grouse in the high desert of central Oregon: results of a study, 1988-1993. - Bureau of Land Management, Portland, Oregon, USA, 67 pp.

Hausleitner, D. 2003: Population dynamics, habitat use and movements of greater sage-grouse in Moffat County, Colorado. - M.Sc. thesis, University of Idaho, Moscow, USA, 162 pp.

Heath, B.J., Straw, R., Anderson, S.H., Lawson, J. & Holloran, M.J. 1998: Sage-grouse productivity, survival, and seasonal habitat use among three ranches with different livestock grazing, predator control, and harvest management practices. - Project Completion Report, Wyoming Game and Fish Department, Cheyenne, USA, 71 pp.

Hedges, L.V. 1982: Estimation of effect size from a series of independent experiments. - Psychological Bulletin 92: 490-499.

Hedges, L.V. & Olkin, I. 1985: Statistical methods for meta-analysis. - Academic Press, San Diego, California, USA, 369 pp.

Holloran, M.J. 1999: Sage grouse (Centrocercus urophasianus) seasonal habitat use near Casper, Wyoming . - M.Sc. thesis, University of Wyoming, Laramie, USA, 123 pp.

Johnson, G.D. & Boyce, M.S. 1991: Survival, growth, and reproduction of captive-reared sage grouse. - Wildlife Society Bulletin 19: 88-93.

Klott, J.H., Smith, R.B. & Vullo, C. 1993: Sage grouse habitat use in the Brown's Bench area of south-central Idaho. - United States Department of Interior, Bureau of Land Management, Idaho State Office, Technical Bulletin 93-4, Boise, Idaho, USA, 14 pp.

Lyon, A.G. 2000: The potential effects of natural gas development on sage grouse near Pinedale, Wyoming. - M.Sc. thesis, University of Wyoming, Laramie, USA, 121 pp.

Popham, G.P. & Gutiérrez, R.J. 2003: Greater sage-grouse Centrocercus urophasianus nesting success and habitat use in northeastern California. - Wildlife Biology 9: 327-334.

Rosenberg, M.S. 2005: The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. - Evolution 59: 464-468.

Rosenberg, M.S., Adams, D.C. & Gurevitch, J. 2000: Metawin: statistical software for Meta-analysis Version 2.0. - Sinauer Associates, Sunderland, Massachusetts, USA, 128 pp.

SAS Institute 2000: SAT/STAT user's guide, Release 8.0 Edition. - SAS Institute, Inc. Cary, North Carolina, USA. Available at: http://v8doc.sas.com/sashtml/

Schroeder, M.A. 1995: Productivity and habitat use of sage grouse in north-central Washington. Job Progress Report W-96-R. -Washington Department of Fish and Wildlife, Olympia, USA, 23 pp.

Schroeder, M.A., Aldridge, C.L., Apa, A.D., Bohne, J.R., Braun, C.E., Bunnell, S.D., Connelly, J.W., Diebert, P., Gardner, S.C., Hilliard, M.A., Kobriger, G.D., McAdam, S.M., McCarthy, C.W., McCarthy, J.J., Mitchell, D.L., Rickerson, E.V. & Stiver, S.J. 2004: Distribution of sage-grouse in North America. - Condor 106: 363-376.

Schultz, B. 2004: Analysis of studies used to develop herbaceous height and cover guidelines for sage grouse nesting habitat. - Cooperative Extension Special Publication SP-04-11, University of Nevada, Reno, USA, 25 pp.

Slater, S.J. 2003: Sage-grouse (Centrocercus urophasianus) use of different-aged burns and the effects of coyote control in southwestern Wyoming. - M.Sc. thesis, University of Wyoming, Laramie, USA, 177 pp.

Sveum, C.M. 1995: Habitat selection by sage-grouse hens during the breeding season in south-central Washington. - M.Sc. thesis, Oregon State University, Corvallis, USA, 86 pp.

Sveum, C.M., Edge, W.D. & Crawford, J.A. 1998: Nesting habitat selection by sage grouse in south-central Washington. - Journal of Range Management 51: 265-269.

Wakkinen, W.L. 1990: Nest site characteristics and spring-summer movements of migratory sage grouse in southeastern Idaho. - M.Sc. thesis, University of Idaho, Moscow, USA, 57 pp.

Wambolt, C.L., Frisina, M.R., Knapp, S.J. & Frisina, R.M. 2006: Effect of method, site, and taxon on line-intercept estimates of sagebrush cover. - Wildlife Society Bulletin 34: 440-445.

Wik, P.A. 2002: Ecology of greater sage-grouse in south-central Owyhee County, Idaho. - M.Sc. thesis, University of Idaho, Moscow, USA, 141 pp.

# GREATER SAGE-GROUSE (*Centrocercus urophasianus*) POPULATION RESPONSE TO NATURAL GAS FIELD DEVELOPMENT IN WESTERN WYOMING

by
Matthew J. Holloran

A dissertation submitted to the Department of Zoology and Physiology
and The Graduate School of The University of Wyoming
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY
in
ZOOLOGY AND PHYSIOLOGY

Laramie, Wyoming
December, 2005

To The Graduate School:

The members of the committee approve the dissertation of Matthew J. Holloran presented on October 20, 2005.

Stanley H. Anderson, Chair in Memoriam

Wayne A. Hubert, Co-Chair

David E. Legg

David B. McDonald

Archie F. Reeve

Daniel C. Rule

APPROVED:

Graham Mitchell, Head, Department of Zoology and Physiology

Don A. Roth, Dean, The Graduate School

Holloran, Matthew J., Greater Sage-Grouse (*Centrocercus urophasianus*) Population Response to Natural Gas Field Development in Western Wyoming. PhD, Department of Zoology and Physiology, December, 2005.

Sage-grouse (*Centrocercus* spp.) populations have declined dramatically throughout the western United States since the 1960s. Increased gas and oil development during this time has potentially contributed to the declines. I investigated impacts of development of natural gas fields on greater sage-grouse (*C. urophasianus*) breeding behavior, seasonal habitat selection, and population growth in the upper Green River Basin of western Wyoming. Greater sage-grouse in western Wyoming appeared to be excluded from attending leks situated within or near the development boundaries of natural gas fields. Declines in the number of displaying males were positively correlated with decreased distance from leks to gas-field-related sources of disturbance, increased levels of development surrounding leks, increased traffic volumes within 3 km of leks, and increased potential for greater noise intensity at leks. Displacement of adult males and low recruitment of juvenile males contributed to declines in the number of breeding males on impacted leks. Additionally, responses of predatory species to development of gas fields could be responsible for decreased male survival on leks situated near the edges of developing fields and could extend the range-of-influence of gas fields. Generally, nesting females avoided areas with high densities of producing wells, and brooding females avoided producing wells. However, the relationship between selected nesting sites and proximity to gas field infrastructure shifted between 2000 – 2003 and 2004, with females selecting nesting habitat farther from active drilling rigs and producing wells in 2004. This suggests that the long-term response of nesting populations is avoidance of natural gas development. Most of the variability in population growth between populations that were impacted and non-impacted by natural gas development was explained by lower annual survival buffered to some extent by higher productivity in impacted populations. Seasonal survival differences between impacted and non-impacted individuals indicates that a lag period occurs between when an individual is impacted by an anthropogenic disturbance and when survival probabilities are influenced, suggesting negative fitness consequences for females subjected to natural gas development during the breeding or nesting periods. I suggest that currently imposed development stipulations are inadequate to protect greater sage-grouse, and that stipulations need to be modified to maintain populations within natural gas fields.

TABLE OF CONTENTS

Acknowledgments x

Preface 1

Goals and Objectives 2

Dissertation Organization 3

Literature Cited 5

Chapter 1: GREATER SAGE-GROUSE POPULATION RESPONSE TO NATURAL GAS FIELD DEVELOPMENT IN WESTERN WYOMING: ARE REGIONAL POPULATIONS AFFECTED BY RELATIVELY LOCALIZED DISTURBANCES?

Introduction 6

Greater Sage-grouse Population Response to Gas Development 8

Are Regional Populations Affected? 10

Concluding Comments 11

Acknowledgments 13

References 13

Chapter 2: GREATER SAGE-GROUSE RESPONSE TO NATURAL GAS FIELD DEVELOPMENT IN WESTERN WYOMING.

Introduction 16

Study Area 18

Field Methods

Lek Analyses 19

Lek Counts 19

Trapping 19

Male Habitat Selection 19

Female Habitat Selection and Demographic Analyses 20

Female Nesting Habitat Selection 20

Female Brood-rearing Habitat Selection and Productivity 21

Female Annual Survival 21

Female Chick Winter Survival 21

Statistical Methods
Lek Analyses 21
Male Habitat Selection 23
First Level: Initial Determination of Treatment and Control Leks 24
Second Level: Refinement of Potential Treatment Effect and Within Treatment Level Influences 25
Drilling Rig 25
Producing Well 26
Main Haul Road 26
Third Level: Inclusive Gas Field Infrastructure Impacts 27
Female Habitat Selection Analyses 28
Consecutive Years' Nests 29
Adult versus Yearling Nest 30
Used versus Available and Successful versus Unsuccessful Nest Locations 30
Used versus Available and Successful versus Unsuccessful Early Brood-rearing Locations 32
Female Demographic Analyses
Vital Rate Estimation 33
Deterministic Analysis 35
Life Table Response Experiment 37
Stochastic Simulations 37
Results
Lek Analyses 38
First Level: Initial Determination of Treatment and Control Leks 38
Second Level: Refinement of Potential Treatment Effect and Within Treatment Level Influences
Drilling Rig 39
Producing Well 39
Main Haul Road 40
Third Level: Inclusive Gas Field Infrastructure Impacts 42

Female Habitat Selection Analyses 42
Consecutive years' nests 43
Adult versus Yearling Nest 43
Used versus Available Nests 44
Successful versus Unsuccessful Nests 44
Used versus Available and Successful versus Unsuccessful Early Brood-rearing Locations 45
Female Demographic Analyses 45
Vital Rate Estimation 45
Deterministic Analysis 47
Life Table Response Experiment 48
Stochastic Simulations 48
Discussion
Lek Analyses 49
Female Habitat Selection Analyses 52
Female Demographic Analyses 54
Summary 56
Management Implications 57
Acknowledgements 60
Literature Cited 60
Tables
Table 1. List of acronyms. 68
Table 2. Mean annual declines in the number of greater sage-grouse males attending leks in western Wyoming, 1998-2004 by the total number of potential natural gas field-related impacts occurring within specified distances of the lek. 70
Table 3. Mean nest-to-natural gas field related disturbance distances for adult and yearling greater sage-grouse in western Wyoming, 2000-2004. 71
Table 4. Parameter coefficients for $AIC_c$ weighted logistic regression models comparing selected nesting sites and random locations for greater sage-grouse in western Wyoming, 2000-2004. 72
Table 5. Parameter coefficients and cumulative $AIC_c$ weights for independent variables included in $AIC_c$ weighted logistic regression models comparing successful to unsuccessful nesting sites for greater sage-grouse in western Wyoming,

2000-2004. 73
Table 6. Mean distances to natural gas field related disturbances for early brood-rearing used and available sites, and mean nest-to-disturbance source distances for successful and unsuccessful brooding greater sage-grouse in western Wyoming, 2000-2004. 74
Table 7. Apparent nest propensity, adjusted nest success probabilities, and brood survival probabilities for adult and yearling greater sage-grouse females in southwestern Wyoming, 1998-2004. 75
Table 8. Investigation of year, age and breeding status effect on annual survival of greater sage-grouse broods and females in southwestern Wyoming, 1998-2004. 76
Table 9. Annual survival estimates for yearling and adult female greater sage-grouse based on nesting status in southwestern Wyoming, 1998-2004. 77
Table 10. Annual survival estimates for female greater sage-grouse based on brooding status in southwestern Wyoming, 1998-2004. 78
Table 11. Seasonal period survival estimates for female greater sage-grouse in southwestern Wyoming, 1998-2004. 79
Table 12. Lower level vital rate estimates for female greater sage-grouse in southwestern Wyoming, 1998-2004. 80
Table 13. Upper level elacticities and stable age distribution for matrix population growth models analyzing demographic information collected from female greater sage-grouse in southwestern Wyoming, 1998-2004. 81
Table 14. Population growth rate estimates (λ) and treatment effect for matrix population growth models analyzing demographic information collected from female greater sage-grouse in southwestern Wyoming, 1998-2004. 83
Table 15. Mean extinction time and estimated change in population growth (λ) with the addition of stochasticity to demographic information collected from female greater sage-grouse in southwestern Wyoming, 1998-2004. 84

Figures

Figure 1. Greater sage-grouse study location in southwestern Wyoming, 1998-2004. 85

Figure 2. Greater sage-grouse study location in southwestern Wyoming, 1998-2004 (illustrating the level of natural gas development that occurred during the duration of the study). 87
Figure 3. Greater sage-grouse study location in southwestern Wyoming, 1998-2004 (representing the spatial area used for nesting and early brood-rearing habitat selection analyses). 89
Figure 4. Regression relationship between overall change in the number of greater sage-grouse males attending leks in southwestern Wyoming, 1998-2004 and principal component 1 scores. 91
Figure 5. Regression relationships between overall change in the number of greater sage-grouse males attending leks in southwestern Wyoming, 1998-2004 and average annual distance from leks to closest drilling rig active during the breeding season, closest producing natural gas well, and closest point on a main haul road. 93
Figure 6. Mean annual change in the number of greater sage-grouse males attending leks in southwestern Wyoming, 1998-2004 by lek-to-closest drilling rig active during the breeding season distance categories, lek-to-closest producing natural gas well distance categories, and lek-to-closest point on a main haul road distance categories. 95
Figure 7. Nest probabilities relative to natural gas development levels generated from an $AIC_c$ weighted logistic regression model comparing selected nesting sites and random locations for greater sage-grouse nesting in southwestern Wyoming, 2000-2004. 97
Figure 8. Annual sample size and percent normal precipitation for female greater sage-grouse in southwestern Wyoming, 1998-2004. 99
Figure 9. Life-cycle diagram and matrix for a 5 stage population growth model of female greater sage-grouse in southwestern Wyoming, 1998-2004. 101
Figure 10. Life table response experiment results from population growth models analyzing demographic information collected from female greater sage-grouse in southwestern Wyoming, 1998-2004 (groups considering all individuals). 103
Figure 11. Life table response experiment results from population growth models analyzing demographic information collected from female greater sage-grouse in southwestern Wyoming, 1998-2004 (groups considering nesting

individuals). 105

Chapter 3: NATURAL GAS DEVELOPMENT IMPACTS TO GREATER SAGE-GROUSE POPULATIONS: A SUMMARY OF RESEARCH CONDUCTED IN WESTERN WYOMING WITH THOUGHTS ON MANAGEMENT AND FUTURE RESEARCH OPTIONS.

Introduction 107

Results 108

Discussion 109

Management Considerations 111

Research Needs 112

Literature Cited 113

Appendix A: SPATIAL DISTRIBUTION OF GREATER SAGE-GROUSE NESTS IN RELATIVELY CONTIGUOUS SAGEBRUSH HABITATS. A1 - A18

Abstract A1

Introduction A2

Methods

Study Area A4

Field Techniques A4

Statistical Analysis A5

Results A7

Discussion A9

Acknowledgments A13

Literature Cited A13

Figures

Figure 1. Distribution of Greater Sage-Grouse nests based on lek-of-capture to nest distances in central and western Wyoming, 1994-2003 and expected numbers assuming uniformly distributed nests within 8.5 km of a lek. A17

Appendix B: GREATER SAGE-GROUSE EARLY BROOD-REARING HABITAT USE AND PRODUCTIVITY IN WYOMING. B1 - B19

Abstract B1

Introduction B2

Study Area B4
Methods B4
Statistical Analysis B6
Habitat Use B6
Productivity B7
Results B8
Habitat Use B8
Productivity B9
Discussion B9
Acknowledgments B13
Literature Cited B13
Tables
Table 1. Candidate models used to explain early brood-rearing habitat use of greater sage-grouse in Pinedale (1999-00, 2002-03), Lander (2001-2003), and Kemmerer (2002), WY. B18
Table 2. Total and standardized cumulative $AIC_c$ weights of variables used to predict juveniles per female and the proportion of females with confirmed chicks 14 days post-hatch of greater sage-grouse in Pinedale (1999-00, 2002-03), Lander (2001-2003), and Kemmerer (2002), WY. B19

Appendix C: GREATER SAGE-GROUSE RESEARCH IN WYOMING: AN OVERVIEW OF STUDIES CONDUCTED BY THE WYOMING COOPERATIVE FISH AND WILDLIFE RESEARCH UNIT BETWEEN 1994 AND 2005. C1 - C59
Abstract C1
Acknowledgements C2
Table of Contents C3
Introduction C4
Historical Sage-grouse Information C6
Factors Potentially Contributing to Historic Population Changes C8
Study Areas and Objectives by Study
Farson C10
Rawlins C10
Casper C11

Pinedale C12
Kemmerer C12
Jackson C13
Lander C14
Pinedale C15
Seasonal Habitat Selection
Nesting Habitat Selection C15
Nesting Success C18
Early Brood-rearing Habitat Selection and Success C20
Late Brood-rearing Habitat Selection and Success C22
Winter Habitat Selection C23
Seasonal Adult Survival C25
Livestock Grazing C26
Sagebrush Manipulation C29
Mineral Extractive Activities C32
Predator Control C36
Future Sage-grouse Research in Wyoming C39
Literature Cited C41
Tables
Table 1. Productivity estimates for greater sage-grouse populations studied by the Wyoming Cooperative Research Unit in central and western Wyoming, 1994-2004. C57
Figures
Figure 1. Study area locations for greater sage-grouse research projects conducted by the Wyoming Cooperative Research Unit, 1994-2005. C58

# ACKNOWLEDGMENTS

I have specifically acknowledged those that made each portion of this dissertation possible within each chapter; thus I will use this space to acknowledge those that made the entire project successful. The students and faculty associated with the Wyoming Cooperative Research Unit have been a tremendous help from the beginning. I would especially like to thank Linda Ohler, Amanda Barry, and Laurie Kempert for all of their technical assistance. Mark McKinstry, Michael Quist, Steven Slater, Charles Anderson, and David Edmunds deserve special recognition. Kristen Thompson has been especially helpful during the long writing process. I also want to give special recognition to my advisor, Stanley H. Anderson; his guidance throughout the process was invaluable. My original committee members, Dr. David Legg, Dr. David McDonald, Dr. Daniel Rule, Dr. Archie Reeve, and Dr. Elizabeth Williams have assisted greatly in their own unique ways, even if it was to make me sweat during my prelims. Additionally, Dr. Wayne Hubert assisted when times were difficult towards the end of the dissertation. Most of all, I would like to thank my beautiful family. Alison and Sage have provided the emotional support necessary to bring this ordeal to fruition.

**PREFACE**

According to the U.S. Department of Energy (www.doe.gov), natural gas consumption in North America is projected to increase by 1.5% annually between 2002 and 2025. The American Gas Association (AGA; www.aga.org) reports that domestic natural gas production is expected to account for at least 60% of the total U.S. supply through 2025. Much of the onshore natural gas in the 48 contiguous states is in the Uinta-Piceance Basin of Colorado and Utah, the Green River Basin of southwestern Wyoming, the San Juan Basin of New Mexico and Colorado, the Montana Thrust Belt, and the Powder River Basin of Wyoming and Montana (Connelly et al. 2004). Most of these Intermountain West reserves are under Bureau of Land Management (BLM) jurisdiction (Connelly et al. 2004) and in sagebrush dominated landscapes (Knick et al. 2003). The Federal Land Policy and Management Act of 1976 established the BLM's multiple-use mandate to serve present and future generations. Multiple-use includes natural resource conservation, recreation, livestock grazing, and resource extraction (www.blm.gov).

The Energy Policy Act of 2005 was signed into law by President George W. Bush in August of 2005, and represents the first major energy legislation passed by Congress since the original Energy Policy Act of 1992. One of the primary focuses of the new law is to increase production of domestic fossil fuels (natural gas, oil and coal). According to the AGA, the law will result in increased domestic oil and gas production on non-park federal lands by increasing leasing, expediting the permitting process in the Intermountain West, and removing stipulations on exploration and development operations.

Currently, Wyoming's economy depends heavily upon natural resource industries, with mining (including oil and gas extraction) generating approximately 23% of the state's gross state product for 2001 (Federal Deposit Insurance Corporation; www.fdic.gov). According to the Petroleum Association of Wyoming (www.pawyo.org), in fiscal year 2004 Wyoming's petroleum industry directly employed 18,000 people with an annual payroll of $730 million, and oil and gas production contributed $1.27 billion to state and local governments. However, natural gas, oil, and coal are non-renewable natural resources. Although the Wyoming state government is attempting to ensure that the current petroleum-based "boom" is not followed by a "bust" as has been historically experienced by the state, this type of cycle is inevitable given the non-renewable nature of fossil fuels.

Quantifying the monetary value of Wyoming's wildlife and open spaces is difficult, but these natural resources are vital for long-term sustainable state revenue. The Wyoming state office of travel and tourism (www.wyomingbusiness.org) estimated that in 2004 tourists spent $2 billion in Wyoming, and the tourism industry employed over 28,600 people with an annual payroll of $540 million. Of the

marketable overnight stays, between 51 and 73% of those visiting the state were interested in outdoor type experiences including wildlife, natural environments, and wilderness areas. Additionally, the Wyoming Game and Fish Department estimated that over 230,000 hunting and fishing licenses were sold, hunting accounted for 3.36 million recreation days, and hunters spent $380 million in license fees and expenditures in Wyoming in 2004 (2005 Annual Report; Wyoming Game and Fish Department, Cheyenne, WY, USA).

Sagebrush ecosystems dominate much of Wyoming, and they are critical to the survival of many of the state's most charismatic wildlife. Approximately 100 bird species and 70 mammal species rely on sagebrush-dominated habitats during at least portions of their life-cycle (Braun et al. 1976, Paige and Ritter 1999). Many of the state's big game herds (including elk [*Cervus canadensis*], mule deer [*Odocoileus hemionus*], and pronghorn [*Antilocapra americana*]) depend on sagebrush habitats during the winter. Additionally, several species of concern within the state are sagebrush obligates (including greater sage-grouse [*Centrocercus urophasianus*] and pygmy rabbits [*Brachylagus idahoensis*]) and rely on sagebrush habitats throughout all life stages.

The magnitude of energy development impacts on wildlife resources throughout North America is relatively unknown. Generally, gregarious species are more severely affected by disturbances than are solitary species, and hunted species will exhibit a greater avoidance of road-related disturbances than will their unhunted conspecifics (PRISM Environmental Management Consultants 1982). Sagebrush-obligate bird species may be important indicators of the health of an ecosystem, and changes in their population levels may be symptomatic of long-term regional habitat condition (Knick et al. 2003, Crawford et al. 2004). Given that the health of sagebrush-dominated ecosystems is paramount to maintaining viable populations of many species of wildlife, the reaction of greater sage-grouse populations to habitat alterations caused by energy development could imply reactions of a wide array of wildlife species.

**Goals and Objectives**

This study investigating the potential impacts of natural gas development to greater sage-grouse was initiated by the U.S. Department of Energy and the Bureau of Land Management in 1998. The goal was to determine if and how the development of natural gas resources was influencing greater sage-grouse populations in the upper Green River Basin of western Wyoming. The study was designed to compare differences between areas where natural gas disturbance potentially influenced greater sage-grouse behavior (i.e., treatment areas) and areas where there was no gas related disturbance (i.e., control areas). The assumption was made that the behavior of birds in control areas mimicked that of birds in a

natural setting with natural variation, thus the study could identify changes in behavior resulting from gas development regardless of annual variations in habitat conditions, weather, grazing, or other factors. Each question and hypothesis was centered on control versus treatment comparisons, thereby isolating the measured effects of the potential impacts of natural gas field development on greater sage-grouse.

I organized the objectives based on several increasingly specific questions: Are breeding greater sage-grouse populations impacted by natural gas development? What aspects of a developing field are influencing breeding populations? Are individuals dispersing from natural gas development or are population sizes declining?

Objective 1: Determine if breeding populations of greater sage-grouse are negatively influenced by the development of a natural gas field.

Objective 2: Determine responses of breeding populations to three independent components of natural gas field development: (1) drilling rigs, (2) producing wells, and (3) main haul roads. To determine if specific characteristics of each component influenced breeding populations, I investigated the influence of distance, density (i.e., well density, total length of main haul road), visibility, and direction of these natural-gas-field developments. I also investigated the influence of traffic levels on main haul roads.

Objective 3: Determine if breeding season habitat selection, survival, and lek tenacity of individual male greater sage-grouse are influenced by natural gas field development.

Objective 4: Determine if nesting and early brood-rearing habitat selection of individual female greater sage-grouse are influenced by natural gas field development.

Objective 5: Determine if growth of female greater sage-grouse populations is influenced by natural gas field development.

Objective 6: Assess the adequacy of BLM-imposed development stipulations.

I used variation in the maximum number of males occupying leks to address objectives 1 and 2, and collected data from radio-equipped individuals to address objectives 3 through 5.

**Dissertation Organization**

The objectives outlined above are addressed in chapters 1 through 3 of the dissertation. I included as appendices manuscripts written with non-gas field related information collected during the study to support methods used in chapters 2 and 3. Throughout the dissertation, I used “greater sage-grouse” or “Gunnison sage-grouse” (*Centrocercus minimus*) when reporting information from other

studies or results from this study that were specific to the species, and used "sage-grouse" to suggest both species in general.

Chapter 1 was written in conjunction with a presentation given at the 70th North American Wildlife and Natural Resource Conference, and is to be published in the transactions from that conference (Wildlife Management Institute, Washington DC, USA). I included this manuscript because it introduces the overriding question plaguing those dealing with the impacts of natural resource extraction: Are sage-grouse dispersing from anthropogenic disturbances or are regional population levels negatively influenced? The manuscript also introduces potential mitigation options not presented elsewhere in the dissertation. Chapter 1 is presented verbatim to the manuscript submitted for publication; this chapter could be altered slightly in published form per the editor's final comments.

I present the bulk of the information on the impacts of natural gas development in Chapter 2. This chapter is organized the same as the objectives, and progresses from the question "are breeding populations influenced?" to "what specific aspects or components of a developing field appear to be influencing populations?" and concludes with "how are individual birds and populations responding to development (i.e., dispersal or population size influences?)". The management implications section of Chapter 2 addresses the adequacy of currently imposed stipulations (objective 6). The chapter is written in *Journal of Wildlife Management* (The Wildlife Society, Bethesda, MD, USA) format.

I include a summary of information on natural gas impacts as Chapter 3. This chapter is formatted as an executive summary, and includes introductory material as well as a summary of Chapters 1 and 2. It also includes sections on potential mitigation options and future research needs.

Three appendices that represent supporting or non-natural gas field related analyses are included. These appendices are included as separate documents, thus page numbering for each is unique. Appendix A presents an investigation of the spatial distribution of greater sage-grouse nests relative to lek location using data collected from throughout Wyoming since 1994. The manuscript is to be published in *The Condor* (Cooper Ornithological Society, Bend, OR, USA; Condor 107:742-752), and is presented here verbatim to the published manuscript. I used the results presented in this manuscript to establish the spatial area of interest for investigating female greater sage-grouse nesting and early brood-rearing habitat selection relative to natural gas field development (discussed in Chapter 2).

Appendix B is an investigation of habitat selection during the early brood-rearing period in terms of vegetative and invertebrate conditions. The analyses used data collected from throughout southwestern Wyoming from 1999 to 2003. Kristin M. Thompson was the primary author of the manuscript, which is to be published in the *Western North American Naturalist* (Brigham Young

University, Provo, UT, USA). The appendix is verbatim to the submitted manuscript, and could be altered slightly in published form per the editor's final comments.

Appendix C summarizes eight completed and two ongoing projects related to greater sage-grouse conducted by the Wyoming Cooperative Fish and Wildlife Research Unit since 1994. I included this appendix so that land and wildlife managers in Wyoming had relatively easy access to the major results from the separate studies. The chapter is formatted as a report for ease of reproduction, and includes a title page and table of contents.

**LITERATURE CITED**

Braun, C. E., M. F. Baker, R. L. Eng, J. S. Gashwiler, and M. A. Schroeder. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulleting 88:165-171.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, WY, USA.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal Range Management 57:2-19.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634.

Paige, C., and S. A. Ritter. 1999. Birds in a sagebrush sea: managing sagebrush habitats for bird communities. Partners in Flight Western Working Group, Boise, ID, USA.

PRISM Environmental Management Consultants. 1982. A review of petroleum industry operations and other land use activities affecting wildlife. The Canadian Petroleum Association, Calgary, Alberta, Canada.

## CHAPTER 1

# Greater Sage-grouse Population Response to Natural Gas Development in Western Wyoming: Are Regional Populations Affected by Relatively Localized Disturbance?

**Matthew J. Holloran**
Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, Wyoming.
**Stanley H. Anderson**
Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, Wyoming.

Holloran, M. J., and S. H. Anderson. *In Press*. Greater Sage-grouse Population Response to Natural Gas Development in Western Wyoming: Are Regional Populations Affected by Relatively Localized Disturbance? Transactions North American Wildlife and Natural Resources Conference 70:000-000.

## Introduction

Current sage-grouse (Centrocercus spp.) breeding populations throughout western North America are approximately two to three times lower than those during the late 1960s, and populations have declined 2% annually from 1965 to 2003 (Connelly et al. 2004). In 2000, greater sage-grouse (Centrocercus urophasianus) occupied 56% of their pre-European settlement distribution (Schroeder et al. 2004). Throughout Wyoming since 1965, greater sage-grouse populations have declined 5.2% annually and the average number of males per lek has declined 49% (Connelly et al. 2004). Although no single factor has been responsible for sage-grouse population declines, the discovery and subsequent development of gas and oil fields throughout the western United States beginning in the 1930s and 1940s has been identified as one potential causative agent (Braun 1987, Connelly et al. 2004). Generally, gregarious [e.g., sage-grouse during the breeding season] and hunted species are more severely affected by land use disturbances than are solitary and unhunted species (PRISM Environmental Management Consultants 1982). Additionally, Braun et al. (2002) indicate that a review of available information suggests that all sagebrush obligate species are negatively influenced by habitat alterations resulting in sagebrush (Artemesia spp.) removal and reduced shrub patch size.

Potential impacts of gas and oil development to sage-grouse include direct habitat loss and fragmentation from well, road, and pipeline construction, and increased human activity causing the displacement of individuals through avoidance behavior. In addition, these impacts may vary through time in that development may negatively influence sage-grouse populations over the short-term (site

preparation and drilling), long-term (road development and producing well maintenance), and permanently (processing facilities and pumping stations; Braun 1987). Braun et al. (2002) suggested that greater sage-grouse leks within 0.25 miles (0.4 km) of coalbed methane wells in Wyoming had significantly fewer males per lek and lower annual rates of population growth compared to less disturbed leks. Additionally, the extirpation of three different lek complexes within 220 yards (0.2 km) of oil field infrastructure in Alberta, Canada, was associated with the arrival of oil field-related disturbance sources (Braun et al. 2002).

Coal mining activity and oil field development in North Park, Colorado, resulted in decreased greater sage-grouse lek attendance on leks within 1.2 miles (2 km) of development activities relative to leks located more than 1.2 miles (2 km) from these activities (Braun 1986, 1987, Remington and Braun 1991). Braun (1986) attributed declines to decreased recruitment of juvenile males (i.e., first-year breeders). Failure to recruit juvenile males could have resulted from juvenile male dispersal to different lek sites, poor nesting success or decreased survival of young resulting in fewer available replacement juveniles, or acoustical or physical factors that deterred juveniles from becoming established (Schoenburg and Braun 1982, Braun 1986, 1987). Although Remington and Braun (1991) indicated that leks closely associated with mining activity declined relative to control leks, overall greater sage-grouse population trends in the area did not change, suggesting that the distribution rather than the number of breeding grouse was altered.

Greater sage-grouse females disturbed on leks during the breeding season by natural gas field-related activity in western Wyoming exhibited lower nest initiation rates and those that initiated a nest selected nesting habitats farther from the lek compared to females breeding on undisturbed leks (Lyon and Anderson 2003). Reduced initiation rates, when combined with inherently low probabilities of reproductive success in sage-grouse (Connelly and Braun 1997), could potentially lower annual productivity rates below sustainable levels. Additionally, if leks are located within or adjacent to potential nesting habitat (Connelly et al. 2000) and gas field-related activities result in females nesting farther from leks, then these impacted females may use sub-optimal nesting sites and thus experience lower nest success. Further, sage-grouse lekking behavior, combined with annual nest site fidelity potentially passed to female offspring (Lyon 2000), could result in relatively clumped nest distributions on a landscape scale. As a result, isolated habitat alterations could impact a relatively large number of nesting individuals.

If declines in the number of males on disturbed leks can be attributed to decreased juvenile male recruitment, what happens to these juvenile males? Remington and Braun (1991) theorize that they disperse to different lek sites. However, Lyon and Andersons' (2003) observations suggest decreased

productivity resulting in fewer available replacement juveniles. This paper investigates the response of greater sage-grouse populations to natural gas development in western Wyoming. We examine changes in the number of males on leks relative to the level of activity occurring around those leks, and use these relative changes to ascertain how individual birds and regional populations might be influenced by natural gas field development.

**Greater Sage-grouse Population Response to Gas Development in Western Wyoming**

We investigated the potential impacts of gas field development on greater sage-grouse populations on a study area designated by 3.1-mile (5-km) buffers around known leks in the upper Green River Basin near the town of Pinedale, in western Wyoming. The study area was located primarily within the boundaries of the Pinedale Anticline Project Area (PAPA), but included portions of the Jonah I and Jonah II gas fields (Bureau of Land Management 2000). The study area encompassed approximately 421 square miles (1090 $km^2$), and was dominated by big sagebrush (Artemesia tridentata spp.) and high-desert vegetation. The first natural gas well was drilled in the PAPA in 1939, but only 23 additional wells had been drilled in the project area by 1997. In May 1998, the Bureau of Land Management (BLM) approved limited exploratory drilling of 45 wells prior to completion of the Environmental Impact Statement (EIS). The final EIS was approved in July 2000. Full development of the field is expected to continue for the next 10 to 15 years and be concentrated within a 3.1 mile (5-km) buffer around the anticline crest. However, areas designated as "hot spots" outside the buffer may also be developed as the BLM has leased all but 7.3 square miles (19 $km^2$) of the PAPA (total area approximately 313 square miles [810 $km^2$]) for potential development. The BLM's record of decision approved the construction of 700 producing well pads with minimum spacing of 40 acres (16 ha) between pads (equivalent to 16 wells per section; Bureau of Land Management 2000). In the spring of 1999, approximately 75 producing gas wells were situated within the designated study area; by the summer of 2004, the study area contained approximately 450 producing wells.

One of the primary objectives of this study was to determine if increased levels of gas field development near known greater sage-grouse leks influenced breeding behavior. We categorized each lek based on the total number of producing gas wells located within 3.1 miles (5 km) of the lek by year (i.e., because gas field development continued through the project, the number of producing wells for each lek year was a unique value), and we considered leks with less than 5 wells to be controls (minimal gas field-related disturbance; n = 49 lek years), leks with 5 to 15 wells to be lightly impacted (n = 19 lek years), and leks with greater than 15 wells to be heavily impacted (n = 31 lek years). We assessed lek attendance as the annual maximum number of males estimated through lek counts

(Connelly et al. 2003). Gas development influences on breeding greater sage-grouse were estimated by calculating either the total change in the maximum number of males attending all leks within a given impact status from the year prior to impact through 2004, or by calculating average annual change in the maximum number of males by lek impact status. In certain instances the impact status of individual leks changed as the field developed (i.e., from lightly to heavily impacted). We calculated overall change in the number of attending males by impact status for these leks using lek counts from the year prior to impact status change.

The total maximum number of males declined 51% on heavily impacted leks from the year prior to impact to 2004 (control leks declined 3% during the same time period). Further, the total maximum number of males on three heavily impacted leks situated centrally within the developing field declined 89%, and two of the three leks were essentially inactive in 2004 (one male counted on one of the leks on one morning in 2004). Additional anecdotal evidence from southern and western Wyoming has also indicated that leks historically situated within areas developed for natural gas extraction became inactive as well densities increased (Jonah gas fields, K.J. Andrews, personal communication 2001; Great Divide Basin gas fields, G.S. Hiatt, personal communication 2000). The evidence appears to suggest greater sage-grouse are ultimately excluded from breeding within the development boundaries of natural gas fields.

This leads us to a fundamental question associated with the ultimate extirpation and subsequent exclusion of greater sage-grouse leks from a region as the probable result of an anthropogenic disturbance source: are greater sage-grouse displaced from impacted leks to breed on leks away from the disturbance source; or does the disturbance result in the impacted birds not breeding? Braun (1986) hypothesized that adult males (i.e., individuals over 1.5 years old, or at least second-year breeders) returned to leks where they had established territories until they died and juvenile males establishing territories replaced those adults, and attributed declines on leks influenced by coal mining activity in northern Colorado to decreased juvenile male recruitment. Our results generally support Braun's (1986) hypothesis. Zablan et al. (2003) used band return rates over 18 years in Colorado to estimate adult male annual survival and found that survival varied from 35 to 45% (95% CI). Following inclusion in the heavy impact category, average annual declines on the three leks located centrally within the developing Anticline field was 48% (±SE; ±9%). Further, using maximum male lek counts from the year prior to inclusion in the heavily impacted category as a starting value and assuming 37% adult male annual survival (Zablan et al. 2003), we were able to reproduce observed overall declines on these leks with 15.6% annual recruitment (approximately 55 to 65% annual recruitment required for

stability). These observations suggest that declines on the three centrally situated leks resulted from adult male tenacity with minimal juvenile male recruitment.

**Are Regional Populations Affected?**

Average annual declines in the maximum number of males differed relative to impact status [heavy 16% (excluding the three centrally situated leks discussed above); light 19%; control 2%], suggesting that juvenile males were being displaced by gas field-related disturbance. This leads to an amendment of the fundamental question: are displaced juvenile males establishing territories on less-impacted leks, or are they not breeding?

To investigate this question, an annual male population growth rate estimate is needed to compare with annual changes in the number of strutting males throughout the region. We assessed average annual change in the regional number of strutting males by combining annual estimates (2000-2004) of the maximum number of males from 20 leks with consistently accurate counts (Connelly et al. 2003) situated within the study area. Annual male population growth was estimated using average demographic information from 190 radio-equipped females captured (Wakkinen et al. 1992) throughout the study area between 1999 and 2003 in the following equation:

$$\lambda = [(Initiate \times Success \times Brood) \times \male Chick] + (\male\ Annual\ Survival)$$

Where $\lambda$ is male population growth rate; *Initiate* is annual nest initiation; *Success* is annual nest success; *Brood* is annual brooding period chick survival; ♂*Chick* is male chicks produced annually [based on average August brood size, a brood sex ratio of 45.4 males to 54.6 females (Swenson 1986) and 75% chick winter survival (J.W. Connelly, personal communication 1998)]; and ♂ *Annual Survival* is adult and juvenile male annual survival (56.4%; survival estimate is average from Schroeder et al. 1999 and Zablan et al. 2003). Demographic values derived from our data were apparent values.

The regional number of strutting males counted on leks declined annually by an average of 13% (±5%). Using the demographic information, male population growth rates declined 8% (±4%) annually. The interval estimates for population growth and annual change in the number of strutting males overlapped, suggesting that a proportion of the displaced juveniles were establishing territories on leks somewhere within the study area. However, the 5% difference in the annual estimates and the population growth rate interval being skewed to the left of the male count interval further implies that a proportion of the juvenile males were not counted on leks, suggesting that these individuals were not establishing breeding territories.

Two potential alternative explanations to the conclusion that a proportion of the juvenile population was not breeding exist. These birds may have established territories on leks beyond the

spatial scope of the study area. The sub-sample of leks used to formulate the estimate for the regional change in the number of males included eight leks that we had designated as controls. The average distance between these control leks and heavily impacted leks was 15.5 miles (25 km), and average distance from control to closest heavily impacted lek was 6.2 miles (10 km [±0.5 miles [±0.8 km]]). In Colorado, juvenile males typically established on natal leks (63%), with the remaining juveniles establishing on leks within 8.1 miles (13 km) of their natal lek (Dunn and Braun 1985). Additionally, 82% of interlek movements (i.e., movement of individual males between different leks during the breeding season) were between leks separated by less than 5 miles (8 km; Dunn and Braun 1985). These results suggest that the scope of our study area was sufficient to encompass the area typically exploited by juvenile males searching for lek establishment sites. The second possibility is that these birds were breeding without visiting a lek. Because sage-grouse males provide neither resources nor parental care to their mates, mate choice does not provide direct benefits to the females, suggesting that indirect benefits may be the main evolutionary force behind females' mate selection (Gibson 1990). The ability of females to recognize high relative fitness in individual males potentially requires a venue for direct comparison (i.e., the lek; Beehler and Foster 1988), and the possibility that off-lek breeding was occurring would constitute a significant change in breeding behavior. We cannot be certain that a proportion of the displaced population abstained from breeding, but the alternatives would represent unlikely deviations from normal behavior.

**Concluding Comments**

Although it is difficult, if not impossible to implicate a single factor or group of factors responsible for recent range-wide sage-grouse population declines, Braun (1998) suggests that complexities of factors related to human-caused habitat changes are responsible. Changes rendered across the landscape include habitat loss (e.g., agricultural conversion, mineral and energy development, community building, roads, reservoirs), fragmentation (e.g., fences, power lines, roads), and degradation (e.g., sagebrush treatments, grazing, exotic plant species introduction), with other factors such as drought, hunting, and predation playing contributory roles. Greater sage-grouse populations in southern and western Wyoming appear to be ultimately displaced to surrounding areas by the development of natural gas fields. A proportion of the displaced birds appeared to establish on leks adjacent to the developed area. However, a proportion of the displaced population apparently did no breed. These conclusions suggest that natural gas field development contributes to localized greater sage-grouse extirpations, but that regional population levels, although negatively impacted, are not as severely influenced.

Research investigating juvenile responses to a developing gas field would improve our understanding of specifics. For example: what proportion of the juvenile male population does not breed; what is the spatial extent of the area searched by disturbed juvenile males prior to establishing a territory on a lek (spatial extent of gas field influence); is territorial establishment timing of juvenile males influenced by displacement; what are the well densities within a given distance from an active lek when juvenile male establishment probabilities become negatively influenced; do increased rates of dispersal influence juvenile male survival? Future research should further address potential impacts to the juvenile female cohort. In addition to the questions asked concerning juvenile males, information relative to female seasonal habitat selection and productivity is needed. What is the proportion of the juvenile female population displaced from their natal nesting or natal brooding areas; are vital rates (i.e., survival, nesting initiation and success probabilities, and chick productivity rates) of the juvenile females displaced from their natal lek, nesting, or brooding areas negatively influenced? These and additional questions are currently (2005-06) being investigated by researchers at the University of Wyoming with assistance from the BLM, Department of Energy, and Wyoming Game and Fish Department.

Braun et al. (2002) suggest that the oil and gas industry should mitigate for habitat and population decreases associated with mineral extraction activities, considering potential cumulative effects [e.g., livestock impacts to surrounding landscapes (Kuipers 2004), habitat treatment consequences (Slater 2003)]. Additionally, mitigation measures aimed at increasing not only productivity in but carrying capacity of surrounding areas could be important because of potential density-dependent difficulties (i.e., nest spacing influences on nest success probabilities; Holloran and Anderson 2005) arising from artificially high populations caused by the shifting of some of the juvenile cohort. Mitigation measures aimed at minimizing the negative numerical consequences of gas development to regional sage-grouse populations implies a refugia approach to species conservation. By protecting and enhancing these reservoir populations surrounding the developing gas field, mitigation theoretically ensures that sage-grouse will be present to recolonize the field following reclamation. However, this approach requires lengthening the time-frame between the development of additional gas fields surrounding the one currently under construction to the life-expectancy of the original field, thus ensuring that surrounding refugia areas are maintained (individual gas well life-expectancy estimated at 25 to 40 years for the types of formations encountered in the Pinedale Anticline area; Wyoming Oil and Gas Conservation Commission, personal communication 2005). Following reclamation of the existing field, the area then potentially becomes a refuge for reservoir populations associated with the next gas field slated for development.

The current energy situation in the United States will likely encourage the development of natural gas reserves in many western states harboring substantial sage-grouse populations. According to the American Gas Association (www.aga.org), natural gas consumption in the U.S. is expected to increase by 50 to 60% over the next 20 years, and that to ensure economic stability and energy security, the U.S. must reduce its dependence on unstable imports of foreign petroleum. However, the environmentally safe development of America's natural gas reserves is of equal importance to the strength and perseverance of this country. Sage-grouse population maintenance initially requires a recognition of the intrinsic value of sagebrush dominated landscapes, followed by the development of a comprehensive approach to sagebrush habitat conservation that involves commitments and partnerships between state and federal agencies, academia, industry, private organizations, and landowners; "only through this concerted effort and commitment can we afford to be optimistic about the future of sagebrush ecosystems and their avifauna" (Knick et al. 2003:627).

## ACKNOWLEDGMENTS

Financial support was provided by the Bureau of Land Management, Department of Energy, Wyoming Game and Fish Department, Ultra Petroleum, Yellowstone-to-Yukon Initiative, EnCana Oil & Gas Inc., and the Cowboy 3-Shot Sage-Grouse Foundation. We thank all the landowners in the upper Green River Basin that allowed access. Field assistance was provided by R. A. Holloran, B. K. Holtby, R. C. Powell, M. S. Stotts, C. G. Taber, and G. L. Wilson. Telemetry flights and lek surveys were conducted with the assistance of Mountain Air Research (Driggs, Idaho). Our manuscript was greatly improved through reviews by A. G. Lyon, M. C. Quist, T. E. Rinkes, and S. J. Slater.

## REFERENCES

Beehler, B.M., and R.S. Foster. 1988. Hotshots, hotspots, and female preference in organization of lek mating systems. *The American Naturalist* 131:203-219.

Braun, C.E. 1986. Changes in sage grouse lek counts with advent of surface coal mining. In *Proceedings: Issues and Technology in the Management of Impacted Western Wildlife,* 227-231. Boulder, Colorado: Thorne Ecological Institute.

Braun, C.E. 1987. Current issues in sage grouse management. In *Proceedings of the Western Association of Fish and Wildlife Agencies,* 134-144. Cheyenne, Wyoming: Western Association of Fish and Wildlife Agencies.

Braun, C.E. 1998. Sage grouse declines in western North America: what are the problems? *Proceedings Western Association of Fish and Wildlife Agencies,* 139-156. Cheyenne, Wyoming: Western Association of Fish and Wildlife Agencies.

Braun, C.E., O.O. Oedekoven, and C.L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage grouse. In *Transactions North American Wildlife and Natural Resources Conference,* 337-349. Washington, DC: Wildlife Management Institute.

Bureau of Land Management. 2000. *Record of decision, environmental impact statement for the Pinedale anticline oil and gas exploration and development project Sublette County, Wyoming.* Pinedale Field Office, Wyoming.

Connelly, J.W., and C.E. Braun. 1997. Long-term changes in sage grouse (Centrocercus urophasianus) populations in western North America. *Wildlife Biology* 3:229-234.

Connelly, J.W., S.T. Knick, M.A. Schroeder, and S.J. Stiver. 2004. *Conservation assessment of greater sage-grouse and sagebrush habitats.* Cheyenne, Wyoming: Western Association of Fish and Wildlife Agencies.

Connelly, J.W., K.P. Reese, and M.A. Schroeder. 2003. *Monitoring of Greater Sage-grouse habitats and populations.* College of Natural Resources Experiment Station publication No. 979, Moscow, Idaho: University of Idaho.

Connelly, J.W., M.A. Schroeder, A.R. Sands, and C.E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. *Wildlife Society Bulletin* 28:967-985.

Dunn, P.O., and C.E. Braun. 1985. Natal dispersal and lek fidelity of sage grouse. *Auk* 102:621-627.

Gibson, R.M. 1990. Relationships between blood parasites, mating success and phenotypic cues in male sage grouse Centrocercus urophasianus. *American Zoologist* 30:271-278.

Holloran, M.J., and S.H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. *Condor* 107:742-752.

Knick, S.T., D.S. Dobkin, J.T. Rotenberry, M.A. Schroeder, W.M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611-634.

Kuipers, J.L. 2004. *Grazing system and linear corridor influences on greater sage-grouse (Centrocercus urophasianus) habitat selection and productivity.* M. S. Thesis, Laramie, Wyoming: Department of Zoology and Physiology, University of Wyoming.

Lyon, A.G. 2000. *The potential effects of natural gas development on sage grouse (Centrocercus urophasianus) near Pinedale, Wyoming.* M. S. Thesis, Laramie, Wyoming: Department of Zoology and Physiology, University of Wyoming.

Lyon, A.G., and S.H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. *Wildlife Society Bulletin* 31:486-491.

PRISM Environmental Management Consultants. 1982. *A review of petroleum industry operations and other land use activities affecting wildlife.* Calgary, Alberta: The Canadian Petroleum Association.

Remington, T.E., and C.E. Braun. 1991. How surface coal mining affects sage grouse, North Park, Colorado. In *Proceedings, Issues and Technology in the Management of Impacted Western Wildlife,* 128-132. Boulder, Colorado: Thorne Ecological Institute.

Schoenburg, T.J., and C.E. Braun. 1982. *Potential impacts of strip mining on sage grouse movements and habitat use.* Federal Aid Project W-37-R-35, Denver, Colorado: Colorado Division of Wildlife.

Schroeder, M.A., C.L. Aldridge, A.D. Apa, J.R. Bohne, C.E. Braun, S.D. Bunnell, J.W. Connelly, P.A. Deibert, S.C. Gardner, M.A. Hilliard, G.D. Kobriger, S.M. McAdam, C.W. McCarthy, J.J. McCarthy, D.L. Mitchell, E.V. Rickerson, and S.J. Stiver. 2004. Distribution of sage-grouse in North America. *Condor* 106:363-376.

Schroeder, M.A., J.R. Young, and C.E. Braun. 1999. Sage grouse (Centrocercus urophasianus). In *The birds of North America, No. 425,* eds. A. Poole and F. Gill, 1-28. The Birds of North America, Inc., Philadelphia: Pennsylvania.

Slater, S.J. 2003. *Sage-grouse (Centrocercus urophasianus) use of different-aged burns and the effects of coyote control in southwestern Wyoming.* M. S. Thesis, Laramie, Wyoming: Department of Zoology and Physiology, University of Wyoming.

Swenson, J.E. 1986. Differential survival by sex in juvenile sage grouse and gray partridge. *Ornis Scandinavica* 17:14-17.

Wakkinen, W.L., K.P. Reese, J.W. Connelly, and R.A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. *Wildlife Society Bulletin* 20:425-426.

Zablan, M.A., C.E. Braun, and G.C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. *Journal of Wildlife Management* 67:144-154.

# CHAPTER 2
# GREATER SAGE-GROUSE RESPONSE TO NATURAL GAS FIELD DEVELOPMENT IN WESTERN WYOMING

Populations of greater sage-grouse (*Centrocercus urophasianus*) throughout North America are one half to one third the size of those during the late 1960s (Connelly et al. 2004). Populations currently occupy 56% of the species' pre-European settlement distribution (Schroeder et al. 2004). Throughout Wyoming between 1965 and 2003, greater sage-grouse populations declined an average of 5.2% annually and the average number of males per lek declined 49% (Connelly et al. 2004). Among the potential causes of these declines are habitat alterations associated with oil and gas development (Braun 1998).

Currently the BLM controls approximately 2.7 million ha that are in production status for oil, natural gas, or geothermal energy (Knick et al. 2003). Connelly et al. (2004) estimated that in 2003 a minimum of 25-28% of the total area delineated by a 50-km buffer around the pre-settlement distribution of sage-grouse (*Centrocercus* spp.) within western North America was influenced by oil and natural gas well pads, pipelines, and roads. Development of oil resources began in Wyoming in the early 1880s (Salt Creek and Dallas Dome oil fields), but the industry has placed emphasis on the development of natural gas resources since the 1960s (Braun et al. 2002, Connelly et al. 2004, T. E. Rinkes, Bureau of Land Management, Lander, Wyoming; personal communication). In 2003, 6 major oil and gas producing fields in the Green River Basin of southwestern Wyoming covered over 8,740 $km^2$, and active and potential wells numbered 7,890; by 2015, natural gas development in the region is expected to increase by 40% (Connelly et al. 2004).

Potential impacts of gas and oil development to sage-grouse include physical habitat loss, habitat fragmentation, spread of exotic plants, increased predation probabilities, and greater anthropogenic activity and noise resulting in displacement of individuals through avoidance behavior (Connelly et al. 2004). Greater sage-grouse leks within 0.4 km of coalbed methane (CBM) wells in northern Wyoming had fewer males per lek and lower annual rates of population growth compared to leks situated >0.4 km from a CBM well (Braun et al. 2002). The extirpation of 3 lek complexes within 0.2 km of oil field infrastructure in Alberta, Canada, was believed to be associated with oil-field-related disturbances (Braun et al. 2002, Aldridge and Brigham 2003). Additionally, the number of displaying males on 2 leks within 2 km of active coal mines in northern Colorado declined by 94% over a 5-year period following an increase in mining activity (Braun 1986, Remington and Braun 1991).

Identifying causes of population declines has remained elusive. Remington and Braun (1991) theorized that regional distributions rather than numbers of breeding greater sage-grouse were altered by coal mining activity in Colorado. This displacement theory is supported by several studies. Female greater sage-grouse disturbed on leks during the breeding season by natural gas development activities in Wyoming moved farther from the lek to nest compared to less disturbed females (Lyon and Anderson 2003). Greater sage-grouse in Alberta, Canada avoided nesting in areas with increased levels of human development (e.g., roads, well sites, urban habitats, cropland), and females with chicks avoided areas with high densities of visible oil wells (Aldridge 2005). Lesser prairie-chickens (*Tympanuchus pallidicinctus*) in Kansas selected habitats removed from anthropogenic features (Hagen 2003). Patch occupancy probabilities of Gunnison sage-grouse (*Centrocercus minimus*) in Colorado were positively correlated with distance to roads (Oyler-McCance 1999).

However, potential negative effects on population levels also have been suggested. Female greater sage-grouse disturbed at leks had lower nesting propensity relative to less disturbed individuals in Wyoming (Lyon and Anderson 2003). Aldridge (2005) reported that greater sage-grouse chick survival decreased as well densities within 1 km of brooding locations increased in Canada. Hagen (2003) suggested that a lesser prairie-chicken population impacted by anthropogenic activity in Kansas had lower nest success and female survival probabilities compared to a non-impacted population.

In central and western Wyoming, greater sage-grouse populations and habitats are considered to be an internationally significant stronghold for the species (Connelly et al. 2004). Currently, existing and proposed oil and gas wells in Wyoming are located primarily within sagebrush (*Artemisia* spp.) dominated landscapes (Knick et al. 2003) that are important for greater sage-grouse populations. Although evidence exists that greater sage-grouse are negatively influenced by the development of oil and gas reserves (Braun et al. 2002, Aldridge and Brigham 2003), the reaction of populations to specific components of developing fields are not well understood, and it is unknown if population declines are resulting from displacement or reduced population growth. Additionally, land management agencies stipulate restrictions on some types of development during breeding and nesting seasons to protect sage-grouse, but the effectiveness of those stipulations is unknown.

I investigated potential impacts of natural-gas-field development on greater sage-grouse populations in the upper Green River Basin of western Wyoming. The specific gas-field components that I investigated were drilling rigs, producing wells, and main haul roads. I compared temporal changes in the number of displaying males with respect to lek-to-drilling rig, producing-well, and main-haul-road distances, producing-well and haul-road densities within specific distances of leks, and traffic activity levels and timing on main haul roads near leks to test the null hypothesis that natural gas

development has no effect on greater sage-grouse breeding populations. I also investigated survival, lek tenacity, and breeding season habitat selection by males relative to cumulative levels of gas field development surrounding leks to address the question of individual male responses to energy development.

Because natural gas development in the upper Green River Basin occurs primarily within sagebrush dominated landscapes, my investigation of the responses of female greater sage-grouse to energy development concentrated on 2 demographic stages dependent on these habitats (nesting and early brood-rearing [hatch through 2 weeks post-hatch]). I examined distances moved between consecutive years' nests, used versus available nesting and early brood-rearing habitats, and successful (i.e., hatched or survived) versus unsuccessful nests and broods with respect to gas-field-development levels to test the null hypothesis that natural gas development has no effect on greater sage-grouse nesting and brooding habitat selection, nest success probabilities, or brood survival. Finally, I used population modeling and life table response experiments to investigate the effect of natural gas development on female greater sage-grouse population growth. I compared populations of individuals impacted by natural gas infrastructure during the breeding and nesting season(s) to individuals in non-impacted populations to test the null hypothesis that natural gas development has no effect on growth or demographic rates of female greater sage-grouse populations.

**STUDY AREA**

The study area (42°60′ N, 109°75′ W) was primarily within the boundaries of the Pinedale Anticline Project Area (PAPA), but included portions of the Jonah II gas field (Figure 1; Bureau of Land Management 2000). The study area encompassed 51,550 ha and was dominated by big sagebrush (*Artemesia tridentata* spp.) and high-desert vegetation. Elevations ranged from 2,100 to 2,350 m and precipitation averaged 30 cm annually (Western Regional Climate Center, Reno, Nevada, USA). The first natural gas well was drilled in the PAPA in 1939, but only 23 additional wells were drilled in the area by 1997. In May 1998, the BLM approved exploratory drilling of 45 wells prior to completion of the Environmental Impact Statement (EIS). The final EIS and the BLM's Record of Decision were approved in 2000. Full development of the PAPA is expected to continue for the next 10-15 years, and the minimum life-expectancy of the field has been estimated at 59 years. The BLM's record of decision approved construction of 700 producing well pads with maximum densities of 1 well pad per 16 ha (equivalent to 16 well pads per 2.59 $km^2$ [1 $mile^2$]), 645 km of pipeline, and 445 km of road (Bureau of Land Management 2000). According to information supplied by the Wyoming Oil and Gas

Conservation Commission (Casper, WY, USA), 780 natural gas wells were drilled within the PAPA and Jonah gas fields between 1998 and 2004.

## FIELD METHODS

### Lek Analyses

*Lek Counts.*--Known leks within 6.4 km of the PAPA borders were used for the lek count analyses (Figure 2; Bureau of Land Management 2000). The 6.4 km represents twice the distance suggested in the sage-grouse management guidelines (Connelly et al. 2000b) for non-manipulation surrounding a lek in contiguous habitats. Annual lek counts were conducted by personnel with the Wyoming Cooperative Fish and Wildlife Research Unit (COOP), the Wyoming Game and Fish Department (WGFD), and the BLM Pinedale Field Office. Lek counts were conducted according to standardized methods outlined by the WGFD's Sage-Grouse Technical Committee (Cheyenne, WY, USA; also see Connelly et al. 2003:19-20). Each lek was visited ≥3 times from March 20 through May 15. Data recorded during each visit included: (1) total number of males; (2) total number of females; (3) total number of unclassifiable grouse; (4) ground condition (i.e., snow, clear) on lek at time of count; (5) precipitation (i.e., snow, rain, sleet) at time of count; (6) percent cloud cover at time of count; (7) estimated wind speed at time of count; (8) estimated temperature at time of count; (9) the time of day the count was conducted; and (10) any comments relevant to the count.

In addition, the number of vehicles using haul roads between 0 and 1.3 km from a lek was recorded during each count (i.e., early morning hours) for 7 leks counted from a main haul road. To monitor traffic volumes, I installed pneumatic axle counters from April 1 through April 30 on roads closely associated with 9 leks. Since the pneumatic counters counted axles, not vehicles, and much of the traffic associated with the Pinedale Anticline gas field consisted of vehicles with multiple axles (i.e., tractor-trailers), the numbers represent an index of traffic volumes rather than actual vehicles.

*Trapping.*--I captured male and female greater sage-grouse on or near 14 leks from mid-March through April, 2000-2004 by spot-lighting and hoop-netting (Giesen et al. 1982, Wakkinen et al. 1992). Each captured grouse was classified as a yearling (first breeding season) or adult (≥ second breeding season) based on the shape of the outermost wing primaries (Eng 1955). I secured radio transmitters with a PVC-covered wire necklace (Advanced Telemetry Systems Inc., Isanti, MN, USA). Transmitters weighed 19.5 or 25.5 g with a battery life expectancy of 530 or 610 days, respectively, and were equipped with motion sensors (i.e., radio-transmitter pulse rate influenced by activity).

*Male Habitat Selection.*--To identify roost locations of males during the day, I used hand-held receivers and Yagi antennae to locate radio-equipped males between 1000 and 1500 hrs 1 to 2 times

from April 1 to April 30. Locations were recorded with a hand-held, 12-channel Global Positioning System (GPS; Garmin 12; Garmin International, Olathe, KS, USA).

**Female Habitat Selection and Demographic Analyses**

*Female Nesting Habitat Selection.*--I monitored radio-marked females at least twice weekly through pre-laying (April) and nesting (May-June). I located nests of radio-marked birds by circling the signal source until females could be visually observed. Rubber boots were worn while confirming nest locations to reduce human scent. I monitored incubating females after nest identification from a distance of 60 m or more to minimize the chance of human-induced nest predation or nest abandonment. I recorded nest fate (successful or unsuccessful) when radio monitoring indicated the female had left the nesting area. Nests were considered successful if ≥1 egg hatched, indicated by presence of detached eggshell membranes (Wallestad and Pyrah 1974). Nest locations were recorded with a hand-held, 12-channel GPS. The area around depredated nests was searched for hairs, scat, tracks, or other signs left by the predatory species, and condition of the nest area and eggshell fragments were noted. Hairs and scat were sent to the Wyoming Game and Fish Laboratory (Laramie, WY, USA) for species identification. Sargeant et al. (1998) described nest conditions following depredation by several species and I used their descriptions to assist in identification of nest predators. I monitored unsuccessful females twice weekly to assess re-nesting attempts.

I evaluated vegetation between late May and early June at nest sites. To minimize differences resulting from herbaceous growth, I measured vegetation at successful and unsuccessful nests concurrently beginning from the first successful hatch. I evaluated vegetation along 2 perpendicular 30-m transects that intersected the nest bowl. Orientation of the first transect was randomly assigned. I measured herbaceous vegetation characteristics within a 20×50-cm quadrat using the Daubenmire (1959) canopy-cover method at 0.0 m (transect intersection), 1.0 m, and 2.5 m from the intersection along each 15-m portion of the 30-m transect radiating from the nest (12 points measured). Herbaceous vegetation variables included total herbaceous cover, standing grass cover, and forb cover (including winterfat [*Eurotia lanata*] and fringed sagewort [*A. frigida*]). I grouped and classified grass species as either new or residual (i.e., standing-dead). I estimated maximum droop height (i.e., the highest naturally growing portion of the plant excluding flowering stalks) of new and residual grasses by measuring the average tallest grasses (estimated visually) occurring within each quadrat. Categorical estimates of herbaceous cover were converted to percentages (1 = 2.5%, 2 = 15%, 3 = 37.5%, 4 = 62.5%, 5 = 85%, 6 = 97.5%; Daubenmire 1959) for each of 12 quadrats, and I averaged height and converted cover estimates from the 12 points to derive a single estimate for each variable per nest.

*Female Brood-rearing Habitat Selection and Productivity.*--I located females that nested successfully weekly from hatch through 15 August. Females with ≥1 chick were considered successful through each brooding stage (week). Brooding locations of females successful through early brooding stages (i.e., ≥1 chick 14 days post-hatch) were recorded with a hand-held, 12-channel GPS. I based chick existence on either visual confirmation of chick(s) or reactions of brooding females to the presence of a potential predator (i.e., researcher; Schroeder et al. 1999). Successfully nesting females recorded as having no chicks were relocated 2-4 days following the initial location to confirm brood loss. Fledge estimates were obtained through flush counts during the last 2 weeks in August, and were an estimate of the number of chicks produced per brood.

*Female Annual Survival.*—Survival of brooding females was assessed weekly from hatch through August. Non-brooding females were monitored from long-range weekly from nest loss through June, and bi-weekly from 1 July through August. I assessed female survival from 1 September through March using a fixed-wing aircraft (Mountain Air Research, Driggs, ID, USA); flights were conducted at least bi-monthly during fall and winter. I used mortality sensors to evaluate female survival during these stages.

*Female Chick Winter Survival.*--I captured chicks (birds hatched that spring) in August 2004 by spotlighting radio-equipped brood-rearing females. Chicks present with the brooding females were captured using hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992). Blood samples were collected from captured chicks and sent to the Wyoming Game and Fish Laboratory (Laramie, WY, USA) to determine sex. I secured 16-g radio transmitters with a battery life expectancy of 500 days and equipped with motion-sensors to chicks with PVC-covered wire necklaces (ATS, Isanti, MN, USA). Chicks were weighed to ensure radio transmitters could be safely attached (Caccamise and Hedin 1985). I assessed chick survival from 1 September through March using a fixed-wing aircraft (Mountain Air Research, Driggs, ID, USA), and used the motion-sensors to evaluate survival.

## STATISTICAL METHODS

### Lek Analyses

I defined the area of interest as the area within 10 km of study leks (Figure 2; Bureau of Land Management 2000). Gas field infrastructure was spatially mapped within the area of interest using ArcGIS 9 (Environmental Systems Research Institute, Redlands, CA, USA). Well locations were obtained from the Wyoming Oil and Gas Conservation Commission (WOGCC; Casper, WY, USA); because the WOGCC well locations sometimes represent bottom-hole versus well-head (i.e., location on surface) location, I verified well locations using a hand-held, 12-channel GPS (Garmin 12; Garmin

International, Olathe, KS, USA). Road locations were provided by the BLM (Pinedale Field Office, Pinedale, WY, USA) and verified using maps provided by Western EcoSystems Technology, Inc. (Cheyenne, WY, USA). Dates corresponding to well pad construction, drilling, and production timing were obtained from the Wyoming Oil and Gas Conservation Commission. The information associated with each well was sent to the responsible gas company (i.e., operator) to verify location, date, and well status. Road construction dates were estimated as occurring 1 week prior to initiation of drilling for the well accessed by that road. Gas-field-infrastructure layers were dynamic and were modified annually.

I considered the annual breeding period to be from March 1-April 30. Sites with drilling rigs operating during any portion of the strutting period were considered drilling locations; sites with gas wells yielding gas during any portion of the strutting period were considered producing gas well locations; and roads built prior to or during the strutting period were considered active road locations. Producing well locations represent all producing wells and do not represent well pads (i.e., multiple wells located on a single well pad are considered independently). Roads accessing ≥5 producing wells were categorized as main haul roads, and those accessing <5 wells were categorized as secondary roads. Traffic volumes on main haul roads during the breeding season were estimated as average axle hits per day (axle/day). I categorized leks as having vehicle influence during the strutting period if ≥1 vehicle was recorded on roads within 1.3 km during ≥1 lek counts.

Measured variables are summarized in Table 1. Lek-to-drilling-location distances (km; Drill_Dist) and lek-to-producing-well-location distances (km; Well_Dist) were estimated from lek center to well-head location, and lek-to-main-haul-road distances (km; Road_Dist) were estimated from lek center to the closest point along main haul roads. Direction to drilling locations and producing well locations were direct bearings. Direction to roads was the bearing to the closest point along the road. The total length of main haul road (km; Road_TotalLength) and the total number of producing wells (Well_Density) were calculated within 1-km buffers radiating from lek centers (i.e., total length of main haul road within 1 km, within 2 km, etc.). To quantify the position of a lek in relation to gas field infrastructure, the number of quadrats (i.e., directionally based quarter circle wedges delineated by the 4 cardinal directions radiating from leks) occupied by ≥1 producing well (1 through 4; Well_Occupied) was estimated within 1-km buffers radiating from lek centers.

To guard against clumped (i.e., contagious) data distribution effects (Sokal and Rohlf 1995) for the variables estimated within 1-km buffers (i.e., Well_Occupied and Road_TotalLength), I selected the first buffer distance at which ≥67% of the leks had non-zero values for the 2 independent variables. The number of quadrats containing a well within 5 km (Well_Occupied5) and total length of main haul

road within 3 km (Road_TotalLength3) of the lek were the first distance buffers containing ≥67% non-zero values; these selected distance buffers were used for subsequent analyses.

Digital elevation maps (DEM; Wyoming Geographic Information Science Center [WyGISC], University of Wyoming, Laramie, WY, USA) were used to identify viewsheds (i.e., the area visible from lek centers) from ground level at lek centers to ground level and to a height of 50 m at drilling locations. Drilling locations visible at ground level were considered to be within full view of leks (Full_Sight), drilling locations visible at 50 m but not at ground level were considered to be within partial view of leks (Partial_Sight), and drilling locations not visible at ground level or 50 m were considered to be blocked from view of leks (No_Sight). I also used the viewsheds for each lek at ground level to estimate the total linear distance of main haul road visible from the lek. All distance, direction, visibility, and numerical estimates were calculated using ArcGIS 9 (ESRI, Redlands, CA, USA), Animal Movement 2.04 (Hooge and Eichenlaub 2000) and Hawth's Analysis Tools 3.04 (Beyer 2004).

Greater sage-grouse response was estimated as the change in the maximum number of males attending an individual lek through time. For lek counts to be considered reliable, leks had to be counted ≥3 times annually and the counts had to be separated by ≥5 days (Connelly et al. 2003). I used the average number of males from the 3 highest male counts annually to estimate the maximum number of males attending a lek. Overall change in the number of males attending an individual lek (Overall_Change) was estimated as the proportional change in the maximum number of males from 1999 to 2004. For leks where reliable counts were not available in 1999, Overall_Change was calculated from the first year with reliable counts. Annual change in the number of males attending an individual lek (Annual_Change) was estimated as the proportional change in the maximum number of males annually (i.e., maximum male attendance estimate differences between 1999 and 2000, 2000 and 2001, etc.). I calculated Annual_Change for years with reliable counts; if lek counts on an individual lek for a specific year were deemed unreliable, Annual_Change was not calculated for that lek that year or the following year. Overall_Change and Annual_Change were apparent estimates. I did not weight proportional change estimates by the maximum number of males occupying the lek, thus the actual numerical change in the number of males represented by the proportional change estimate was dependent on lek size. Annual variation in the number of males attending an individual lek was estimated as the standard deviation of all counts from that lek.

*Male Habitat Selection.*--Adult male lek tenacity (i.e., probability of a male remaining on a lek throughout the breeding season) and breeding season survival probabilities were assessed using radio-equipped individuals. I considered those individuals that were never located on or near the lek where

they were captured (i.e., lek-of-capture), but documented alive during the breeding season, to have deserted the originally attended lek (assumed to be the lek-of-capture). I did not attempt to document these individuals at alternative leks, thus desertion probability estimates solely reflect the probability of not attending the lek-of-capture. Breeding season (March 15-April 30) survival probabilities were calculated using known-fate models (logit link functions) in program MARK (White and Burnham 1999) for those individuals that remained at the lek-of-capture. Three 2-week observation occasions were used and survival data were left-censored to date-of-capture. I estimated the annual percentage of yearling males as the ratio of trapped yearlings to total number of trapped males by lek, and annual date of peak male attendance was estimated as the date when the annual high count was recorded. Distances (km) from lek to male roost locations were estimated from lek-of-capture centers for those individuals attending the original lek.

I used an ordered approach to the statistical analyses. Results from each level of analysis were used to designate treatment and control categories for subsequent analyses. Initially, I considered leks as the sample units and investigated relationships between Overall_Change and independent gas-field-related variables averaged by lek (Drill_Dist, Well_Dist, Road_Dist, Well_Occupied5, and Road_TotalLength3). Using control levels suggested from these analyses, I investigated differences in mean Annual_Change by categories defined by the independent variables (e.g., lek-years categorized by annual Drill_Dist, annual Well_Dist, etc.). For these second-level analyses, categories were used as the sample units, and results from the first-level analyses were used to delineate treatment and control leks by year. Second-level analyses were used to refine treatment effect levels and investigate within-treatment-level influences (e.g., direction to drilling rig, drilling rig visibility, etc.). The final analyses investigated gas-field-infrastructure impacts by comparing mean Annual_Change of leks categorically delineated by the total number of potential gas-field-related influences. The second-level results were used to designate treatment and control leks for third-level analyses. I also used the third-level categorization to compare lek tenacity, survival, and habitat selection of individual males. Because of the nature of this approach, results necessary for explaining how I investigated second- and third-level relationships are presented in the methods.

**First Level: Initial Determination of Treatment and Control Leks**

I used a principal components analysis (PCA) to summarize covariation patterns present in the 5 primary gas field-related independent variables (Drill_Dist, Well_Dist, Road_Dist, Well_Occupied5, Road_TotalLength3) because of potential collinearity problems identified through correlation analysis

(Philippi 1993). Principal components (PC) with eigenvalues >1 were retained (Hair et al. 1995), and Overall_Change was regressed against retained PC scores.

Using leks as the sample units, I regressed Overall_Change against Drill_Dist, Well_Dist, Road_Dist, Well_Occupied5, and Road_TotalLength3 independently. General relationships were initially assessed by plotting mean distance and numerical estimates against Overall_Change using SigmaPlot (SPSS Inc., Chicago, IL, USA). I used the scatterplot-suggested shape of the relationship to determine regression equations, and refined those equations using PROC NLIN or PROC REG (SAS Institute Inc., 1990).

To estimate the level at which male lek attendance appeared to be influenced by independent variables for curvilinear relationships, I used the portion of the regression equation that approximated independent variable effect. This effect is approximated by the slope coefficient [*b*] portion of equation with general form of $[e^{(-bX)}]$ (see Figure 5). I determined the variation in Overall_Change expected from a non-impacted group of leks through visual assessment of the curved relationships. Variation among non-impacted populations was estimated as the standard deviation of the Overall_Change for the group of leks located obviously within the flattened portion of the curve. By setting the effect portion of the regression equation $[e^{(-bX)}]$ equal to control variation and solving for *X*, I estimated the level of the independent variable where the total change in the slope of the regression line past that point was equal to the expected variance in the Overall_Change of the control population. This point represented the level of independent variable effect influencing male lek attendance. These techniques are similar to those used to find range-of-influence distances in geostatistical analyses of semivariograms (Royle et al. 1980).

**Second Level: Refinement of Potential Treatment Effect and Within Treatment Level Influences**

I investigated univariate relationships using independent variables designated by distance or numerical categories as sample units. The impact distances of lek-to-disturbance-source estimated from the curvilinear relationships were used to designate treatment and control categories for the distance relationships (Drill_Dist; Well_Dist; Road_Dist). Within the treatment distances, each lek-year was categorized into 1-km designated groups based on annual distance to individual disturbance source. Control leks for the distance relationships were situated beyond impact distances estimated from the curvilinear relationships.

*Drilling Rig.*--Drill_Dist treatment categories included 6 groups: 0-1.0 km, 1.1-2.0 km, 2.1-3.0 km, 3.1-4.0 km, 4.1-5.0 km, 5.1-6.2 km; leks situated >6.2 km from a drilling rig were considered controls. Mean differences in Annual_Change between individual treatment groups and controls were

assessed using separate-variance two sample *t*-tests ($t_{df}$, *p*-value; *t*-tests). Treatment leks were additionally compared in terms of direction from lek to drilling rig and drilling rig visibility. The directions from leks to drilling rigs were categorized northeast, northwest, southeast, or southwest based on cardinal direction from the closest drilling rig. To ensure that direction and visibility relationships were not compounded by distances to drilling rigs, I used one-way analysis of variance ($F_{df}$, *p*-value) to compare Drill_Dist between direction and visibility categories. If drill distances differed significantly, lek-years were removed from the category with the largest sample until Drill_Dist were statistically similar between categories. Mean differences in Annual_Change between direction and visibility categories were assessed using one-way analysis of variance, and mean differences in Annual_Change between treatment categories and controls were assessed using *t*-tests.

*Producing Well.*--Well_Dist treatment categories included 5 groups: 0-1.0 km, 1.0-2.0 km, 2.1-3.0 km, 3.1-4.0 km, 4.1-4.7 km; leks situated >4.7 km from a producing gas well were considered controls. Mean differences in Annual_Change between individual treatment groups and controls were assessed using *t*-tests. Mean total number of producing wells within 3 km (Well_Density3; 3 km based on Dist_Well *t*-test results) was compared to Overall_Change using regression. Because the relationship was curvilinear, the number of wells at which male lek attendance was influenced was estimated using methods previously outlined. Additionally, Well_Density3 was categorized to reflect the distribution of the data (1-3, 4-6, 7-9, 10-15, >15 wells). Mean differences in Annual_Change between Well_Density3 treatment groups and controls (i.e., leks >4.7 km from a producing well) were assessed using *t*-tests. Total number of quadrats containing wells within 5 km (Well_Occupied5) was categorized as 1, 2, 3, or 4 well-occupied quadrats. Mean difference in Annual_Change between Well_Occupied5 categories and controls (i.e., leks with no wells within 5 km) were assessed using *t*-tests. Annual_Change was additionally compared in terms of categorical direction to closest producing well within 3 km. The directions from leks to producing wells were categorized northeast, northwest, southeast, or southwest based on cardinal direction from closest well to lek. To ensure that direction relationships were not compounded by distance to producing well, I used one-way analysis of variance to compare Well_Dist between direction categories. If well distances differed significantly, lek-years were removed from the category with the largest sample until Well_Dist were statistically similar between categories. Mean differences in Annual_Change between direction categories were assessed using one-way analysis of variance.

*Main Haul Road.*--Road_Dist treatment categories included 6 groups: 0-1.0 km, 1.1-2.0 km, 2.1-3.0 km, 3.1-4.0 km, 4.1-5.0 km, 5.1-6.1 km. Treatment categories for total length of main haul road within 3 km (Road_TotalLength3) were developed to represent the distribution in the data (0.1-5.0 km,

5.1-7.0 km, 7.1-9.0 km, 9.1-12.0 km, >12.1 km). Leks situated >6.1 km from a main haul road were considered controls for both comparisons. Mean differences in Annual_Change between Road_Dist and Road_TotalLength3 treatment groups and controls were assessed using *t*-tests. The total length of main haul road visible within 3 km of a lek (Road_Visible3) was expressed as a proportion of Road_TotalLength3; proportional differences were compared between treatment groups using Chi-squared analysis. Additionally, Road_Visible3 was categorized to represent the distribution in the data (0-0.5 km, 0.6-1.0 km, 1.1-2.0 km, >2.1 km) and direction to closest point on main haul road was categorized based on the cardinal directions (i.e., 1 through 4); mean differences in Annual_Change among treatment groups were assessed using one-way analysis of variance.

Traffic volume influences on male lek attendance were assessed by regressing mean axle/day against Overall_Change. Mean axle/day were additionally categorized to represent the distribution in the data (1-20, 21-50, 51-100, 101-200, >200 axle/day) and mean Annual_Change of treatment categories were compared to controls (i.e., leks >6.1 km from a main haul road) using *t*-tests. Mean Annual_Change of treatment leks within 1.3 km of a main haul road categorized as having vehicle influence during the strutting period were compared to treatment leks categorized as not having vehicle influence during the strutting period using *t*-tests.

**Third Level: Inclusive Gas Field Infrastructure Impacts**

Using estimated potential influence distances from the categorical analyses, I refined the total distance of potential impact for each of the 5 primary impact sources: Drill_Dist ≤5 km, Well_Dist ≤3 km, Road_Dist ≤3 km, Well_Density3 ≥5 wells, and Well_Occupied5 ≥3 occupied quadrats. Each lek-year was subsequently categorized based on the number of potential influences occurring within these distances (i.e., ≤2 impacts and ≥3 impacts); control lek-years were those with none of these factors occurring within the specified levels. Mean Annual_Change of overall treatment categories was compared to controls using *t*-tests. Expected adult male desertion probabilities were estimated using the proportion of deserting control individuals. Observed desertion probabilities were compared to expected probabilities inclusively and by treatment category using Chi-squared analysis; due to sample sizes <25 in certain instances, I corrected Chi-square estimates with a continuity correction (Dowdy and Wearden 1991). Male breeding season survival differences between treatment categories were based on confidence interval overlap. Because the magnitude of the standard deviation could be related to lek size, I standardized annual lek attendance variation estimates by dividing the standard deviation by the maximum number of males attending the lek. Mean standardized annual variation in male lek attendance and mean lek-to-day roost distances were compared between treatment categories and

control leks using *t*-tests. Average annual differences in the Julian date of peak lek attendance were compared between treatment leks combined (i.e., ≤2 and ≥3 impact categories combined; combined due to sample size constraints) and controls using paired *t*-tests. The average annual proportion of yearling males was compared between treatment categories combined and controls using Chi-squared analysis. Expected annual proportions were estimated from yearling to total male proportions captured from non-impacted leks.

All statistical procedures in the lek analyses were performed using SAS 8.2 (Statistical Analysis Software, Cary, NC, USA) and MINITAB 13.1 (Minitab Inc., State College, PA, USA); statistical significance was assumed at $p < 0.05$.

**Female Habitat Selection Analyses**

I delineated the spatial area of interest based on the potential for female habitat selection to be influenced by gas field infrastructure because delineating the boundaries used to define the area of available habitat (i.e., the spatial scale of resource availability) could influence selection analyses (Erickson et al. 2001). I used known leks ($n = 12$) within 3.2 km (distance the sage-grouse management guidelines [Connelly et al. 2000b] suggest for non-manipulation surrounding a lek in contiguous habitats) of the Pinedale Anticline crest (Figure 3; Bureau of Land Management 2000) as an initial delineation of the area of interest. Because greater sage-grouse nests are spatially associated with lek location within 5 km (Holloran and Anderson 2005), I delineated the final area of interest with 5-km buffers around those leks. Females that nested within this area between 2000 and 2004 were used for analyses.

To identify potentially suitable nesting habitat within this area, I initially used Gap Analysis Program (GAP) landcover layers (WyGISC, University of Wyoming, Laramie, WY, USA) to identify all areas dominated by sagebrush. Within these sagebrush dominated areas, I identified potentially suitable (i.e., available) nesting habitat as all areas within 1 standard deviation of the mean slope and aspect of the nest sample ($n = 162$) using digital elevation maps (DEM; WyGISC, University of Wyoming, Laramie, WY, USA). Identification of suitable early brood-rearing habitat initially considered all areas within the area of interest except those areas dominated by bare ground or exposed rock (GAP; WyGISC, University of Wyoming, Laramie, WY, USA). Within these areas, I designated available early brood-rearing habitats as those areas within 1 standard deviation of the mean slope and aspect (DEM; WyGISC, University of Wyoming, Laramie, WY, USA) of identified early brood-rearing sites ($n = 49$).

I spatially mapped gas field infrastructure within the delineated area of interest (5-km buffer around known leks within 3.2 km of Pinedale Anticline crest). Locations of drilling rigs, producing wells, and roads established for the lek analyses described above were used for the analyses of females. I considered the annual nest initiation period to be from April 15-May 15, the annual nest incubation period to be May 1-June 15, and the annual early brood-rearing period to be June 1-July 1. Sites with drilling rigs operating during any portion of these periods were considered drilling locations. Sites with gas wells yielding gas during any portion of these periods were considered producing gas well locations. Roads built prior to or during these periods were considered active road locations and were categorized as main haul roads if they accessed ≥5 individual producing wells. Distances from nests and early brood-rearing locations to drilling rigs and producing gas wells were estimated to well-head locations. Distances to main haul roads were estimated to the closest point on the roads.

The potential area of influence surrounding nests was estimated as twice the mean distance between consecutive years' nests (1,480 m; Holloran and Anderson 2005). The potential area of influence surrounding early brood-rearing locations was estimated as the maximum daily distance traveled by broods during the early brood-rearing period (1,000 m; N. A. Burkepile, University of Idaho, Moscow, ID, USA; personal communication). I calculated the total number of producing wells and the total length of main haul road within these distances. Distance variables used for nesting and early brood-rearing habitat selection analyses included: distance from nest or early brood-rearing site to closest active drilling rig (Drill_Dist), distance to closest producing gas well (Well_Dist), and distance to closest point on a main haul road (Road_Dist). Density variables used for nesting habitat selection analyses included the total number of producing gas wells within 1,480 m of the nest (Well_Density1480) and the total length of main haul road within 1,480 m of the nest (Road_TotalLength1480). Density variables used for early brood-rearing habitat selection included the total number of producing gas wells within 1,000 m of the early brood-rearing site (Well_Density1000) and the total length of main haul road within 1,000 m of the early brood-rearing site (Road_TotalLength1000). Spatial mapping of gas-field-related variables was accomplished using ArcGIS 9.0 (ESRI, Redlands, CA, USA). I calculated distance and numerical estimates using Animal Movement 2.04 (Hooge and Eichenlaub 2000) and Hawth's Analysis Tools 3.04 (Beyer 2004) within ArcView GIS 3.3 (ESRI, Redlands, CA, USA). See Table 1 for variable summary.

*Consecutive Years' Nests.*--To investigate whether temporal changes in the level of development within an individual female's nesting area (i.e., potential area of influence surrounding nests; 1,480 m radius area) influenced habitat selection, I used individuals with identified consecutive years' nests. I calculated Drill_Dist, Well_Dist, Road_Dist, Well_Density1480, and

Road_TotalLength1480 during the nest initiation period from the first year's nest location for that year and the following year. Because of differing development levels surrounding first year nests and the need to standardize for these initial levels, I investigated distances moved between consecutive years' nests in terms of changes in the level of development (versus total development levels) between years. For example, if an individual female nested in 2000 and 2001, was the distance between these 2 nests related to changes in the level of gas field development that occurred within the individual's nesting area between these 2 years? I categorized females based on the total number of differences in gas field infrastructure that occurred between years: ≥3 gas field factors numerically higher or closer, 2 factors changed, 1 factor changed; nests where no change in gas field infrastructure occurred between years were considered controls. One-way analysis of variance ($F_{df}$, *p*-value) was used to assess consecutive years' nest-to-nest distance differences between change categories. I used Chi-squared analysis ($\chi^2_{df}$, *p*-value) to investigate proportional differences in the number of females that moved >930 m (95% confidence interval around mean nest-to-nest distance upper limit; Holloran and Anderson 2005) among categories; expected proportions were estimated from the control sample. Because fate of the first year's nest could influence the distance moved between consecutive years' nests (Holloran and Anderson 2005), I used a Chi-squared test of homogeneity (Dowdy and Wearden 1991) to test for proportional differences in first year successful and unsuccessful nests by treatment category.

*Adult versus Yearling Nest.*--I compared adult and yearling females in terms of Drill_Dist, Well_Dist, Road_Dist, Well_Density1480, and Road_TotalLength1480 during the nest initiation period using 2-sample separate-variance *t*-tests ($t$-value$_{df}$, *p*-value; *t*-test). Due to potential lack of independence associated with nest site fidelity (Holloran and Anderson 2005), consecutive year nests ($n$ = 47) and re-nests ($n$ = 3) were not included in the comparison.

*Used versus Available and Successful versus Unsuccessful Nest Locations.*--I used logistic regression to compare used and available nesting locations from 2000-2004. Again, due to potential lack of independence associated with nest site fidelity (Holloran and Anderson 2005), consecutive year and re-nests were removed from analyses. Available nesting locations were obtained from randomly generated points located within potentially suitable nesting habitat (Beyer 2004). The number of generated random locations equaled the number of nests used for analyses ($n$ = 112). To ensure that random points were distributed throughout the area of interest, I stratified the area into 1.6-km$^2$ blocks based on existing township and range section boundaries (BLM 2000). No more than 2 random points per section were generated. Because of proportional differences in the amount of potentially suitable nesting habitat identified within sections, the stratified technique was employed to guard against excessive clumping of random points. The gas field related variables used to compare used and

available nesting locations included: Drill_Dist, Well_Dist, Road_Dist, Well_Density1480, and Road_TotalLength1480 during the nest initiation period (April 15-May 15).

Logistic regression was also used to compare successful and unsuccessful nests identified from 2000-2003 (2004 data were incomplete and therefore were removed from analyses). Nests of unknown fate (e.g., female killed while feeding during incubation but nest not disturbed; $n = 2$) and nests abandoned due to researcher disturbance ($n = 2$) were removed from the nest fate analyses. All remaining identified nests ($n = 108$; includes consecutive year [$n = 31$] and re-nests [$n = 3$]) were considered. The gas field related variables used to compare successful and unsuccessful nests included Drill_Dist, Well_Dist, Road_Dist, Well_Density1480, and Road_TotalLength1480 during the nest incubation period (May 1-June 15); the habitat variables included residual grass cover and residual grass height (Holloran et al. 2005).

Because gas-field-development variables potentially differed among years (due to increased levels of development through time), I investigated variable differences by year using one-way analysis of variance. Values of gas-development variables for identified nest and available locations were combined for the used versus available analysis. Only variable values for identified nest locations were used for the successful versus unsuccessful analysis. If >2 variables differed significantly by year, I investigated used versus available and successful versus unsuccessful relationships among years independently. If ≤2 variables differed significantly among years, those variables that differed were standardized by year (Sokal and Rohlf 1995) and years were combined for analysis. Due to inherent annual differences in residual grass cover and height resulting from differing environmental conditions (i.e., precipitation levels), I standardized these habitat variables by year.

I considered 18 logistic regression models for the used versus available and 56 models for the successful versus unsuccessful analyses. Models included all 1-, 2- and 3-variable combinations, except where combinations included variables correlated by Pearson's Correlation Coefficients ($r$) ≥ 0.7. To avoid over-parameterizing models (Hosmer and Lemeshow 1989), combinations of 4 variables or more were not investigated. I ranked models using a small-sample size bias adjusted Akaike's Information Criterion ($AIC_c$), and calculated Akaike weights ($w_i$) for each model (Burnham and Anderson 2002). I calculated a relative importance estimate for each independent variable by summing $w_i$-values for all models containing the variable (Burnham and Anderson 2002). I also used a model averaging procedure to calculate weighted mean parameter coefficients for each variable, weights were based on the $w_i$-likelihood for each model in the group of models considered (Burnham and Anderson 2002).

Where I had standardized and combined data among years, I calculated 90% CI around weighted average parameter coefficients (using weighted average standard error estimates) to investigate individual variable potential affect on nest site selection or success probabilities. Averaged model fit was assessed using correct classification contingency tables (predicted probability = 0.5; Menard 1995) adjusted for chance agreement due to differences in sample sizes (Titus et al. 1984).

Where I had separated logistic regression analyses by year, the same group of 18 or 56 models was investigated annually. I obtained a weighted average model for each year, and investigated annual differences in nest site selection or success probabilities through a comparison of 90% confidence intervals (90% CI; calculated using $AIC_c$ weighted average standard errors). Differences in individual gas field related variable parameter coefficients were based on 90% CI overlap. To investigate overall differences associated with annual models by year (i.e., the relationship between probability of a nest or a successful nest and the 5 gas field related variables inclusively), I generated 350 random points in potentially suitable nesting habitat (Beyer 2004). This random sample was run through each year's model and estimated probabilities per random sample point were obtained. Standard errors per probability estimate were generated following Hosmer and Lemeshow (1989) and used to estimate 90% CI around each probability. Averaged annual models were subsequently compared based on the proportion of confidence interval overlap. Nest and random data from years with ≥95% overlap were combined, and the same set of models was used to generate a single overall weighted average model for investigating the relationship of nest site selection or success probabilities relative to gas field infrastructure through the duration of the study. To investigate the relationship suggested by the overall model, I plotted the probability estimates associated with the range of independent variable values against the level of development (e.g., probability of a nest in the presence of inclusively high to low levels of development). To assess averaged model(s) fit, I used correct classification contingency tables (predicted probability = 0.5; Menard 1995).

*Used versus Available and Successful versus Unsuccessful Early Brood-rearing Locations.*-- Because of limited chick mobility during the initial stages of brooding (Patterson 1952), available early brood-rearing habitat depends on nest location (i.e., the entire study area does not represent available early brood-rearing habitat). Therefore, a buffer equal to the upper 95% CI limit of the mean nest-to-early brood-rearing location distance was created around nesting locations for each successfully nesting female with an identified early brood-rearing location (i.e., females with ≥1 living chick 14 days post-hatch). Within each nest buffer area, I generated 1 random point within potentially suitable early brood-rearing habitat; random points were paired with early brood-rearing locations. Used and available locations were compared using paired *t*-tests. Only females included in the nesting analyses

were considered for the early brood-rearing analyses (i.e., females nesting within 5 km of leks located within 3.2 km of Pinedale Anticline crest). Because the fate of the brood was unknown for females killed during the early brood-rearing period, these birds were removed from the early brood-rearing analyses (6 birds). Additionally, females that lost their entire brood prior to our identifying early brood-rearing locations (15 birds) potentially were not selecting brooding habitat, and were removed from the used versus available analysis (these individuals represented the unsuccessful sample in the early brood-rearing chick survival analysis). The gas field related variables for the early brood-rearing selected versus available analysis included Drill_Dist, Well_Dist, Road_Dist, Well_Density1000, and Road_TotalLength1000 during the early brood-rearing period (June 1-July 1).

Because females that lost their entire brood prior to the identification of early brood-rearing locations (15 birds) potentially were not selecting brooding habitat, I did not have accurate brood-rearing locations for these individuals. Therefore, I used levels of development surrounding successful nests to compare successful (i.e., females with ≥1 living chick 14 days post-hatch) and unsuccessful (i.e., females that hatched successfully but with no living chicks 14 days post-hatch) brooding females. I estimated the total number of producing wells and total length of main haul road within the area designated by the upper 95% CI limit of the mean nest-to-early brood-rearing location distance. Additional gas field related variables included Drill_Dist, Well_Dist, and Road_Dist during the early brood-rearing period (June 1-July 1). Successful and unsuccessful brooding females were compared using *t*-tests.

All statistical procedures in the female analyses were performed using SAS 8.2 (Statistical Analysis Software, Cary, NC, USA) and MINITAB 13.1 (Minitab Inc., State College, PA, USA); statistical significance was assumed at $p < 0.05$.

**Female Demographic Analyses**

*Vital Rate Estimation.*--For matrix population modeling (examples: Crouse et al. 1987, McDonald and Caswell 1993, Johnson and Braun 1999, Wisdom et al. 2000, Hoekman et al. 2002, and Hagen 2003), individuals were classified into discrete age or life-history stages, and stage importance was evaluated based on the sensitivity of population growth to variations in stage-specific vital rates (i.e., survival, chick production). The first step in population modeling is to accurately estimate stage-specific vital rates.

The latest recorded hatch date for a first nest (vs. re-nest) was 1 July. Assuming 27 days to incubate (Schroeder et al. 1999), the latest documented initiation of incubation occurred on 4 June. Therefore, I estimated apparent nesting propensity as the number of nesting females divided by the total

number of females surviving to 4 June. Potential age and year effects on nesting propensity were investigated by 95% confidence limit overlap; standard errors were calculated using annual nesting propensity differences between yearling and adult females and between years.

The total number of eggs per clutch was estimated from counts conducted at nests where females were flushed during nest site identification field procedures. Because I attempted not to flush females from nests during the nest search process, clutch size estimates are a sub-sample of individuals. I estimated the number of female eggs per clutch based on juvenile sex ratios established from fall harvest data (54.6% female; Swenson 1986).

Nest success probability estimates were adjusted following Mayfield (1975). For this adjustment, I estimated length of incubation period at 27 days (Schroeder et al. 1999). Because of small sample sizes, re-nests were not considered independently and were grouped with initial nests for annual nest success estimates. Potential age and year effects to nest success probabilities were investigated by 95% confidence interval overlap; standard error estimates for yearling and adult females and per year were calculated following Hensler and Nichols (1981). Because I typically identified a nest following the initiation of incubation (i.e., following clutch completion) and I potentially missed nests destroyed during the egg-laying or early incubation stages (females classified as non-nesters), apparent nesting propensity was a minimum and adjusted nest success could be overestimated.

Survival of broods from hatch through 15 August and associated standard error were estimated using known-fate models in program MARK (White and Burnham 1999); models were developed using design matrices and logit link functions (Cooch and White 2004). Broods were considered to have survived the weekly censor period if chick presence was suggested (see Field Methods). Because the first documented successful hatch was 17 May, I left-censored (staggered entry) broods from 17 May based on hatch date. Additionally, the fate of a brood was unknown if the brooding female was killed during the brooding period, thus I right-censored these broods to date of female mortality. I investigated potential effects of brooding female age and year on brood survival by comparing models using a small-sample size bias adjusted Akaike's Information Criterion ($AIC_c$; Burnham and Anderson 2002). I used respective model ranking to determine potential age and year effects.

Apparent fledge rates (chicks per brood) were estimated by dividing the total number of chicks produced by the total number of females with ≥1 chick the end of August; females that lost their entire brood during brooding stages were not included in chick per brood estimates. Potential age and year effects on fledge rates were investigated by 95% confidence interval overlap; standard errors were calculated from brood size distribution differences between yearling and adult females and between years. Chick summer survival (from eggs to fledge [15 Aug]) was calculated by dividing chick per

brood estimates by the total number of eggs per clutch. Standard error estimate for chick summer survival was calculated following error propagation techniques outlined by Burrough and McDonnell (1998).

Annual survival of females (April-March) and associated standard error were estimated using known-fate models in program MARK (White and Burnham 1999); models were developed using design matrices and logit link functions (Cooch and White 2004). I based survival on monthly census intervals, staggered individual entry into census periods based on date-of-capture, and right-censored lost individuals. Spring and summer mortalities were assumed to have occurred mid-way between census dates (outlined above). Because of relatively long time intervals between winter flights and to be conservative, mortalities documented during the winter flights were assumed to have occurred 1 day after the previous flight date. I investigated potential annual survival effects of age, breeding status (i.e., nesting or non-nesting; brooding or non-brooding), and year by comparing models using $AIC_c$ values (Burnham and Anderson 2002). I used respective model ranking to determine potential age, breeding status, and year effects. Chick winter survival (September - March) also was estimated using program MARK (White and Burnham 1999). Chick loss within 2 weeks of capture was assumed to have been caused by trapping-related influences or lost radio transmitters; these individuals were removed from the sample.

*Deterministic Analysis.*--Individual females were categorized as treatments or controls based on the level of natural gas field development occurring within given distances of the lek-of-capture or nest location. Designation of these groups was based on results obtained from the third level lek analyses and the female habitat selection analyses. Females breeding on leks found to be influenced by natural gas development were categorized as lek treatment individuals; females breeding on non-impacted leks were categorized as control. Additionally, females nesting within 1,480 m of any gas field related structure (i.e., drilling rig, producing well, main haul road) were considered nest treatment individuals; females nesting farther than 1,480 m from gas field development were categorized as controls.

I categorized all individuals potentially impacted either on the lek or at the nest as treatments (All_Treat). All individuals not impacted by natural gas development on the lek or at the nest were categorized controls (All_Control). Females were further separated into treatment groups to isolate the potential effects of gas field related disturbance during specific demographic periods. Individuals that were impacted on the lek but not at the nest were considered lek treatments (Lek_Treat); individuals impacted at the nest but not on the lek were nest treatments (Nest_Treat); and individuals impacted both on the lek and at the nest were lek and nest treatments (LekNest_Treat). Because these groups required individuals to survive the breeding period (required a nest), they were represented by a biased sub-

sample of the population. To remain consistent between group comparisons, I used the nesting sub-sample of the lek impacted individuals, and compared these treatment groups to the nesting portion of the control population (Nest_Control). Additionally, because these groups required a nest (i.e., the sub-sample represented by these groups had 100% nesting propensity rates), I used apparent nesting propensity estimates from all females combined for demographic modeling (constant between groups). Between 1998-2004, females were captured from 5 leks where gas field development levels surrounding leks changed from a control to a treatment situation during the study. Individuals captured from these leks were categorized as pre (Pre_Treat) and post-treatment (Post_Treat) based on annual lek-of-capture impact status. Variables are summarized in Table 1.

I constructed female-based, stage-class population matrices (best visualized by life-cycle graphs) based on vital rate comparisons outlined above. Different life-stages were developed based on potential age or breeding status effects detected through comparison of the vital rates (e.g., if an age effect was detected for annual survival, individuals were differentiated into yearling [$1^{st}$ year breeder] or adult stages). Transfer of individuals between stages was based on the probability of remaining in a stage. Demographic models for separated groups (i.e., treatments and controls) were analyzed using similarly structured matrices. Given the potential bias associated with the sub-sample of individuals represented in the groups requiring a nest (Nest_Control, Lek_Treat, Nest_Treat, LekNest_Treat), population growth estimates for these groups should not be interpreted beyond the life table response experiment comparisons outlined below.

Investigating the sensitivity of population growth to variation in vital rates is a method of evaluating life-stage importance (Wisdom and Mills 1997). By standardizing sensitivity values (the effect on $\lambda$ of absolute changes in vital rates) to a scale between 0 and 1 (represented by elasticity values), proportional effects of vital rate variation on population growth can be investigated (Wisdom and Mills 1997, Mills et al. 1999); elasticity values have the advantage of allowing interpretable comparisons between vital rates (Wisdom and Mills 1997). I used upper level (i.e., matrix entries) elasticity values to compare relative sensitivities between matrix elements within and between groups. Deterministic analysis of the population matrices was accomplished using program MatrixCrunch (D. B. McDonald, University of Wyoming, Laramie, WY, USA) with Mathematica 4.2 (Wolfram Research Inc., Champaign, IL, USA) software.

Because of the annual shift associated with the pre- vs. post-treatment comparison data, population growth could have been influenced by environmental factors not related to gas field development level differences between these groups (i.e., drought). I graphically compared annual sample sizes of pre and post-treatment categories with annual percent normal precipitation levels to

investigate the potential for drought related population growth effects. I averaged monthly precipitation totals from weather stations within and near the study area, and calculated percent normal precipitation by dividing annual levels by long-term averages (average period of record 24 years) to standardize these estimates (Western Regional Climate Center, Reno, NV, USA). Other group comparisons were made between individuals impacted concurrently, thus extrinsic concerns beyond the level of development were essentially standardized.

*Life Table Response Experiment.*--Life table response experiments can be used to quantify population level effects of potential impacts on populations by comparing matrix models developed using vital rates collected from individuals subjected to differing environmental conditions (i.e., treatment vs. control; Caswell 1989, 1996). I was interested in comparing lower-level vital rates (e.g., nesting propensity, nest success, brood survival; as compared to the matrix entries themselves) and the relative effect of variation in each to differences in population growth between treatment and control populations. For these analyses, I followed life table response experiment methods outlined by Caswell (1989 and 1996). For each comparison (e.g., All_Treat vs. All_Control), I calculated a mean matrix using the projection matrices of the groups being compared; sensitivities of these mean matrices were computed. Using the sensitivity values computed from the mean matrix, I derived partial sensitivities for the mean of each lower level vital rate (Caswell 1989). I multiplied the difference (control subtracted from treatment) of each vital rate to the lower level sensitivity to establish the contribution changes in each vital rate had to the overall treatment effect on population growth (Caswell 1996). Caswell (1996) suggests that the contributions represent a measure of the effect of the treatment on the vital rate relative to the sensitivity of population growth to that effect.

*Stochastic Simulations.*--I assessed the effect of demographic stochasticity for each group by conducting simulations using program BetaStoch05 (D. B. McDonald, University of Wyoming, Laramie, WY, USA) with Mathematica 4.2 (Wolfram Research Inc., Champaign, IL, USA) software. The mean and standard error of each vital rate were used to establish beta distributions; for each of 1,000 iterations, a value for each vital rate was selected from these distributions and used in matrix building procedures. Starting population size for each simulation was 1,000,000 individuals, and each simulation was followed for 2,000 years. I investigated differences in population growth between the different groups through 95% confidence interval overlap of the mean time (years) to population extinction. The effect of variability in vital rates on each group was assessed through the estimated change in population growth occurring as a result of the addition of stochasticity. I additionally investigate mean time to extinction of the estimated size of the Pre_Treat population under Post_Treat conditions. Pre-treatment population size was estimated from the maximum number of males on

Pre_Treat leks the year prior to entering Post_Treat status. I assumed the maximum male counts represented 75% of the male population, and assumed twice as many females as males (C. E. Braun; Colorado Division of Wildlife, Denver, CO, USA; personal communication). This population estimate was used as the starting population size for 5,000 iterations through the stochastic model developed for the Post_Treat population.

## RESULTS

### Lek Analyses

I used lek-count information from 21 leks. Overall_Change was calculated from 1999-2004 for 8 leks, from 2000-2004 for 8 leks, from 2001-2004 for 4 leks, and from 2002-2004 for 1 lek, yielding Annual_Change data for 86 lek years. Maximum male lek attendance for the first year of reliable information ranged from 20 to 131 males. I captured and radio-equipped 78 males from 12 leks between 2000-2003.

### First Level: Initial Determination of Treatment and Control Leks

Because of high correlations between independent variables (Pearson's correlation values ≥0.67), I used principal components analysis. The first principal component (PC1) explained 82.3% of the variability among independent variables; based on eigenvalues (>1.0), none of the other principal components were considered. The loadings associated with the independent variables ranged between 0.42 and 0.46, suggesting nearly equal weight was associated with each of the variables (Ramsey and Schafer 1997). The regression relationship between PC1 scores and Overall_Change had a positive slope (Figure 4). The loadings associated with Drill_Dist, Well_Dist, and Road_Dist were positive, whereas those with Well_Occupied5 and Road_TotalLength3 were negative. In general, the loadings suggest that as Drill_Dist, Well_Dist, and Road_Dist decreased, and Well_Occupied5 and Road_TotalLength3 increased, Overall_Change approached a 100% decline (Figure 4).

The relationships between Overall_Change and Drill_Dist, Well_Dist, and Road_Dist were curvilinear (Figure 5). Based on the slope coefficients, the distance from leks at which drilling rigs appeared to have no influence on overall male lek attendance (i.e., variation in the regression relationship equaled control variation) was >6.2 km. For producing gas wells, the regression relationship suggested no influence on leks >4.7 km from a well. Main haul roads did not influence leks >6.1 km from a road. Regression relationships between Overall_Change and Well_Occupied5 (Overall_Change = -0.014 - 0.197[Well_Occupied5]; $R^2$ = 54.6%) and Road_TotalLength3 (Overall_Change = -0.073 - 0.066[Road_TotalLength3]; $R^2$ = 60.6%) were linear with negative slopes.

**Second Level: Refinement of Potential Treatment Effect and Within Treatment Level Influences**

*Drilling Rig.*--The number of males occupying leks within 5 km of a drilling rig declined relative to controls with the exception of leks between 2.1-3.0 km from a drilling rig. Mean Annual_Change among leks categorized by 1-km Dist_Drill buffers and leks >6.2 km from a drilling rig (i.e., controls) suggested that leks within 0-1.0 km ($n$ = 3, $t_{18}$ = -12.49, $p < 0.000$), 1.1-2.0 km ($n$ = 5, $t_8$ = -4.72, $p$ = 0.002), 3.1-4.0 km ($n$ = 11, $t_{11}$ = -2.38, $p$ = 0.037), and 4.1-5.0 km ($n$ = 9, $t_{13}$ = -3.79, $p$ = 0.002) of a drilling rig had significantly greater annual rates of decline than control leks (n = 34). Average annual rates of change on leks within the 2.1-3.0 km ($n$ = 10, $t_{11}$ = -1.64, $p$ = 0.130) and 5.0-6.2 km ($n$ = 12, $t_{24}$ = -1.96, $p$ = 0.061) buffers did not differ significantly from controls (Figure 6).

There did not appear to be visual effects of drilling rigs on lek attendance by males, but the number of males occupying leks generally east of drilling rigs declined. There were no significant differences ($F_3$ = 0.55, $p$ = 0.649) among average Annual_Change in terms of the direction from leks to drilling rigs after standardizing for distance. However, the comparisons between directions to drilling rig categories and controls Annual_Change indicated that leks situated southeast (mean change -24.7%, $n$ = 10, $t_{11}$ = -2.50, $p$ = 0.029) and northeast (mean change -20.7%, $n$ = 15, $t_{25}$ = -3.66, $p$ = 0.001) of an operating drilling rig had significantly greater annual rates of decline, while leks situated southwest (mean change -11.4%, $n$ = 13, $t_{17}$ = -1.76, $p$ = 0.096) and northwest (mean change -11.8%, $n$ = 10, $t_{11}$ = -1.47, $p$ = 0.171) of a drilling rig did not differ from controls (mean change +4.7%, $n$ = 34). Additionally, there were no mean Annual_Change differences ($F_2$ = 0.72, $p$ = 0.493) among treatment leks in terms of drilling rig visibility. However, all three visibility categories declined significantly compared to controls (Full_Sight mean change -27.1%, $n$ = 10, $t_{11}$ = -2.65, $p$ = 0.023; Partial_Sight mean change -14.2%, $n$ = 17, $t_{35}$ = -3.15, $p$ = 0.003; No_Sight mean change -14.8%, $n$ = 21, $t_{30}$ = -2.40, $p$ = 0.023; control mean change +4.7%, $n$ = 34).

*Producing Well.*--The number of males occupying leks within 3 km of a producing well declined relative to controls. The relationships between distance to the closest producing gas well and average annual change in the number of males indicated that leks 0-1.0 km ($n$ = 15, $t_{20}$ = -3.24, $p$ = 0.004), 1.1-2.0 km ($n$ = 11, $t_{21}$ = -3.83, $p$ = 0.001), and 2.1-3.0 km ($n$ = 16, $t_{37}$ = -2.47, $p$ = 0.018) from a well had significantly greater average annual declines in male numbers relative to control leks (i.e., leks >4.7 km from a producing well; $n$ = 30). Average annual change in the number of males on leks situated 3.1-4.0 km ($n$ = 4, $t_4$ = 1.22, $p$ = 0.290) and 4.1-4.7 km ($n$ = 9, $t_{16}$ = -0.38, $p$ = 0.708) did not differ significantly from controls (Figure 6).

Well densities were also related to annual changes in the number of males. The number of males occupying leks declined where there were more than 5 wells within 3 km of the lek. Leks with

>15 producing wells within 3 km (mean change -33.1%, $n = 9$, $t_9 = -2.28$, $p = 0.048$), 10-15 producing wells within 3 km (mean change -37.5%, $n = 4$, $t_6 = -5.12$, $p = 0.002$), 7-9 producing wells within 3 km (mean change -23.2%, $n = 6$, $t_7 = -2.37$, $p = 0.050$), and 4-6 producing wells within 3 km (mean change -26.8%, $n = 7$, $t_{11} = -3.46$, $p = 0.005$) had significantly greater average annual declines compared to control leks (leks >4.7 km from a producing well; mean change +3.5%, $n = 30$). Average annual change in the number of males on leks with 1-3 producing wells within 3 km did not differ significantly from controls (mean change -9.5%, $n = 17$, $t_{35} = -1.76$, $p = 0.088$). The regression relationship between Overall_Change and average number of wells within 3 km (Well_Density3) was curvilinear [Overall_Change = $-0.73+0.66(e^{-0.47(\text{Well_Density3})})$; $R^2 = 61.1\%$]. Using the slope coefficient to solve for the number of wells where total variation in the regression line reached control variation indicated that leks with ≥4.7 producing wells within 3 km were negatively influenced by those wells.

Male lek attendance declined on leks where at least half of the directions from the lek were occupied by a producing well within 5 km. The relationships between the number of quadrats containing a producing well within 5 km and mean Annual_Change indicated that leks with wells in 3 quadrats (mean change -17.9%, $n = 21$, $t_{38} = -2.65$, $p = 0.012$) and 4 quadrats (mean change -28.5%, $n = 12$, $t_{15} = -2.87$, $p = 0.012$) had significantly greater declines in male numbers compared to control leks (leks >5 km from a producing well; mean change +3.5%, $n = 30$). Mean Annual_Change on leks with wells located in 1 quadrat (mean change +2.4%, $n = 9$, $t_{15} = -0.13$, $p = 0.900$) and 2 quadrats (mean change -12.1%, $n = 14$, $t_{24} =$ -1.85, $p = 0.076$) did not differ from controls. Mean Annual_Change did not differ in terms of direction to producing well ($F_3 = 1.41$, $p = 0.254$).

*Main Haul Road*.--The number of males occupying leks within 3 km of a main haul road declined relative to controls. The relationships between distances to nearest main haul road and average annual change in the number of males revealed that leks located within 0-1.0 km ($n = 9$, $t_{19} = -4.02$, $p = 0.001$), 1.1-2.0 km ($n = 30$, $t_{51} = -3.53$, $p = 0.001$), and 2.1-3.0 km ($n = 6$, $t_{15} = -2.70$, $p = 0.017$) of a main haul road declined significantly compared to control leks (leks >6.1 km from a main haul road; $n = 24$). Mean Annual_Change on leks 3.1-4.0 km ($n = 5$, $t_4 = -0.20$, $p = 0.851$), 4.1-5.0 km ($n = 6$, $t_{12} = -1.55$, $p = 0.146$) and 5.1-6.1 km ($n = 6$, $t_7 = -0.40$, $p = 0.703$) from a main haul road did not differ significantly from controls (Figure 6).

When there was more than 5 km of main haul road within 3 km of a lek numbers of males were negatively influenced, but male lek attendance was not influenced by the proportion of road visible from a lek or the direction from the lek to the closest main haul road. The relationships between the total length of main haul road within 3 km and mean Annual_Change indicated that leks with 5.1-7.0 km of main haul road (mean change -14.7%, $n = 11$, $t_{20} = -2.46$, $p = 0.023$), 7.1-9.0 km of main haul

road (mean change -20.2%, $n$ = 10, $t_{17}$ = -3.03, $p$ = 0.008), 9.1-12.0 km of main haul road (mean change -28.4%, $n$ = 11, $t_{16}$ = -3.32, $p$ = 0.004), and >12.1 km of main haul road (mean change -56.4%, $n$ = 4, $t_3$ = -3.86, $p$ = 0.031) had significantly greater declines compared to changes on control leks (leks >6.1 km from a main haul road; mean change +7.2%, $n$ = 24). Average Annual_Change on leks with 0.1-5.0 km of main haul road within 3 km (mean change -1.6%, $n$ = 14, $t_{29}$ = -1.08, $p$ = 0.286) did not differ from controls. The proportion of visible main haul road within 3 km of treatment leks did not differ between treatment buffer groups ($\chi^2_4$ = 8.23, $p$ = 0.083). Additionally, categorizing treatment leks by total distance of visible main haul road within 3 km and comparing average annual change in the number of males by category indicated no significant differences ($F_3$ = 0.11, $p$ = 0.957). Mean Annual_Change for leks with 0-0.5 km of road visible was -19.9% ($n$ = 31), 0.6-1.0 km of road visible was -15.0% ($n$ = 10), 1.1-2.0 km of road visible was -20.2% ($n$ = 5), and >2.1 km of main haul road visible was -13.9% ($n$ = 4). Mean Annual_Change on road treatment leks where the closest main haul road was generally east (-18.5%, $n$ = 20), west (-15.5%, $n$ = 23), north (-11.8%, $n$ = 10), and south (-9.7%, $n$ = 9) did not differ significantly ($F_3$ = 0.23, $p$ = 0.874).

The rate of male lek attendance decline was related to traffic volumes, and vehicle activity on roads during the daily strutting period had an influence on male lek attendance. The regression relationship between average number of axle hits per day (axle/day) and Overall_Change was linear with a negative slope (Overall_Change = -0.18-0.005[axle/day]; $R^2$ = 73.3%). After categorizing lek years based on average number of axle hits per day, I found that leks with 1 to 20 axle/day (mean change -12.8%, $n$ = 9, $t_{22}$ = -2.72, $p$ = 0.013), 21 to 50 axle/day (mean change -13.2%, $n$ = 8, $t_{16}$ = -2.46, $p$ = 0.025), 51 to 100 axle/day (mean change -45.8%, $n$ = 3, $t_3$ = -4.98, $p$ = 0.016), 101 to 200 axle/day (mean change -21.0%, $n$ = 3, $t_5$ = -3.55, $p$ = 0.016), and >200 axle/day (mean change -57.5%, $n$ = 7, $t_8$ = -4.73, $p$ = 0.001) all differed significantly from average annual change on control leks (leks >6.1 km from main haul road; mean change +7.2%, $n$ = 24). Additionally, average axle hits per day for all traffic categories differed significantly ($p \leq 0.041$) from controls designated by leks >3 km from a main haul road (mean change +4.2%, $n$ = 41). Comparing mean Annual_Change between leks at which vehicles used or did not use main haul road within 1.3 km during the daily strutting time period (i.e., vehicle activity during the early morning) indicated that average Annual_Change on leks with traffic (mean change -34.8%; $n$ = 16) declined significantly more than leks without traffic (mean change -11.0%; $n$ = 11, $t_{24}$ = 2.22, $p$ = 0.036).

**Third Level: Inclusive Gas Field Infrastructure Impacts**

Desertions of leks by adult males were higher where there were 3 or more impacts compared to control leks. Average annual change in the number of males on leks with ≥3 impacts ($t_{65}$ = -4.85, $p$ = 0.000) declined significantly relative to changes in control leks; change on leks with ≤2 impacts did not differ from control changes ($t_{19}$ = -2.91, $p$ = 0.072; Table 2). Lek desertion probabilities of adult males captured on treatment leks differed significantly from desertion probabilities of control adult males (i.e., expected desertion probabilities; $\chi^2_1$ = 9.41, $p$ = 0.002). Males deserted leks impacted by ≥3 factors significantly more than expected ($\chi^2_1$ = 6.10, $p$ = 0.014; Table 2).

Male survival probabilities during the breeding season were lower for lightly impacted compared to heavily impacted leks, but habitat selection by males during the breeding season was not influenced by development levels surrounding a lek. Male survival probabilities did not differ at the 70% level between treatment and control leks; however, male survival differed between leks impacted by ≥3 factors and leks impacted by ≤2 factors at the 80% level (Table 2). Additionally, survival probabilities of leks impacted by ≤2 factors and control leks combined (42.2% [±11.6]; combined due to small sample sizes; Table 2) differed from leks impacted by ≥3 factors at the 70% level. Mean standardized variation in lek counts was significantly higher at leks impacted by ≤2 factors compared to control leks (mean standard deviation 0.46; $n$ = 13, $t_{16}$ = 2.48, $p$ = 0.023), but did not differ significantly between leks impacted by ≥3 factors (mean standard deviation 0.35; $n$ = 35, $t_{69}$ = 1.11, $p$ = 0.270) and controls (mean standard deviation 0.30; $n$ = 37). Additionally, mean distance from lek to day roost locations during the breeding season did not differ significantly between leks impacted by ≥3 factors (mean distance 753 m; $n$ = 22, $t_4$ = 0.13, $p$ = 0.903) and leks impacted by ≤2 (mean distance 783 m; $n$ = 3, $t_4$ = 0.24, $p$ = 0.819) relative to control leks (mean distance 727 m; $n$ = 4).

Treatment leks had fewer yearling males and earlier peak attendance dates compared to control leks. The average annual ratio of trapped yearling males to total number of trapped males was 20.3% higher for controls compared to treatment leks combined, but did not significantly differ ($\chi^2_3$ = 5.81, $p$ = 0.121). Average annual date of peak male attendance was significantly later on control leks compared to treatment leks combined (mean difference 4.5 days; paired-$t$ = 2.61, $p$ = 0.048).

**Female Habitat Selection Analyses**

I captured and radio-equipped 209 females from 14 leks between 2000-2004. The proportions of radio-equipped adults to yearlings for birds captured from leks used to delineate the area of interest (i.e., leks within 3.2 km of the Pinedale Anticline crest) were 0.4 in 2000, 2.0 in 2001, 3.2 in 2002, 5.4 in 2003, and 1.2 in 2004; adult-to-yearling ratios were 1.2 in 1998 and 0.8 in 1999 (A. G. Lyon,

unpublished data). I located 213 total nests and 162 nests within the delineated area of interest (i.e., nests ≤5 km from leks within 3.2 km of the Pinedale Anticline crest). Mean apparent annual nest success (±standard error [SE]) for all nests was 46.2% (±4.7%) and for nests within the area of interest was 46.9% (±6.3%). Mean adjusted annual nest success (Mayfield 1975) was 43.3% (±1.9%) and 44.1% (±2.7%), respectively. Based on conditions at destroyed nests (Sargeant et al. 1998), I identified predators (mammalian or avian) responsible for the destruction of 82% of the 78 unsuccessful nests within the designated area of interest; mammals were responsible for 77% and birds for 23% of the depredated nests (avian predators were responsible for 13% of the destroyed nests in 2000 [$n$ = 8 total predator identified nests], 11% in 2001 [$n$ = 9], 13% in 2002 [$n$ = 16], 33% in 2003 [$n$ = 21], 40% in 2004 [$n$ = 10]). I used 47 consecutive years' nests (7 in 2000-01, 9 in 2001-02, 15 in 2002-03, 16 in 2003-04) for the consecutive years analyses, 112 nest and random locations (16 in 2000, 13 in 2001, 25 in 2002, 27 in 2003, 31 in 2004) for the nest habitat selection and adult versus yearling habitat selection analyses, and 108 nests (16 in 2000, 20 in 2001, 30 in 2002, 42 in 2003) for the nest success analyses. For the early brood-rearing habitat selection analysis, I used 49 early brood-rearing locations (6 in 2000, 5 in 2001, 7 in 2002, 10 in 2003, 21 in 2004); 64 females were used for the early brood fate analysis.

*Consecutive years' nests.*--Nesting adult females remained within selected nesting areas regardless of gas development levels within those areas. Mean consecutive years' nest-to-nest distances did not differ significantly relative to the level of development change between years ($F_3$ = 0.59, $p$ = 0.62); mean (±SE) nest-to-nest distance for females where ≥3 changes occurred within the nesting area between years was 565 m (±153 m; $n$ = 10), where 2 changes occurred 933 m (±282 m; $n$ = 7), where 1 change occurred 664 m (±164 m; $n$ = 20), and where no changes occurred 879 m (±240 m; $n$ = 6). The proportion of control females moving >930 m between nesting locations was 33% (proportion used to estimate expected proportions); the proportion of females moving >930 m relative to the number of changes occurring within nesting areas between years did not differ from expected ($\chi^2_2$ = 2.67, $p$ = 0.26). The proportion of successful to unsuccessful nests by treatment category did not differ ($\chi^2_3$ = 1.69, $p$ = 0.64), suggesting that distances moved between nests were not biased by first year's nest fate.

*Adult versus Yearling Nest.*--Nesting yearling females showed avoidance of road related disturbances compared to adults. Yearling females nested significantly farther from main haul roads compared to adult females ($t_{48}$ = 2.4, $p$ = 0.02) and nested in areas with significantly less total length of main haul road within 1480 m compared to adult females ($t_{75}$ = 3.5, $p$ < 0.01). Mean Drill_Dist ($t_{34}$ =

1.9, $p = 0.07$), Well_Dist ($t_{59} = 0.3$, $p = 0.74$), and Well_Density1480 ($t_{75} = 1.3$, $p = 0.21$) did not differ significantly by age (Table 3).

*Used versus Available Nests.*--Compared to available sites, nests were located farther from drilling rigs and gas wells in 2004, whereas nests were closer to these structures in 2000-2003. When used and available nesting sites were combined, mean Drill_Dist ($F_4 = 35.0$, $p < 0.01$), Well_Dist ($F_4 = 4.0$, $p < 0.01$), Road_Dist ($F_4 = 5.7$, $p < 0.01$), and Road_TotalLength1480 ($F_4 = 4.5$, $p < 0.01$) differed significantly by year; mean Well_Density1480 did not differ significantly by year ($F_4 = 1.7$, $p = 0.16$). Therefore, $AIC_c$ weighted logistic regression models with 90% CI around the parameter estimates were produced by year (Table 4). The annual models correctly classified between 54 and 76% of the points used to build the models (63% correct 2000, 65% correct 2001, 76% correct 2002, 54% correct 2003, 74% correct 2004). Based on 90% CI overlap, the parameter estimates associated with Drill_Dist and Well_Dist for the 2004 model differed consistently from the parameter estimates for all other years' models. The parameter estimate for Road_Dist associated with the 2002 model differed consistently from other years (Table 4).

Nests were closer to wells but in areas with decreased well densities compared to available sites. Between 97 and 100% of the 90% CI around the probability estimates for the annual averaged models computed for the sample of 350 random locations overlapped. Therefore, nests (used) and available locations for all years were combined to derive an $AIC_c$ weighted overall logistic regression model assessing the relationship between selected and available habitats relative to overall gas field infrastructure levels (Table 4; Figure 7). The overall model correctly classified 55% of the points used to build the model. Relative importance of the independent variables suggested that Well_Dist and Well_Density1480 best distinguished used from available sites (Table 4).

*Successful versus Unsuccessful Nests.*--Successful nests had increased residual grass cover and height and were closer to wells but in areas with lower well densities relative to unsuccessful nests. For nest (used) sites only, mean Drill_Dist differed significantly among years ($F_4 = 27.5$, $p < 0.01$); mean Well_Dist ($F_4 = 0.7$, $p = 0.58$), Road_Dist ($F_4 = 1.8$, $p = 0.15$), Well_Density1480 ($F_4 = 1.4$, $p = 0.26$), and Road_TotalLength1480 ($F_4 = 2.7$, $p = 0.05$) did not differ among years. Therefore, Drill_Dist was standardized by year, and nest data were combined across years for logistic regression analysis. The $AIC_c$ weighted model (Table 5) correctly classified 58% of the points used to build the model, which was 37% better than chance ($K = 0.37$, $Z = 5.3$). Although the relative importance estimates associated with the independent variables suggested that variables were similar, the skewed nature of the 90% CI around Well_Dist, Well_Density1480, residual grass cover, and residual grass height suggested these variables could have influenced nest success (Hosmer and Lemeshow 1989; Table 5). However, the

difference in $AIC_c$ between the best and worst ranked models was 5.56, and 36 of the 56 models considered were within 4 $AIC_c$ units of the best model. Considerable empirical evidence exists suggesting that models within 4 units of the AIC ranked best model should be considered as candidates for the Kullback-Leibler best model (Burnham and Anderson 2002). Because 64% of the models considered could potentially be the best model and high model selection uncertainty was indicated (Burnham and Anderson 2002), relationships between variables and nest success probabilities were not conclusive.

*Used versus Available and Successful versus Unsuccessful Early Brood-rearing Locations.*- Brooding females avoided producing wells during early brood-rearing, but development levels surrounding nesting locations did not appear to influence brood success. Mean distance from nest-to-early brood-rearing location was 1,033 m (95% CI 549-1,582 m). Therefore, random points were generated within 1,580 m of successful nests in suitable early brood-rearing habitat. Additionally, the 1,580 m buffer was used to estimate the total number of producing wells (Well_Density1580) and total length of main haul road (Road_TotalLength1580) for the successful versus unsuccessful brood analyses. Early brood-rearing locations were significantly farther from producing wells compared to random locations (paired-$t$ = 3.2; $p < 0.01$). Mean difference in Drill_Dist (paired-$t$ = 0.9; $p$ = 0.37), Road_Dist (paired-$t$ = 1.7; $p$ = 0.10), Well_Density1000 (paired-$t$ = 1.4; $p$ = 0.16), and Road_TotalLength1000 (paired-$t$ = 1.6; $p$ = 0.11) did not differ significantly (Table 6). None of the 5 variables describing gas field development differed significantly between successful and unsuccessful early brooding hens (Drill_Dist $t_{19}$ = 0.1, $p$ = 0.90; Well_Dist $t_{17}$ = 0.6, $p$ = 0.54; Road_Dist $t_{26}$ = 1.3, $p$ = 0.22; Well_Density1580 $t_{19}$ = 1.0, $p$ = 0.32; Road_TotalLength1580 $t_{22}$ = 1.2, $p$ = 0.24; Table 6).

**Female Demographic Analyses**

I collected data for 428 individual radio-equipped female-years between 1998 and 2004 (41 in 1998, 40 in 1999, 37 in 2000, 46 in 2001, 76 in 2002, 91 in 2003, 97 in 2004). Because transmitter battery-life allowed birds to be monitored for multiple years, sample sizes represent the annual number of radio-equipped birds with working transmitters, not the number of distinct individuals marked. By treatment group, I included 148 female-years in All_Control, 73 in Nest_Control, 254 in All_Treat, 51 in Lek_Treat, 57 in Nest_Treat, 81 in LekNest_Treat, 88 in Pre_Treat, and 117 in Post_Treat.

*Vital Rate Estimation.*--Reported nesting propensity estimates in greater sage-grouse range from 68 to 93% (Connelly et al. 1993, Schroeder 1997), and fewer 1$^{st}$ year breeding females may initiate nests compared to adults (Connelly et al. 1993). Mean apparent nesting propensity [± standard error (SE)] of adult ($n$ = 244; 84.6% ±2.2) and yearling females ($n$ = 76; 67.2% ±6.3) suggested an age

difference at the 95% level. Using the standard error generated from year differences (±2.1), a year effect was detected at the 95% level (1998 nesting propensity 90.3%, 1999 78.8%, 2000 73.9%, 2001 84.4%, 2002 85.0%, 2003 84.4%, 2004 76.6%). Apparent nesting propensity was estimated separately for adult and yearling females, and SE was generated through year differences (Table 7); this standard error was used for stochastic simulations.

From females flushed during nest site identification (n = 66), I estimated 7.41 (±0.14) eggs per clutch, similar to 7.43 eggs/clutch reported in the literature (Schroeder et al. 1999). Correcting for male to female ratios (Swenson 1986), I estimated 3.96 (±0.16 propagated SE) female eggs per clutch; this estimate was used for all demographic comparisons (i.e., constant between groups).

My nest success estimates fall within the range of those reported for greater sage-grouse, which are typically between 40 and 60% (Wakkinen 1990, Connelly et al. 1991, Connelly et al. 1993, Sveum et al. 1998b, Schroeder et al. 1999). Mayfield (1975) corrected nest success estimates (±SE) of adult ($n$ = 211; 43.7% ±0.8) and yearling females ($n$ = 53; 41.7% ±1.7) suggested no age differences at the 95% level; however a year effect was detected (1998 nest success 43.6 ±2.0, 1999 38.8 ±2.3, 2000 41.3 ±2.9, 2001 37.6 ±2.2, 2002 41.8 ±1.6, 2003 49.5 ±1.5, 2004 44.1 ±1.9). Adult and yearling females were combined for group nest success estimation, and SE was generated through year differences (Table 7).

Limited information exists on sage-grouse chick survival from hatch to 1st breeding attempt; however, Connelly and Braun (1997) reported that long-term (≥17 years pre-1996) chick to female ratios in the fall harvest throughout western North America ranged between approximately 1.3 and 2.5 chicks/female. For all broods ($n$ = 123), the $AIC_c$ (Burnham and Anderson 2002) ranking of brood survival models suggested no year or age effects (White and Burnham 1999; Table 8); both age categories and years were combined for group brood survival estimates (Table 7). Fledge estimates suggested no age (adult 2.39 ±0.19; yearling 2.25 ±0.34 chicks/brood) or year (1998 2.70 ±0.45; 1999 2.50 ±0.87; 2000 2.83 ±0.79; 2001 2.17 ±0.40; 2002 1.94 ±0.30; 2003 2.56 ±0.48; 2004 2.30 ±0.28) effect at the 95% level. Therefore, I pooled ages and years ($n$ = 86 broods) and estimated 2.36 (±0.16) chicks per brood. Although fledge estimates could be biased by difficulty finding chicks (Schroeder 1997), brood mixing, and flock size (i.e., several brooding females summering in a given flock), I believe the estimate is accurate because I was able to pool adults, yearlings, and years. Comparing brood and clutch estimates, I estimated 31.9% (±17.3 propagated SE) summer chick survival. Using chick females captured in fall 2004 ($n$ = 35), I estimated 70.9% (±7.7) winter survival. Female chick summer and winter survival estimates were used for all demographic comparisons (i.e., constant between groups).

For all females ($n$ = 404), survival model $AIC_c$ (Burnham and Anderson 2002) ranking suggested an age and nest status (i.e., nesting vs. non-nesting females) effect (White and Burnham 1999; Table 8); annual survival was calculated separately for nesting and non-nesting adult and yearling females for groups that included all females (All_Control, All_Treat, Pre_Treat, Post_Treat; Table 9). Nesting female ($n$ = 262) survival model ranking suggested a brood effect but no age effect (Table 8); adult and yearling females were combined, and annual survival was estimated separately for brooding and non-brooding females for groups requiring a nest (Nest_Control, Lek_Treat, Nest_Treat, LekNest_Treat; Table 10). Documented age and breeding status effects were used for classifying stages present in the life-cycle graph (see deterministic analysis below).

Annual survival estimates (95% confidence interval) for all adult [54.1% (48.2, 60.0); $n$ = 300] and yearling females [64.5% (54.4, 73.3); $n$ = 104] were similar to those reported in the literature [adult 59.2% (57.1, 61.3); 1st year 77.7% (71.8, 75.3); Zablan et al. 2003]. Comparisons of survival among periods between All_Control and All_Treat groups suggested differential survival primarily during early brooding and summer periods (Table 11). Comparing annual sample size for Pre_Treat and Post_Treat groups and percent normal annual precipitation (Figure 8) suggested that below normal precipitation levels during 2001 and 2002 may have influenced population growth estimates. However, because samples of pre-treatment individuals were included during 2001-2002, potential drought effects in terms of the pre- versus post-treatment comparison were probably minimal. Through the remaining years, annual environmental variation was similar relative to sample size differences between the 2 groups.

*Deterministic Analysis.*--The potential effect comparisons suggest that for groups including all females (All_Control, All_Treat, Pre_Treat, Post_Treat), nesting and non-nesting adult and yearling females had differential survival. Among groups that nested (Nest_Control, Lek_Treat, Nest_Treat, LekNest_Treat), brooding and non-brooding females had different survival. Therefore, a 5-node, stage-based life-cycle diagram and corresponding matrix was constructed for pre-breeding, birth-pulse demographic modeling of greater sage-grouse females (Figure 9). Females entered the model as eggs (m). For groups including all females, the chick (1st year female; node 1) survival associated matrix entry ($P_1$) was the product of nest success, brood survival, and chick female summer and winter survival. Yearling (second year; nodes 2 and 3) and adult (nodes 4 and 5) females were separated into nesting (yearling $P_{2Y}$; adult $P_{AY}$) and non-nesting (yearling $P_{2N}$; adult $P_{AN}$) individuals. Probabilities of breeding matrix entries were adult ($B_A$) and yearling female ($B_2$) nesting propensity (Table 12). For groups requiring a nest, the chick survival associated matrix entry ($P_1$) was the product of brood survival and chick female summer and winter survival. Yearling and adult females were separated into

brooding (yearling $P_{2Y}$; adult $P_{AY}$) and non-brooding (yearling $P_{2N}$; adult $P_{AN}$) individuals; age related survival did not differ. Probabilities of breeding entries ($B_2$ and $B_A$) were the product of nesting propensity (for all individuals) and nest success (Table 12).

The elasticity analysis of the deterministic matrices suggested that population growth was most elastic to relatively consistent arcs between models considering similar groups of birds (Table 13). For groups considering all females, between 52 and 68% of the elasticity in population growth was included in proportional changes to nesting adult productivity and survival and nesting yearling female survival. Between 41 and 56% of the elasticity in $\lambda$ was included in proportional changes to brooding and non-brooding adult and non-brooding yearling female survival for groups requiring a nest. For the populations considering all birds (versus nesting birds only), between 37.7 and 51.5% of the total proportional sensitivity was present in the survival and subsequent productivity of nesting adult females. Approximately 28% of the total elasticity in populations impacted on the lek (Lek_Treat and LekNest_Treat) was present in the survival and subsequent productivity of non-brooding adult females. And, for Nest_Control and Nest_Treat populations, adult female survival accounted for 34.5 and 46.2% of the total elasticity, respectively.

*Life Table Response Experiment.*--The effect of treatment on population growth was generally negative when using control groups as reference populations (Table 14). There were relatively consistent negative contributions from adult and yearling female survival. Nest success (NS) had generally negative contributions except the comparison between LekNest_Treat vs. Nest_Control. Brood survival (BS) had generally positive contributions, which acted to buffer the treatment effect, in all comparisons except Nest_Treat vs. Nest_Control, where its contribution was distinctly negative. A distinctly positive contribution of adult nest propensity [NP(a)] occurred in the All_Treat vs. All_Control comparison (Figures 10 and 11).

*Stochastic Simulations.*--Mean extinction times generated through stochastic simulations suggested that population growth rates between groups were different at the 95% level (Table 15). Large changes in population growth resulting from the addition of stochasticity to All_Control, Lek_Treat, and LekNest_Treat suggested relatively high variability in these groups' vital rates. Mean extinction time (±SE) for the Pre_Treat population (estimated population size = 1,203 individuals) under Post_Treat conditions was 19 (±0.09) years.

## DISCUSSION

### Lek Analyses

My results support the suggestion that greater sage-grouse leks situated relatively near extractive mineral developments ultimately will become unoccupied. The evidence suggests that natural gas field development within 3-5 km of an active greater sage-grouse lek will lead to dramatic declines in breeding populations. Overall declines in male lek attendance approached 100% (i.e., lek inactivity) when distances from leks to drilling rigs, producing wells, and main haul roads decreased, and as the number of quadrats containing wells within 5 km and the total length of main haul road within 3 km of leks increased. Conversely, as distances from leks to disturbance sources increased and the level of development surrounding leks decreased, male lek attendance remained stable. These observations were similar to 3 lek complexes in southern Canada that were disturbed by oil and gas activities occurring within 200 m between 1983-1985; none of these leks has been active since the disturbance (Braun et al. 2002, Aldridge and Brigham 2003). In northern Colorado, the numbers of males counted on 3 of 4 leks within 2 km of coal mine development declined as mining activity increased (Braun 1986, Remington and Braun 1991). Following the increase in activity, 1 lek became inactive in 3 years, 1 lek became inactive in 5 years, and 1 lek declined by approximately 88% in 4 years (Braun 1986, Remington and Braun 1991). Further, 2 of the 3 most heavily impacted leks in my study became essentially inactive over a 3-4 year period (Holloran and Anderson *In Press*).

Greater sage-grouse leks appeared to be negatively influenced if situated within 5 km of a drilling rig that was operating during the breeding season. Male lek attendance declines were not associated with drilling rig visibility, suggesting that something other than the potentially negative effects of structure (Braun 1998) were influencing drill-disturbed leks. Attendance on leks situated generally east of operating drilling rigs (i.e., drilling rig-to-lek directions northeast and southeast) declined significantly relative to control leks, whereas when drilling rig-to-lek directions were generally west, male lek attendance changes did not statistically differ from controls. Using hourly wind direction estimates from March 15 through April 30, 2000-2004 at a station approximately 18 km from the study area (Western Regional Climate Center, Reno, NV, USA; Big Piney AP station), I estimated that the wind blew from the west 62% of the time during the breeding season. Sound waves propagating upwind of the source enter a shadow zone >100 m from the source, resulting in substantial reductions (typically ≥20 dB) in sound intensity; downwind on the other hand, sound waves are bent in the opposite direction resulting in the opposite effect (Taylor 1970, Piercy and Daigle 1991). This suggests that noise emitted from drilling rigs could negatively influence male lek attendance.

Well densities exceeding 1 well every 283 ha (1 well/699 acres) appeared to negatively influence male lek attendance. Male lek attendance declined on leks situated where at least half of the quadrats radiating from that lek contained a producing well within 5 km. Additionally, leks located within 3 km of ≥5 producing gas wells were negatively influenced. Because lek-to-producing well direction did not influence male lek attendance, I combined these results and assumed equal well spacing (i.e., assumed 5 wells located within a 3 km radius semicircle). This resulted in a conservative well density estimate.

Main haul roads within 3 km of leks, and a length of >5 km of main haul road within 3 km of leks negatively influenced greater sage-grouse male lek attendance. Although there was no confounding influence of road visibility from leks or road direction to leks, the number of displaying males declined in response to road activity (i.e., traffic volume). Rates of male lek attendance were negatively associated with increased traffic volumes. Additionally, vehicle activity on roads during the daily strutting period (i.e., early morning) had a greater influence on male lek attendance compared to those roads with no vehicle activity during the daily strutting period. Although portions of 2 of the leks used for the traffic analyses were located on main haul roads, direct mortalities resulting from vehicle collisions were rarely observed. Further, because declines were associated with traffic volumes, they appeared to be related to male avoidance of traffic activity. Remington and Braun (1991) reported that the upgrade of haul roads associated with surface coal mining activity in Colorado was correlated with declines in the number of displaying males on leks situated relatively near the road.

Male lek attendance on heavily impacted leks (i.e., leks influenced by ≥3 gas field-related factors) declined significantly relative to control leks. Lek desertion probabilities were higher than expected for adult males captured on leks impacted by ≥3 gas field-related factors, suggesting that adult male displacement partially explained lek attendance declines. Braun (1986) attributed the witnessed rates of lek attendance decline on leks disturbed by coal mining activity to adult male lek tenacity with decreased annual recruitment of yearling males. Using information from the same study, Remington and Braun (1991) theorized that the distribution rather than the number of breeding grouse was altered, suggesting that males were being displaced by anthropogenic disturbances. However, desertion probabilities were not high enough to explain witnessed rates of decline on impacted leks in Pinedale.

Although not significant, the proportion of yearling males captured from impacted leks was 20% lower than that from non-impacted leks. Additionally, because yearling males establish territories on leks later in the breeding season compared to adults (Walsh et al. 2004), peak male attendance occurring 4.5 days earlier on impacted compared to non-impacted leks further suggests lower yearling male numbers on impacted leks. Therefore, lek attendance declines could also be explained by reduced

yearling male recruitment onto impacted leks, supporting the hypothesis of Braun (1986). Annual declines in the number of displaying males on leks influenced by gas field development could be partially explained by adult male displacement and reduced yearling male recruitment, however, the proportion of displaced adult and yearling males that established breeding territories on leks beyond the gas field's influence is unknown. Using data collected during this study, Holloran and Anderson (*In Press*) suggested that a proportion of the displaced yearlings were establishing territories on leks somewhere within the study area.

Lek count variability and potential breeding season male survival differences on lightly impacted leks suggest cumulative impacts resulting from predator responses to development. Mean standardized variation in daily male lek attendance was significantly higher at lightly impacted leks (i.e., leks influenced by ≤2 gas field-related factor) compared to heavily impacted (i.e., leks influenced ≥3 factors) and control leks. Based on field observations, days when few or no males were counted on a lek were often days that the lek had been influenced by a predator, typically a golden eagle (*Aquila chrysaetos*) in the study area (field observations supported by Schroeder et al. 1999 and Boyko et al. 2004). These low counts were responsible for increased variation in daily lek attendance. Additionally, breeding season survival probabilities were approximately 32% lower for males captured on leks impacted by ≤2 gas field-related factors compared to heavily impacted leks. These results suggest that predators were responding to gas field development by shifting core-area use patterns away from development, and thus impacting leks situated on the perimeter of the developing field proportionally more than leks situated near development. Golden eagles, Swainson's hawks (*Buteo swainsoni*) and red-tailed hawks (*Buteo jamaicensis*) have been documented avoiding anthropogenic disturbances (Fitzner 1985, Andersen et al. 1986, Andersen et al. 1990, Marzluff et al. 1997). Lek attendance on leks influenced by ≤2 gas field-related factors did not differ from controls, but increased predation pressure on the lightly impacted leks could have been partially masked by establishment of displaced adult males and proportionally increased yearling recruitment. Changes in raptor foraging behavior could additionally account for the relatively extended influence of gas field-related factors in terms of lek-to-disturbance source distances. Research investigating predator core-area use pattern changes as a result of development is needed to understand potential synergistic effects resulting from the development of natural gas fields.

Greater sage-grouse leks appeared to be negatively influenced if situated within 5 km of a drilling rig. Interestingly, however, average annual changes in male lek attendance on leks situated within 2.1-3.0 km of a drilling rig did not differ from average annual changes witnessed on control leks, but leks situated 3.1-5.0 km from a drilling rig declined significantly relative to controls. The number

of males on leks within 2.1 to 3 km of a drilling rig could have been augmented by adult males displaced from more heavily impacted leks. Additionally, proportionally increased predator pressure on leks 3.1 to 5 km from an operating drilling rig could have resulted in male lek attendance declines through decreased grouse survival probabilities. The results suggest that the witnessed pattern in male lek attendance changes on leks potentially influenced by a drilling rig (Figure 6) probably resulted from a combination of displaced male reestablishment and decreased survival.

The leks I used for these analyses were selected to control for extraneous factors that could influence changes in male lek attendance beyond the potential effects of natural gas development (i.e., habitat condition differences); thus I excluded leks farther than 6.4 km from the Pinedale Anticline Project Area. However, given the potential nature of the breeding population response to natural gas development, my control population could have been influenced by the gas fields. Depending on the range searched by males establishing breeding territories (Dunn and Braun 1985), disproportionate establishment by displaced adult and yearling males could have occurred on control leks. Additionally, my control population could have been subjected to artificially increased predation pressure. These possibilities may have biased lek attendance estimates on control leks.

**Female Habitat Selection Analyses**

Female greater sage-grouse in my study area avoided nesting near the infrastructure of natural gas fields. Aldridge (2005) reported that nesting females avoided areas with high levels of anthropogenic development, and Lyon and Anderson's (2003) results suggested that nesting females avoided road-related disturbances. However, investigating the gas field related factors individually suggested that avoidance was not absolute. Nesting females did not appear to be influenced by distance to main haul road or distance to drilling rig, and selected nest locations tended to be closer to producing gas wells. But, given the high cumulative $AIC_c$ weight (0.874; Table 4) associated with the total number of producing gas wells within 1,480 m, the results here suggest that nesting females were strongly avoiding areas with high well densities.

Site fidelity in breeding birds could delay population response to habitat changes, and a clear response may require the death of most site-tenacious individuals (Wiens et al. 1986). Greater sage-grouse adult females have strong nest site fidelity (Holloran and Anderson 2005), and appear to be tied to specific nesting areas regardless of temporal changes in the level of gas field development occurring within those areas. Mean annual survival estimates for female greater sage-grouse range from 59 to 75% (Connelly et al. 1994, Zablan et al. 2003), suggesting that 5 to 9 years could be required to realize ultimate nesting population responses to gas field development. Investigating habitat selection relative

to gas development levels between years indicated that parameter coefficients associated with distance to an active drilling rig and producing gas well differed at the 90% level in 2004 compared to models generated for 2000 through 2003 (Table 4). Compared to available sites, nests were located farther from drilling rigs and gas wells in 2004, whereas nests were closer in 2000 – 2003. If the 2004 nesting cohort consisted of a substantial number of individual females produced following the onset of extensive development (2000), this suggests that the eventual nesting population response could be avoidance of natural gas development. However, potential long-term avoidance patterns were detected for only 1 year's data; additional research is needed to assess the ultimate response to gas field development.

Relative to adults, yearling females nested farther from main haul roads and in areas with less total length of main haul road within 1,480 m. There did not appear to be age-related avoidance of other aspects of gas field development. Dunn and Braun (1985) suggest that a majority of yearlings attend natal leks (i.e., leks attended by female parent), thus the yearling sample could have consisted primarily of chicks produced by adult females nesting near gas field development (due to capture protocol that concentrated trapping effort on leks relatively close to gas development; Figure 2). Because yearling females could form an affinity for the parent's nesting area (Wiens et al. 1986, Lyon 2000), my yearling sample could have overestimated individuals with an affinity for areas near gas field infrastructure, biasing yearling nesting habitat selection results. However, although not statistically significant in all cases (Table 3), yearling females had a tendency to avoid gas field infrastructure relative to adults. Yearling site affinity could have acted to diminish the magnitude of avoidance.

Nests with dense, tall residual grass that were near a producing well, but were located in areas with low well densities, had higher probabilities of success. However, high model selection uncertainty suggested that the independent variables considered did not conclusively distinguish successful from unsuccessful nests. Aldridge (2005) also found inconclusive effects of anthropogenic features on greater sage-grouse nest success in Canada.

Female greater sage-grouse avoided producing wells during the early brood-rearing period (Table 6). However, early brood survival probabilities were not related to levels of development surrounding successful nests. Aldridge (2005) suggested that greater sage-grouse chick survival decreased as well densities within 1 km of brooding locations increased in Canada. In contrast to Aldridge's (2005) methods, I did not attempt to document the number of chicks per brood during the early brood-rearing stages, but merely assessed if successfully nesting females had chick(s) 2 weeks post-hatch. Therefore, my early brood-rearing success analysis was based on a dichotomous categorization of brood survival (chicks or no chicks), not on the actual number of chicks surviving the

early brood-rearing period. Although I was unable to determine if individual chick survival was affected by development levels surrounding the nest, my results suggest that survival of the entire brood was not influenced. However, brooding females were selecting areas farther from wells compared to available early brood-rearing habitat within 1 km of the nest. Thus, using the levels of development surrounding nests to compare successful and unsuccessful broods might have inaccurately described areas selected by brooding females and could have influenced my ability to detect brood survival differences relative to gas development levels.

**Female Demographic Analyses**

Natural-gas-related impacts negatively influenced female greater sage-grouse population growth. In general, most of the differences in population growth between treatment and control populations were explained by lower annual survival buffered to some extent by higher productivity in treatment populations.

Differences in population growth between females subjected to natural gas development activity near selected nest sites but not influenced by development activity on the lek and individuals nesting and breeding away from development were primarily due to decreased nest success, brood survival, and nesting adult female survival for nest-impacted females. Nest success and brood survival probabilities for females selecting habitats within a 5-km buffer around known leks within 3.2 km of the Pinedale Anticline crest were not influenced by the presence of gas field-related infrastructure within approximately 1.5 km of the nest. However, the successful versus unsuccessful nest and brood analyses (presented in the female habitat selection analyses section) only considered birds occupying areas relatively close to the gas field. This suggests that gas field-related activity negatively influenced greater sage-grouse nesting and brooding potential at least within the spatial scale considered (i.e., areas ≤8.2 km of the Pinedale Anticline crest).

However, the comparison between females breeding and nesting near development and those breeding and nesting far from development indicated that individuals influenced throughout the spring had higher nest success and brood survival probabilities compared to non-impacted individuals. Because the pattern of increased nest success and brood survival was not consistent through the nest-only impacted comparison, this appears to suggest that females impacted both on the lek and at the nest had increased breeding success probabilities compared to individuals impacted only at the nest. Both groups of treatment individuals (i.e., Nest_Treat and LekNest_Treat) were selecting nesting habitats near gas field-related infrastructure, suggesting that breeding success differences were not a result of habitat condition differences (i.e., predator numbers) between treatment and control populations.

Additionally, because nest-site fidelity was likely the reason treatment females selected to nest relatively near gas field infrastructure (Holloran and Anderson 2005), differences in breeding success between treatment groups probably cannot be explained by age related influences (Connelly et al. 2000b). This suggests that individuals subjected to natural gas field impacts throughout the breeding and nesting seasons potentially became habituated to natural gas field-related disturbance. Research investigating avian species' reactions to anthropogenic disturbance (primarily ecotourism related disturbance) demonstrated that individuals frequently subjected to high levels of human-related activity do not respond as strongly to disturbance compared to individuals subjected to lower levels of activity (Fowler 1999, Lord et al. 2001, Müllner et al. 2004), suggesting habituation. However, differential survival that I observed between control and treatment individual greater sage-grouse overrode the potential influence of habituation on productivity.

The direct demographic response of a greater sage-grouse population to the development of a natural gas field was probably best described by the pre- versus post-treatment comparison. The decline in population growth (21%) between these groups was primarily attributed to decreased nest success and adult female annual survival. Although severe drought conditions in 2001 and 2002 may have influenced population growth (Braun 1998), drought effect differences between the 2 groups were probably minimized by having a sample of each during the severe drought years and by precipitation level similarities in 1998-1999 and 2003-2004 (Figure 8). Treatment effect was especially noticeable on annual survival of nesting adults (Figure 10), or those individuals influenced by both anthropogenic and breeding related stressors.

Seasonal survival differences between treatment and control individuals (Table 11) suggests a lag period between the time an individual was impacted by an anthropogenic disturbance and when survival probabilities were influenced. Individuals were directly influenced by natural gas development activity primarily during the breeding and nesting periods, while differential survival occurred primarily during the early brooding and summer periods. Because of limited chick mobility during the early brooding stage (Patterson 1952), females impacted at the nest could have been influenced by gas field development during this period. However, treatment and control individuals summered in the same general areas, and these areas were removed from the gas field. Females that die during the early brooding and summer periods typically are killed by predators (Schroeder et al. 1999), thus disturbance during the spring may predispose individuals to predation later in the year. Increased predation probabilities suggest increased exposure, possibly through a change in foraging behavior (i.e., spending more time feeding), a change in habitat selection (i.e., selecting areas with greater food resources and reduced cover), or a change in self-preservation behavior (i.e., reduced alertness). If these behavioral

changes occurred, it suggests body condition of females subjected to anthropogenic disturbance may have been negatively compromised.

Avian species respond to environmental stress stimuli with elevated blood corticosteroid levels (Siegel 1980). Research investigating the hormonal response of birds to anthropogenic disturbance is limited; however, Northern Spotted Owls (*Strix occidentalis caurina*) subjected to increased logging activity within their home ranges had elevated fecal corticosteroid concentrations relative to non-impacted individuals (Wasser et al. 1997). Although temporary increases of corticosterone in response to acute stress are thought to enhance self-maintenance behavior (i.e., result in a reallocation of effort to foraging and energy uptake; Wingfield et al. 1995, Brown et al. 2005), chronically high levels can be detrimental. Increased corticosteroid levels over an extended period of time negatively affect metabolic processes, reducing fitness of adult individuals by resulting in weight loss, reduced reproductive capabilities, and suppressed immune function (Bartov et al. 1980, Siegel 1980, Fowles et al. 1993). Brown et al. (2005) and Silverin (1986), respectively, reported that cliff swallow (*Petrochelidon pyrrhonota*) and pied flycatcher (*Ficedula hypoleuca*) annual survival was negatively correlated with high corticosterone levels during the breeding season. If female greater sage-grouse were stressed by natural gas development activity and were entering the brooding and summering seasons in a state of reduced condition, they may have responded by altering foraging or vigilance behaviors, thereby increasing predation probabilities. Research investigating hormone level (Wasser et al. 1997, Washburn et al. 2003) and diurnal activity pattern differences relative to anthropogenic disturbance levels is needed to determine stress related responses and consequences of energy development to female greater sage-grouse.

**Summary**

My results suggest that greater sage-grouse in western Wyoming avoid breeding within or near the development boundaries of natural gas fields. The number of displaying males declined as distances from leks to gas-field-related disturbance sources (i.e., drilling rigs, producing wells, and main haul roads) decreased and as traffic volumes within 3 km of leks increased. Well densities exceeding 1 well per 283 ha within 3 km of leks negatively influenced male lek attendance, and rates of decline increased on leks located relatively centrally within the developing gas field (i.e., producing wells occupying ≥3 directions around leks). The results further suggest that increased noise intensity at leks negatively influenced male lek attendance. Although potential gas field-related disturbances were investigated independently, a developing natural gas field simultaneously consists of all the disturbance factors considered plus others not investigated (i.e., well completion activity, compressor stations).

Therefore, greater sage-grouse breeding populations were probably reacting to a combination of these factors' effects.

The evidence suggests that displacement of adult males and low recruitment of yearling males contributed to declines on impacted leks. Additionally, predatory species' responses to gas field development could be responsible for decreased survival of males on leks situated near the edges of developing fields. The results further suggest that although site-tenacious adult females did not engage in breeding dispersal in response to increased levels of gas development, subsequent generations avoided nesting near gas field infrastructure.

Mean extinction time for the population of birds that was present before gas field development was estimated at 19 years. Leks that became inactive during this study (2 leks) did so in 3-4 years (Holloran and Anderson *In Press*). Additionally, the number of males breeding on heavily impacted leks declined on average 24% annually (Table 2), compared to the 8-21% decline in population growth predicted from the effects of gas development on vital rates (Table 14). These comparisons suggest that the extirpation of leks near anthropogenic disturbances resulted from a combination of emigration and decreased survival. Regional greater sage-grouse population levels as well as population distributions appeared to be influenced negatively by the development of natural gas fields.

## MANAGEMENT IMPLICATIONS

The Pinedale Anticline Record of Decision (ROD; Bureau of Land Management 2000) outlined the following development stipulations for protection of greater sage-grouse leks: (1) operators will avoid surface disturbance within 0.25 miles (0.4 km) of greater sage-grouse leks; permanent (life of the project), high profile facilities (i.e., buildings and storage tanks) should not be constructed within 0.25 miles of a lek. (2) From March 1 through May 15, surface use and activities are not allowed between 0000 (i.e., midnight) and 0900 hrs within a 0.5-mile (0.8-km) radius of active leks (i.e., leks occupied by mating birds). (3) Operators will restrict construction and drilling activities from March 1 through May 15 within a 1.0-mile (1.6-km) radius of active leks. To protect nesting and brooding females, the Pinedale Anticline ROD (Bureau of Land Management 2000) stipulated that gas field related construction activities will be restricted from March 1 through July 31 in suitable nesting habitat within 2 miles (3.2 km) of active greater sage-grouse leks; a suitable habitat designation requires that an active nest be located during an on-site review of the proposed development area.

My results suggest that current development stipulations are inadequate to maintain greater sage-grouse breeding populations in natural gas fields. A minimal level of development within 3 km of a lek negatively influences breeding activity. Maintaining well densities of ≤1 well per 283 ha

(approximately 1 well per section) within 3 km of a lek could reduce the negative consequences of gas field development. The distance from disturbance sources that produced substantial levels of noise (i.e., drilling rigs, compressor stations, heavy construction equipment) during the breeding season was conservatively estimated at 5 km, especially if the source was located where sound propagation towards leks was intensified by environmental factors. Therefore, sound muffling devices or other techniques of sound reduction on noisy gas field structures within 5 km of a lek could reduce the negative consequences of these structures on breeding grouse. Declines in lek attendance were positively correlated with vehicle traffic levels, and vehicular activity during the daily strutting period on roads within 1.3 km of a lek intensified the negative influence of traffic. Reducing overall traffic volumes (i.e., offsite condensate collection facilities, car-pooling) and isolating traffic disturbance (i.e., restricting travel to and from the gas field to 1 major artery) within gas fields could reduce road effects. Additionally, enforcement of daily travel timing restrictions could further dampen road effects.

Barring direct disturbance resulting in nest abandonment, the stipulation aimed at protecting nesting females protects only philopatric individuals. Basing suitable designation on habitat conditions rather than habitat occupancy could assist in maintaining nesting areas for future generations. At a minimum, all areas within 5 km (Holloran and Anderson 2005) of known leks meeting the breeding habitat shrub requirements outlined by the sage-grouse habitat management guidelines (Connelly et al. 2000b) should be considered suitable and protected from development. Although adequate buffer distances are unknown, because of the tendency for brooding females and nesting yearling females to avoid gas field infrastructure, areas designated as suitable breeding habitats need to be buffered from gas field development. Additionally, nesting females avoid areas with high well densities. Although actual densities resulting in avoidance are unknown, my results suggest that areas with relatively high well densities present within the area of interest during this study (i.e., 16 ha well spacing present in the Jonah fields; Figure 3) contained well densities that were high enough to exclude nesting females. Because a developing natural gas field consists of multiple disturbance sources that all may influence greater sage-grouse leks and nests, managers need to ensure that all potential factors are addressed concomitantly.

The increase in relative occurrence of nest destruction by avian predators suggests that gas development attracts corvid species. Breeding and non-breeding individuals may be attracted to human developments due to food source availability (Andren 1992, Linz et al. 1992). Ensuring that potential corvid food sources (i.e., trash, road-killed carrion) are removed from the gas field and installing perching deterrents (Avery and Genchi 2004) on gas field related structures could reduce corvid densities within the gas field.

The results from this study suggest that dispersal from developed areas could be contributing to population declines. Although the proportion of potentially displaced adult and yearling males and yearling females breeding and nesting in areas removed from gas field infrastructure is unknown, offsite populations could be artificially enhanced by gas development. Because of potential density-dependent influences on breeding and nesting success probabilities (LaMontagne et al. 2002, Holloran and Anderson 2005), maintenance of these enhanced populations could require increasing the carrying capacity of offsite habitats. Additionally, the deterministic investigation of separate matrices using elasticity values suggested population growth was generally most sensitive to proportional changes in adult female survival. Subsequent productivity associated with the most elastic adult female cohort (i.e., nesting or non-brooding adult females) was also relatively elastic for most groups. Thus, proportional changes in adult female survival and subsequent productivity would have the most pronounced influence on population growth for all populations considered.

Sage-grouse survival and fecundity have been linked to sagebrush-steppe habitat quality. Sage-grouse distributions are clearly aligned with the distribution of big sagebrush (Schroeder et al. 2004), and the dependence of the species on sagebrush through all seasonal periods has been well documented (see Connelly et al. 2004 for review). Suitable sagebrush cover is especially important during the nesting (Wallestad and Pyrah 1974, Connelly et al. 1991, Gregg et al. 1994, Sveum et al. 1998b, Aldridge and Brigham 2002, Holloran et al. 2005), early brood-rearing (Sveum et al. 1998a, Thompson et al. *In Press*), and wintering periods (Patterson 1952, Eng and Schladweiler 1972, Beck 1977, Crawford et al. 2004). Residual herbaceous cover within suitable sagebrush stands has been positively linked with increased nest success probabilities (Connelly et al. 1991, Gregg et al. 1994, Sveum et al. 1998b, Moynahan 2004, Holloran et al. 2005); and brood survival has been positively linked to increased invertebrate abundance and forb cover (Johnson and Boyce 1990, Drut et al. 1994, Fischer et al. 1996, Huwer 2004, Thompson et al. *In Press*). Other factors influencing sage-grouse survival and productivity include the potential additive nature of hunting mortality, West Nile virus, extreme weather conditions, and non-native herbaceous and predatory species proliferation (Braun 1998, Johnson and Braun 1999, Connelly et al. 2000a, Connelly et al. 2000b, Crawford et al. 2004, Moynahan 2004, Naugle et al. 2004). These habitat issues need to be considered to increase greater sage-grouse survival and fecundity and mitigate for population declines.

Regional levels and distributions of greater sage-grouse populations were affected negatively by the development of natural gas fields. Based on the demographic information collected, increasing adult female survival and subsequent productivity would have the most pronounced influence on population growth. I recommend intact sagebrush-dominated habitats be protected and managed for

suitable understory conditions. Managing for high quality seasonal habitats should maximize survival and productivity, could counteract density-dependent consequences of artificially high offsite populations, and may be the best management option for offsetting regional population declines and distributional changes resulting from natural gas field development.

**ACKNOWLEDGEMENTS**

Financial support was provided by the Bureau of Land Management, U.S. Department of Energy, Wyoming Game and Fish Department, Ultra Petroleum, Yellowstone-to-Yukon Initiative, EnCana Oil & Gas Inc., and the Cowboy 3-Shot Sage-Grouse Foundation. We thank all the landowners in the upper Green River Basin who allowed access. Field assistance was provided by R. A. Holloran, B. K. Holtby, R. C. Kaiser, A. G. Lyon, R. C. Powell, S. J. Slater, M. S. Stotts, C. G. Taber, and G. L. Wilson. Technical assistance was provided by TRC Mariah Associates, Inc. (Laramie, WY, USA), Western EcoSystems Technology, Inc. (Cheyenne, WY, USA), BLM Pinedale field office (Pinedale, WY, USA), WGFD Jackson/Pinedale regional office (Pinedale, WY, USA), and Wyoming Wildlife Consultants, LLC (Pinedale, WY, USA). Statistical assistance was provided by K. G. Gerow and D. E. Legg (University of Wyoming, Laramie, WY, USA); D. B. McDonald provided extensive sensitivity analysis assistance; and K. M. Thompson provided extensive GIS assistance. Pneumatic axle counters were provided by the Wyoming Highway Department (Cheyenne, WY, USA). Telemetry flights and lek surveys were conducted with the assistance of Mountain Air Research (Driggs, ID, USA). Our manuscript was greatly improved through reviews by T. J. Christiansen, D. R. Edmunds, W. A. Hubert, D. E. Legg, D. B. McDonald, A. F. Reeve, T. E. Rinkes, D. C. Rule, S. J. Slater, and K. M. Thompson.

**LITERATURE CITED**

Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. PhD Dissertation, University of Alberta, Edmonton, Alberta, Canada.

Aldridge, C. L., and R. M. Brigham. 2002. Greater sage-grouse nesting and brood habitat use in southern Canada. Journal Wildlife Management 66:433-444.

Aldridge, C. L., and R. M. Brigham. 2003. Distribution, abundance, and status of the greater sage-grouse, *Centrocercus urophasianus*, in Canada. Canadian Field-Naturalist 117:25-34.

Andersen, D. E., O. J. Rongstad, and W. R. Mytton. 1986. The behavioral response of a red-tailed hawk to military training activity. Raptor Research 20:65-68.

Andersen, D. E., O. J. Rongstad, and W. R. Mytton. 1990. Home-range changes in raptors exposed to increased human activity levels in southeastern Colorado. Wildlife Society Bulletin 18:134-142.

Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794-804.

Avery, M. L., and A. C. Genchi. 2004. Avian perching deterrents on ultrasonic sensors at airport wind-shear alert systems. Wildlife Society Bulletin 32:718-725.

Bartov, I., L. S. Jensen, and J. R. Veltmann, Jr. 1980. Effect of corticosterone and prolactin on fattening in broiler chicks. Poultry Science 59:1328-1334.

Beck, T. D. I. 1977. Sage grouse flock characteristics and habitat selection in winter. Journal Wildlife Management 41:18-26.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.

Boyko, A. R., R. M. Gibson, and J. R. Lucas. 2004. How predation risk affects the temporal dynamics of avian leks: greater sage-grouse versus golden eagles. American Naturalist 163:154-165.

Braun, C. E. 1986. Changes in sage grouse lek counts with advent of surface coal mining. Proceedings: Issues and Technology in the Management of Impacted Western Wildlife, Thorne Ecological Institute 2:227-231.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139-156.

Braun, C. E., O. O. Oedekoven, and C. L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage grouse. Transactions North American Wildlife and Natural Resources Conference 67:337-349.

Brown, C. R., M. B. Brown, S. A. Raouf, L. C. Smith, and J. C. Wingfield. 2005. Effects of endogenous steroid hormone levels on annual survival in Cliff Swallows. Ecology 86:1034-1046.

Bureau of Land Management. 2000. Record of decision, environmental impact statement for the Pinedale anticline oil and gas exploration and development project Sublette County, Wyoming. United States Bureau of Land Management, Pinedale, WY, USA.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, NY, USA.

Burrough, P. A., and R. A. McDonnell. 1998. Principles of geographical information systems. Oxford University Press Inc., New York, USA.

Caccamise, D. F., and R. S. Hedin. 1985. An aerodynamic basis for selecting transmitter loads in birds. Wilson Bulletin 97:306-318.

Caswell, H. 1989. Analysis of life table response experiments I. decomposition of effects on population growth rate. Ecological Modelling 46:221-237.

Caswell, H. 1996. Analysis of life table response experiments II. alternative parameterizations fro size- and stage-structured models. Ecological Modelling 88:73-82.

Connelly, J. W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000a. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. Wildlife Biology 6:227-232.

Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse Centrocercus urophasianus populations in western North America. Wildlife Biology 3:229-234.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of Greater Sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, WY, USA.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station publication No. 979, University of Idaho, Moscow, ID, USA.

Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage grouse ecology. Idaho Department Fish and Game Job Completion Report W-160-R-19. Boise, ID, USA.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000b. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage grouse use of nest sites in southeastern Idaho. Journal Wildlife Management 55:521-524.

Connelly, J. W., W. L. Wakkinen, A. D. Apa, K. P. Reese, and J. W. Fischer. 1993. Re-nesting by sage grouse in southeastern Idaho. Condor 94:1041-1043.

Cooch, E., and G. C. White. 2004. Program MARK: a gentle introduction. Available online at: www.cnr.colostate.edu/~gwhite.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal Range Management 57:2-19.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for Loggerhead Sea Turtles and implications for conservation. Ecology 68:1412-1423.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33:224-227.

Dowdy, S. M., and S. Wearden. 1991. Statistics for research second edition. John Wiley & Sons, Inc., New York, NY, USA.

Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994. Diets and food selection of sage grouse chicks in Oregon. Journal Range Management 47:90-93.

Dunn, P.O., and C.E. Braun. 1985. Natal dispersal and lek fidelity of sage grouse. Auk 102:621-627.

Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal Wildlife Management 19:267-272.

Eng, R. L., and P. Schladweiler. 1972. Sage grouse winter movements and habitat use in central Montana. Journal Wildlife Management 36:141-146.

Erickson, W. P., T. L. McDonald, K. G. Gerow, S. Howlin, and J. W. Kern. 2001. Statistical issues in resource selection studies with radio-marked animals. Pages 209-242 *in* J. J. Millspaugh and J. M. Marzluff [eds.], Radio Tracking and Animal Populations. Academic Press, San Diego, CA, USA.

Fischer, R. A., K. P. Reese, and J. W. Connelly. 1996. An investigation on fire effects within xeric sage grouse brood habitat. Journal Range Management 49:194-198.

Fitzner, R. E. 1985. Responses of birds of prey to large-scale energy development in southcentral Washington. Issues and Technology in the Management of Impacted Western Wildlife National Symposium Proceedings. February 4-6, Glenwood Springs, Colorado, USA.

Fowler, G. S. 1999. Behavioral and hormonal responses of Magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitation. Biological Conservation 90:143-149.

Fowles, J. R., A. Fairbrother, M. Fix, S. Schiller, and N. I. Kerkvliet. 1993. Glucocorticoid effects on natural and humoral immunity in Mallards. Developmental and Comparative Immunology 17:165-177.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224-231.

Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetational cover and predation sage grouse nests in Oregon. Journal Wildlife Management 58:162-166.

Hagen, C. A. 2003. A demographic analysis of Lesser Prairie-Chicken populations in southwestern Kansas: survival, population viability, and habitat use. PhD Dissertation, Kansas State University, Manhattan, KS, USA.

Hair, J. F. Jr., R. E. Anderson, R. L. Tatham, and W. C. Black. 1995. Multivariate data analysis fourth edition. Simon & Schuster Company, Englewood Cliffs, NJ, USA.

Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin 93:42-53.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analyses of the life cycle of midcontinent Mallards. Journal Wildlife Management 66:883-900.

Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742-752.

Holloran, M. J., and S. H. Anderson. *In Press*. Greater sage-grouse population response to natural gas development in Western Wyoming: are regional populations affected by relatively localized disturbances? Transactions 70th North American Wildlife and Natural Resources Conference, Wildlife Management Institute, Washington DC, USA.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal Wildlife Management 69:638-649.

Hooge, P. N., and B. Eichenlaub. 2000. Animal movement extension to ArcView version 2.04. Alaska Science Center, Biological Science Office, U.S. Geological Survey, Anchorage, USA.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. John Wiley & Sons, New York, NY, USA.

Huwer, S. L. 2004. Evaluating greater sage-grouse brood habitat using human-imprinted chicks. MS Thesis, Colorado State University, Fort Collins, CO, USA.

Johnson, G. D., and M. S. Boyce. 1990. Feeding trials with insects in the diet of sage grouse chicks. Journal of Wildlife Management 54:89-91.

Johnson, K. H. and C. E. Braun. 1999. Viability and conservation of an exploited sage grouse population. Conservation Biology 13:77-83.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634.

LaMontagne, J. M., R. L. Irvine, and E. E. Crone. 2002. Spatial patterns of population regulation in sage grouse (*Centrocercus* spp.) population viability analysis. Journal Animal Ecology 71:672-682.

Linz, G. M., C. E. Knittle, and R. E. Johnson. 1992. Home range of breeding common ravens in coastal southern California. Southwestern Naturalist 37:199-202.

Lord, A., J. R. Waas, J. Innes, and M. J. Whittingham. 2001. Effects of human approaches to nests of northern New Zealand dotterels. Biological Conservation 98:233-240.

Lyon, A. G. 2000. The potential effects of natural gas development on sage grouse near Pinedale, Wyoming. MS Thesis, University of Wyoming, Laramie, WY, USA.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486-491.

Marzluff, J. M., S. T. Knick, M. S. Vekasy, L. S. Schueck, and T. J. Zarriello. 1997. Spatial use and habitat selection of golden eagles in southwestern Idaho. Auk 114:673-687.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

McDonald, D. B. and H. Caswell. 1993. Matrix methods for avian demography. Current Ornithology 10:139-185.

Menard, S. W. 1995. Applied logistic regression analysis. Sage Publications, Thousand Oaks, CA, USA.

Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology 13:815-829.

Moynahan, B. J. 2004. Landscape-scale factors affecting population dynamics of greater sage-grouse (*Centrocercus urophasianus*) in north-central Montana, 2001-2004. PhD Dissertation, University of Montana, Missoula, MT, USA.

Müllner, A., K. E. Linsenmair, and M. Wikelski. 2004. Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). Biological Conservation 118:549-558.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Dato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: pending crisis for greater sage-grouse. Ecology Letters 7:704-713.

Oyler-McCance, S. J. 1999. Genetic and habitat factors underlying conservation strategies for Gunnison sage-grouse. PhD Dissertation, Colorado State University, Fort Collins, CO, USA.

Patterson, R. L. 1952. The Sage grouse in Wyoming. Sage Books, Inc., Denver, CO, USA.

Philippi, T. E. 1993. Multiple regression: herbivory. *In* S. M. Scheiner and J. Gurevitch (eds.). Design and analysis of ecological experiments. Chapman and Hall, New York, NY, USA.

Piercy, J. E., and G. A. Daigle. 1991. Sound propagation in the open air. *In* C. M. Harris (ed.). Handbook of acoustical measurements and noise control, third edition. McGraw Hill, Inc., New York, NY, USA.

Remington, T. E. and C. E. Braun. 1991. How surface coal mining affects sage grouse, North Park, Colorado. Proceedings, Issues and Technology in Management of Impacted Western Wildlife. Thorne Ecological Institute 5:128-132.

Royle, A., I. Clark, P. I. Brooker, H. Parker, A. Journel, J. M. Rendu, and P. Mousset-Jones. 1980. Geostatistics. McGraw-Hill, Inc., New York, NY, USA.

Sargeant, A. B., M. A. Sovada, and R. J. Greenwood. 1998. Interpreting evidence of depredation of duck nests in the prairie potholes region. U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND, USA, and Ducks Unlimited, Inc., Memphis, TN USA.

SAS Institute Inc. 1990. SAS/STAT® User's Guide, Version 6, Fourth Edition, Volume 2. Sas Institute Inc., Cary, NC, USA.

Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99:933-941.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of Sage-grouse in North America. Condor 106:363-376.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Pages 1-28 *in* A. Pool and F. Gill [eds.], The Birds of North America, No. 425. The Birds of North America, Inc. Philadelphia, PA, USA.

Siegel, H. S. 1980. Physiological stress in birds. BioScience 30:529-534.

Silverin, B. 1986. Corticosterone-binding proteins and behavioral effects of high plasma levels of corticosterone during the breeding period in the Pied Flycatcher. General and Comparative Endocrinology 64:67-74.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practices of statistics in biological research. Third edition. W. H. Freeman and Company, New York, NY, USA.

Sveum, C. M., J. A. Crawford, and W. D. Edge. 1998a. Use and selection of brood-rearing habitat by sage grouse in south-central Washington. Great Basin Naturalist 58:344-351.

Sveum, C. M., W. D. Edge, and J. A. Crawford. 1998b. Nesting habitat selection by sage grouse in south-central Washington. Journal Range Management 51:265-269.

Swenson, J. E. 1986. Differential survival by sex in juvenile sage grouse and grey partridge. Ornis Scandinavica 17:14-17.

Taylor, R. 1970. Noise. Penguin Books Ltd., Harmondsworth, Middlesex, England.

Thompson, K. M., M. J. Holloran, S. J. Slater, J. L. Kuipers, and S. H. Anderson. *In Press*. Greater sage-grouse early brood-rearing habitat use and productivity in Wyoming. Western North American Naturalist, Brigham Young University, Provo, UT, USA.

Titus, K., J. A. Mosher, and B. K. Williams. 1984. Chance-correct classification for use in discriminant analysis: ecological applications. American Midland Naturalist 111:1-7.

Wakkinen, W. L. 1990. Nest site characteristics and spring-summer movements of migratory sage grouse in southeastern Idaho. MS Thesis, University of Idaho, Moscow, ID, USA.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425-426.

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. Journal Wildlife Management 38:630-633.

Walsh, D. P., G. C. White, T. E. Remington, and D. C. Bowden. 2004. Evaluation of the lek-count index for greater sage-grouse. Wildlife Society Bulletin 32:56-68.

Washburn, B. E., J. J. Millspaugh, J. H. Schulz, S. B. Jones, and T. Mong. 2003. Using fecal glucocorticoids for stress assessment in Mourning Doves. Condor 105:696-706.

Wasser, S. K., K. Bevis, G. King, and E. Hanson. 1997. Noninvasive physiological measures of disturbance in the Northern Spotted Owl. Conservation Biology 11:1019-1022.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120-138.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1986. A lesson in the limitations of field experiments: shrubsteppe birds and habitat alteration. Ecology 67:365-376.

Wingfield, J. C., K. M. O'Reilly, and L. B. Astheimer. 1995. Modulation of the adrenocortical responses to acute stress in Arctic birds: a possible ecological basis. American Zoologist 35:285-294.

Wisdom, M. J. and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. Journal of Wildlife Management 61:302-312.

Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life stage simulation analysis: Estimating vital-rate effects on population growth for conservation. Ecology 81:628-641.

Zablan, M. A., C. E. Braun, and G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal Wildlife Management 67:144-154.

Table 1. List of acronyms. Order presented reflects the order the acronym was encountered in the text.

| Acronym | Description | Analyses |
|---|---|---|
| Drill_Dist | Distance (km) to active drilling rig. | Lek, Nest, Early Brood-rearing |
| Well_Dist | Distance (km) to producing well. | Lek, Nest, Early Brood-rearing |
| Road_Dist | Distance (km) to closest point on main haul road. | Lek, Nest, Early Brood-rearing |
| Well_Occupied5 | Total number of quadrats (1-4) occupied by a producing well within 5 km (quadrats delineated by cardinal directions). | Lek |
| Road_TotalLength3 | Total length of main haul road (km) within 3 km. | Lek |
| Full_Sight | Drilling locations within full view of lek. | Lek |
| Partial_Sight | Drilling locations within partial view of lek (i.e., top half of drilling rig visible from lek). | Lek |
| No_Sight | Drilling locations not visible from lek. | Lek |
| Overall_Change | Proportional change in maximum number of males occupying a lek between 1999 and 2004. | Lek |
| Annual_Change | Proportional change in maximum number of males occupying a lek annually (i.e., between 1999 and 2000, 2000 and 01, etc.). | Lek |
| Well_Density3 | Total number of producing wells (well) within 3 km. | Lek |
| Road_Visible3 | Total length of main haul road (km) visible within 3 km. | Lek |
| Well_Density1480 | Total number of producing wells (well) within 1480 m. | Nest |
| Road_TotalLength1480 | Total length of main haul road (km) within 1480 m. | Nest |
| Well_Density1000 | Total number of producing wells (well) within 1000 m. | Early Brood-rearing |
| Road_TotalLength1000 | Total length of main haul road (km) within 1000 m. | Early Brood-rearing |
| Well_Density1580 | Total number of producing wells (well) within 1580 m. | Early Brood-rearing |
| Road_TotalLength1580 | Total length of main haul road (km) within 1580 m. | Early Brood-rearing |
| All_Treat | Group of individual females impacted by natural gas development either on the lek or at the nest. | Demographic |
| All_Control | Group of individual females not impacted by natural gas development on the lek or at the nest. | Demographic |
| Lek_Treat | Group of individual females impacted by natural gas development on the lek but not on the nest. | Demographic |
| Nest_Treat | Group of individual females impacted by natural gas development at the nest but not on the lek. | Demographic |
| LekNest_Treat | Group of individual females impacted by natural gas development both on the lek and at the nest. | Demographic |
| Nest_Control | The nesting portion of the All_Control group. | Demographic |

Table 1 continued on next page.

Table 1 (Continued). List of acronyms. Order presented reflects the order the acronym was encountered in the text.

| Acronym | Description | Analyses |
|---|---|---|
| Pre_Treat | Group of individual females captured from leks that were considered controls in 1999 but were considered treatment by 2004 during the years the lek was considered a control. | Demographic |
| Post_Treat | Group of individual females captured from Pre_Treat leks during the years the lek was considered a treatment. | Demographic |

Table 2. Mean annual declines (%) in the number of greater sage-grouse males (Annual_Chng) attending leks in western Wyoming, 1998-2004 by the total number of potential natural gas field-related impacts (Number of Impacts) occurring within specified distances of the lek. The probabilities of lek desertion (Prob_Desert; %) and breeding season survival (Prob_Survive; %) of radio-equipped individual males captured on leks by impact category are additionally provided.

| Number of Impacts[a] | n[b] | Annual_Chng | n[c] | Prob_Desert | n[b] | Prob_Survive (±SE) |
|---|---|---|---|---|---|---|
| ≥3 Impacts | 36 | -24.4 | 62 | 19.4 | 59 | 61.5 (±6.4) |
| ≤2 Impacts | 13 | -8.7 | 8 | 25.0 | 6 | 29.6 (±18.1) |
| 0 Impacts (Control) | 37 | 6.2 | 11 | 9.1 | 13 | 48.5 (±14.4) |

[a] Natural gas field-related impacts included: lek-to-drilling rig distance ≤5 km, lek-to-producing gas well distance ≤3 km, lek-to-main haul road distance ≤3 km, well densities within 3 km ≥5 wells, and ≥3 quadrates containing a well within 5 km.

[b] Number of lek years.

[c] Number of radio-equipped individual males.

Table 3. Mean (SE) nest-to-natural gas field related disturbance distances for adult (≥second breeding season; $n$ = 83) and yearling (first breeding season; $n$ = 29) greater sage-grouse nesting within 5 km of leks located within 3.2 km of the Pinedale Anticline crest (Bureau of Land Management 2000) in western Wyoming, 2000-2004. Note that nesting yearling females generally avoided natural gas related disturbances relative to adult females.

| Variable[ab] | Adult | Yearling |
|---|---|---|
| Drill_Dist (km) | 5.13 (0.53) | 8.22 (1.55) |
| Well_Dist (km) | 2.00 (0.16) | 1.91 (0.22) |
| Road_Dist (km) | 1.34 (0.12) | 1.92 (0.20)[c] |
| Well_Density1480 (wells) | 2.08 (0.43) | 1.28 (0.48) |
| Road_TotalLength1480 (km) | 2.04 (0.19) | 1.07 (0.21)[c] |

[a] Independent variables included: distance to closest active drill rig (Drill_Dist), distance to closest producing gas well (Well_Dist), distance to closest point on a main haul road (Road_Dist), total number of producing gas wells within 1480 m (Well_Density1480) and total linear distance of main haul road within 1480 m (Road_TotalLength1480).

[b] Variables were measured for gas related factor active during the nest incubation period (May 1 through June 15).

[c] Differed significantly from adults (2-sample separate-variance $t$-tests; $p < 0.05$).

Table 4. Parameter coefficients (90% confidence intervals) for $AIC_c$ weighted logistic regression models comparing selected nesting sites and random locations for greater sage-grouse nesting within 5 km of leks located within 3.2 km of the Pinedale Anticline crest (Bureau of Land Management 2000) in western Wyoming, 2000-2004. Models were developed by year and for all years combined (Overall model). Cumulative $AIC_c$ weights ($AIC_c$ weights) for independent variables in the global model were estimated by adding $AIC_c$ weight-values for all models containing the variable. Nesting females were avoiding areas with high well densities (Overall model); note that nests were farther from drilling rigs and gas wells in 2004, whereas nests were closer to these structures in 2000-2003 (annual models).

| Model[ab] | n[c] | Drill_Dist (90% CI) | Well_Dist (90% CI) | Road_Dist (90% CI) | Well_Density1480 (90% CI) | Road_TotalLength1480 (90% CI) |
|---|---|---|---|---|---|---|
| 2000 | 16 | -0.002 (0.005, -0.009) | -0.601 (0.010, -1.211) | 0.044 (0.212, -0.125) | -0.144 (0.094, -0.382) | -0.156 (0.044, -0.355) |
| 2001 | 13 | -0.022 (0.037, -0.081) | -0.118 (0.058, -0.293) | -0.021 (0.089, -0.130) | 0.011 (0.255, -0.233) | -0.009 (0.097, -0.114) |
| 2002 | 25 | -0.041 (-0.004, -0.078) | -0.529 (-0.165, -0.863) | -0.838 (-0.189, -1.487) | -0.324 (-0.081, -0.566) | 0.029 (0.068, -0.011) |
| 2003 | 27 | -0.017 (0.046, -0.080) | -0.017 (0.057, -0.091) | -0.053 (0.064, -0.170) | -0.019 (0.018, -0.056) | -0.014 (0.042, -0.070) |
| 2004 | 31 | 0.183 (0.308, 0.058) | 0.297 (0.496, 0.097) | 0.013 (0.074, -0.048) | -0.083 (-0.016, -0.149) | -0.121 (0.009, -0.250) |
| Overall | 112 | 0.001 (0.053, -0.056) | -0.073 (0.716, -0.861) | -0.023 (0.438, -0.484) | -0.063 (0.397, -0.522) | -0.025 (0.365, -0.415) |
| $AIC_c$ Weights | | 0.161 | 0.458 | 0.279 | 0.874 | 0.302 |

[a] Independent variables included: distance to closest active drill rig (Drill_Dist), distance to closest producing gas well (Well_Dist), distance to closest point on a main haul road (Road_Dist), total number of producing gas wells within 1480 m (Well_Density1480) and total linear distance of main haul road within 1480 m (Road_TotalLength1480).

[b] Variables were measured for gas related factor active during the nest initiation period (April 15 through May 15).

[c] Number of nests (random sample sizes equal).

Table 5. Parameter coefficients (90% confidence intervals) and cumulative $AIC_c$ weights for independent variables included in $AIC_c$ weighted logistic regression models ($n$ = 56) comparing successful ($n$ = 45) to unsuccessful ($n$ = 63) nesting sites for greater sage-grouse nesting within 5 km of leks located within 3.2 km of the Pinedale Anticline crest (Bureau of Land Management 2000) in western Wyoming, 2000-2004. Cumulative $AIC_c$ weights for independent variables were estimated by adding $AIC_c$ weight-values for all models containing the variable. Note the skewed nature of the 90% CI around Well_Dist, Well_Density1480, residual grass cover, and residual grass height which suggests these variables could have influenced nest success.

| Independent variable[ab] | Parameter coefficient | 90% Confidence interval | $AIC_c$ cumulative weight |
|---|---|---|---|
| Drill_Dist | -0.023 | (0.066, -0.112) | 0.247 |
| Well_Dist | -0.097 | (0.025, -0.220) | 0.419 |
| Road_Dist | 0.002 | (0.066, -0.061) | 0.188 |
| Well_Density1480 | -0.040 | (0.008, -0.088) | 0.411 |
| Road_TotalLength1480 | 0.019 | (0.070, -0.033) | 0.273 |
| RGHT | 0.038 | (0.129, -0.054) | 0.241 |
| RGRS | 0.048 | (0.144, -0.048) | 0.257 |

[a] Independent variables included: distance to closest active drill rig (Drill_Dist), distance to closest producing gas well (Well_Dist), distance to closest point on a main haul road (Road_Dist), total number of producing gas wells within 1480 m (Well_Density1480), total linear distance of main haul road within 1480 m (Road_TotalLength1480), residual grass height (RGHT), and residual grass cover (RGRS).

[b] Gas field related variables were measured for gas related factor active during the nest incubation period (May 1 through June 15).

Table 6. Mean (SE) distances to natural gas field related disturbances for early brood-rearing used (between 6 and 14 days post-hatch; $n = 49$) and available (within 1 km of nesting location; $n = 49$) sites, and mean (SE) nest-to-disturbance source distances for successful (i.e., females that successfully hatched and had ≥1 living chick 14 days post-hatch; $n = 49$) and unsuccessful (i.e., females that successfully hatched but had 0 living chicks 14 days post-hatch; $n = 15$) brooding greater sage-grouse nesting within 5 km of leks located within 3.2 km of the Pinedale Anticline crest (Bureau of Land Management 2000) in western Wyoming, 2000-2004. Brooding females avoided producing wells; note that development levels did not influence brood success.

| Variable[ab] | Use | Available | Successful | Unsuccessful |
|---|---|---|---|---|
| Drill_Dist (km) | 4.23 (0.41) | 4.06 (0.42) | 3.92 (0.34) | 4.03 (0.81) |
| Well_Dist (km) | 1.84 (0.21)[c] | 1.38 (0.14) | 1.51 (0.14) | 1.78 (0.40) |
| Road_Dist (km) | 1.75 (0.22) | 1.48 (0.15) | 1.62 (0.16) | 1.25 (0.24) |
| Well_Density1000 (wells) | 0.61 (0.21) | 1.12 (0.33) | | |
| Well_Density1580 (wells) | | | 2.65 (0.54) | 4.00 (1.21) |
| Road_TotalLength1000 (km) | 0.45 (0.12) | 0.63 (0.13) | | |
| Road_TotalLength1580 (km) | | | 1.92 (0.25) | 2.56 (0.46) |

[a] Independent variables included: distance to closest active drill rig (Drill_Dist), distance to closest producing gas well (Well_Dist), distance to closest point on a main haul road (Road_Dist), total number of producing gas wells within 1000 m (Well_Density1000; use vs. available) and within 1580 m (Well_Density1580; successful vs. unsuccessful), and total linear distance of main haul road within 1000 m (Road_TotalLength1000; use vs. available) and 1580 m (Road_TotalLength1580; successful vs. unsuccessful).

[b] Variables were measured for gas related factor active during the early brood-rearing period (June 1 through July 1).

[c] Differed significantly from available distance (paired *t*-tests; $p < 0.05$).

Table 7. Apparent nest propensity (±SE), adjusted nest success probabilities (±SE), and brood survival probabilities (±SE) for adult and yearling greater sage-grouse females in southwestern Wyoming, 1998-2004. Individual female separation based on potential gas field development impacts (Group Designation as defined in Statistical Methods section; Table 1).

| Group Designation | Age | Apparent Nest Propensity[a] | Adjusted Nest Success[bc] | Brood Survival[dc] |
|---|---|---|---|---|
| All_Control | Adult | 75.3 (±8.4) | 43.8 (±4.9) | 60.8 (±9.1) |
| | Yearling | 71.4 (±11.2) | | |
| Nest_Control | Adult | 84.8 (±2.2)[e] | 43.8 (±4.9) | 60.8 (±9.1) |
| | Yearling | 72.4 (±6.3)[e] | | |
| All_Treat | Adult | 90.5 (±2.7) | 39.0 (±4.0) | 63.4 (±5.9) |
| | Yearling | 74.0 (±6.9) | | |
| Lek_Treat | Adult | 84.8 (±2.2)[e] | 40.3 (±9.1) | 73.2 (±11.4) |
| | Yearling | 72.4 (±6.3)[e] | | |
| Nest_Treat | Adult | 84.8 (±2.2)[e] | 38.2 (±3.7) | 47.8 (±11.8) |
| | Yearling | 72.4 (±6.3)[e] | | |
| LekNest_Treat | Adult | 84.8 (±2.2)[e] | 49.6 (±4.5) | 67.1 (±8.1) |
| | Yearling | 72.4 (±6.3)[e] | | |
| Pre_Treat | Adult | 80.4 (±6.0) | 51.6 (±7.1) | 54.4 (±10.5) |
| | Yearling | 68.4 (±13.8) | | |
| Post_Treat | Adult | 82.2 (±3.7) | 42.6 (±5.9) | 61.5 (±10.0) |
| | Yearling | 70.0 (±8.1) | | |

[a] Estimated as the number of nesting females divided by the total number of females surviving to June 4.

[b] Nest success probabilities adjusted following Mayfield (1975). Length of incubation estimated at 27 days; re-nests included in nest success calculation.

[c] No age effect detected; adult and yearling birds grouped for estimate.

[d] Brood survival estimated from hatch – August 15 using program MARK (White and Burnham 1999); broods survived censor period if ≥1 chick documented.

[e] Estimates derived from all individuals as group designation required a nest (see Statistical Methods).

Table 8. Investigation of year, age and breeding status (i.e., nesting or non-nesting; brooding or barren females) effect on annual survival of greater sage-grouse broods and females in southwestern Wyoming, 1998-2004. Effect models were developed in program MARK (White and Burnham 1999) and compared using $AIC_c$ weights of evidence (Burnham and Anderson 2002). Constant models predicted no effect; Year models predicted year effect; Age models predicted age effect (adult vs. yearling); Nest models predicted nesting status effect (nesting vs. non-nesting); and Brood models predicted brooding status effect (brooding vs. barren).

| EFFECT | Model | $AIC_C$ | Delta $AIC_C$ | $AIC_C$ Weights | Model Likelihood | Number Parameters | Deviance |
|---|---|---|---|---|---|---|---|
| YEAR (Brood Survival) | | | | | | | |
| | Constant[a] | 568.081 | 0.000 | 0.685 | 1.000 | 1 | 99.776 |
| | Year[b] | 569.630 | 1.550 | 0.315 | 0.461 | 7 | 89.263 |
| AGE (Brood Survival) | | | | | | | |
| | Constant[a] | 553.079 | 0.000 | 0.697 | 1.000 | 1 | 56.161 |
| | Age[b] | 554.746 | 1.667 | 0.303 | 0.435 | 2 | 55.823 |
| YEAR (All Female Survival) | | | | | | | |
| | Constant[a] | 2414.393 | 0.000 | 0.590 | 1.000 | 1 | 237.903 |
| | Year[b] | 2415.123 | 0.730 | 0.410 | 0.694 | 7 | 226.616 |
| AGE, NEST, BROOD (All Female Survival) | | | | | | | |
| | Age[b] | 1841.135 | 0.000 | 0.298 | 1.000 | 2 | 193.041 |
| | Nest[b] | 1841.152 | 0.017 | 0.295 | 0.992 | 2 | 193.058 |
| | Constant[a] | 1841.164 | 0.029 | 0.293 | 0.986 | 1 | 195.071 |
| | Brood[b] | 1843.052 | 1.916 | 0.114 | 0.384 | 2 | 194.957 |
| YEAR (Nesting Female Survival)[c] | | | | | | | |
| | Constant[a] | 1381.157 | 0.000 | 0.507 | 1.000 | 1 | 163.098 |
| | Year[b] | 1381.215 | 0.058 | 0.493 | 0.971 | 7 | 151.132 |
| AGE, BROOD (Nesting Female Survival)[c] | | | | | | | |
| | Brood[b] | 1211.198 | 0.000 | 0.687 | 1.000 | 2 | 117.070 |
| | Constant[a] | 1213.643 | 2.445 | 0.202 | 0.295 | 1 | 121.517 |
| | Age[b] | 1214.856 | 3.659 | 0.110 | 0.161 | 2 | 120.729 |

[a] Model predicting no effect (i.e., constant annual survival across years, age or breeding status).

[b] Models predicting effect [i.e., annual survival differed between years, age classes (yearling or adult), or breeding status].

[c] No nesting effect investigated as groups required a nest (e.g., no non-nesting individuals represented).

Table 9. Annual survival (±SE) estimates for yearling and adult female greater sage-grouse based on nesting status (Nest; No Nest) in southwestern Wyoming, 1998-2004. Individual female separation based on potential gas field development impacts; survival estimates for groups considering all individuals are included (Group Designation as defined in Statistical Methods section; Table 1).

| Group Designation | Adult Nest ($P_{AY}$) | Adult No Nest ($P_{AN}$) | Yearling Nest ($P_{2Y}$) | Yearling No Nest ($P_{2N}$) |
|---|---|---|---|---|
| All_Control | 67.8 (±6.6) | 58.5 (±7.8) | 88.8 (±7.5) | 62.8 (±11.0) |
| All_Treat | 61.5 (±4.1) | 23.0 (±6.9) | 74.7 (±7.3) | 38.5 (±9.8) |
| Pre_Treat | 73.4 (±7.6) | 59.3 (±15.5) | 91.8 (±7.8) | 69.1 (±18.0) |
| Post_Treat | 53.0 (±6.5) | 24.9 (±9.3) | 85.4 (±9.5) | 31.9 (±16.3) |

Table 10. Annual survival (±SE) estimates for female greater sage-grouse based on brooding status (Brood; Barren) in southwestern Wyoming, 1998-2004. Individual female separation based on potential gas field development impacts; survival estimates for groups considering nesting individuals are included (Group Designation as defined in Statistical Methods section; Table 1).

| Group Designation | Adult and Yearling Brood ($P_{AY}$, $P_{2Y}$) | Adult and Yearling Barren ($P_{AN}$, $P_{2N}$) |
|---|---|---|
| Nest_Control | 75.1 (±8.1) | 85.5 (±6.0) |
| Lek_Treat | 54.5 (±10.5) | 60.9 (±10.1) |
| Nest_Treat | 62.2 (±10.4) | 87.1 (±6.0) |
| LekNest_Treat | 50.5 (±8.4) | 77.2 (±6.7) |

Table 11. Seasonal period survival (±SE) estimates for female greater sage-grouse in southwestern Wyoming, 1998-2004. Individual female separation based on potential gas field development impacts; survival estimates for groups including all individuals (Group Designation as defined in Statistical Methods section; Table 1). The treatment population (All_Treat) was impacted by natural gas development during the breeding and nesting seasons, but note that differential survival between treatment and control (All_Control) populations occurred during the early brooding and summer seasons.

| Group Designation | Breeding Survival[a] | Nesting Survival[b] | Early Brooding Survival[c] | Summer Survival[d] | Winter Survival[e] |
|---|---|---|---|---|---|
| All_Control | 93.2 (±2.3) | 84.9 (±3.0) | 99.2 (±0.8) | 98.2 (±1.2) | 82.5 (±3.9) |
| All_Treat | 96.2 (±1.3) | 89.0 (±2.0) | 92.6 (±1.8) | 90.3 (±2.1) | 77.2 (±3.3) |

[a] April 1 – April 30.

[b] May 1 – May 31.

[c] June 1 – June 30.

[d] July 1 – August 31.

[e] September 1 – March 31.

Table 12. Lower level vital rate estimates for female greater sage-grouse in southwestern Wyoming, 1998-2004 (see Figures 10 and 11). Individual female separation based on potential gas field development impacts (Group Designation as defined in statistical methods section; Table 1). Probability of surviving from egg[a] or chick[b] to yearling ($P_1$), nesting[a] or brooding[b] yearling and adult female annual survival ($P_{2Y}$, $P_{AY}$ respectively), non-nesting[a] or barren[b] yearling and adult female annual survival ($P_{2N}$, $P_{AN}$ respectively), probability of yearling and adult nesting[a] or successfully hatching[b] ($B_2$, $B_A$ respectively), and the estimated number of female eggs per clutch (m) are presented.

| Group Designation | $P_1$ | $P_{2Y}$ | $P_{2N}$ | $P_{AY}$ | $P_{AN}$ | $B_2$ | $B_A$ | m |
|---|---|---|---|---|---|---|---|---|
| All_Control[1] | 6.0 | 88.8 | 62.8 | 67.8 | 58.5 | 71.4 | 75.3 | 3.96 |
| Nest_Control[2] | 13.7 | 75.1 | 85.5 | 75.1 | 85.5 | 31.7 | 37.2 | 3.96 |
| All_Treat[1] | 5.6 | 74.7 | 38.5 | 61.5 | 23.0 | 74.0 | 90.5 | 3.96 |
| Lek_Treat[2] | 16.6 | 54.5 | 60.9 | 54.5 | 60.9 | 29.1 | 34.2 | 3.96 |
| Nest_Treat[2] | 10.8 | 62.2 | 87.1 | 62.2 | 87.1 | 27.6 | 32.4 | 3.96 |
| LekNest_Treat[2] | 15.2 | 50.5 | 77.2 | 50.5 | 77.2 | 35.9 | 42.1 | 3.96 |
| Pre_Treat[1] | 6.3 | 91.8 | 69.1 | 73.4 | 59.3 | 68.4 | 80.4 | 3.96 |
| Post_Treat[1] | 5.9 | 85.4 | 31.9 | 53.0 | 24.9 | 70.0 | 82.2 | 3.96 |

[a] Estimates for groups including all individuals (Group Designation [1]).

[b] Estimates for groups including nesting individuals (Group Designation [2]).

Table 13. Upper level (i.e., matrix entry) elacticities and stable age distribution (see Figure 4) for matrix population growth models analyzing demographic information collected from female greater sage-grouse in southwestern Wyoming, 1998-2004. Individual female separation based on potential gas field development impacts (Group Designation as defined in Statistical Methods section; Table 1). Relatively large elacticities suggest that changes to the vital rates within a stage have a proportionally large influence on population growth.

| | | Group Designation | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Matrix Entries | Arc Type[a] | All_Control | Nest_Control | All_Treat | Lek_Treat | Nest_Treat | LekNest_Treat | Pre_Treat | Post_Treat |
| $P_1B_2m$ | Fertility (yearling) | 0.046 | 0.033 | 0.052 | 0.062 | 0.019 | 0.063 | 0.042 | 0.069 |
| $P_{2Y}B_Am$ | Fertility (2nd year)[b] | 0.035 | 0.009 | 0.045 | 0.014 | 0.004 | 0.015 | 0.033 | 0.067 |
| $P_{2N}B_Am$ | Fertility (2nd year)[c] | 0.010 | 0.022 | 0.008 | 0.039 | 0.015 | 0.040 | 0.012 | 0.011 |
| $P_{AY}B_Am$ | Fertility (adult)[b] | 0.110 | 0.044 | 0.141 | 0.046 | 0.028 | 0.047 | 0.118 | 0.141 |
| $P_{AN}B_Am$ | Fertility (adult)[c] | 0.031 | 0.084 | 0.006 | 0.099 | 0.080 | 0.099 | 0.023 | 0.014 |
| $P_1B_2$ | Survival (1st year)[b] | 0.146 | 0.046 | 0.169 | 0.054 | 0.027 | 0.054 | 0.138 | 0.201 |
| $P_1(1-B_2)$ | Survival (1st year)[c] | 0.041 | 0.112 | 0.031 | 0.145 | 0.100 | 0.147 | 0.048 | 0.032 |
| $P_{2Y}B_A$ | Survival (2nd year)[b] | 0.086 | 0.013 | 0.119 | 0.012 | 0.006 | 0.013 | 0.088 | 0.122 |
| $P_{2N}B_A$ | Survival (2nd year)[c] | 0.024 | 0.031 | 0.022 | 0.034 | 0.022 | 0.034 | 0.030 | 0.019 |
| $P_{AY}B_A$ | Survival (adult)[b] | 0.267 | 0.061 | 0.374 | 0.040 | 0.040 | 0.040 | 0.310 | 0.255 |
| $P_{AN}B_A$ | Survival (adult)[c] | 0.076 | 0.118 | 0.015 | 0.086 | 0.118 | 0.085 | 0.061 | 0.026 |
| $P_{2Y}(1-B_A)$ | Survival (2nd year)[b] | 0.024 | 0.024 | 0.005 | 0.027 | 0.017 | 0.027 | 0.017 | 0.012 |
| $P_{2N}(1-B_A)$ | Survival (2nd year)[c] | 0.007 | 0.059 | 0.001 | 0.073 | 0.063 | 0.073 | 0.006 | 0.002 |
| $P_{AY}(1-B_A)$ | Survival (adult)[b] | 0.076 | 0.118 | 0.015 | 0.086 | 0.118 | 0.085 | 0.061 | 0.026 |
| $P_{AN}(1-B_A)$ | Survival (adult)[c] | 0.021 | 0.227 | 0.001 | 0.184 | 0.344 | 0.179 | 0.012 | 0.003 |

Table 13 continued on next page.

Table 13 (Continued). Upper level (i.e., matrix entry) elacticities and stable age distribution (see Figure 4) for matrix population growth models analyzing demographic information collected from female greater sage-grouse in southwestern Wyoming, 1998-2004. Individual female separation based on potential gas field development impacts (Group Designation as defined in Statistical Methods section; Table 1). Relatively large elacticities suggest that changes to the vital rates within a stage have a proportionally large influence on population growth.

| | | Group Designation | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Matrix Entries | Arc Type[a] | All_Control | Nest_Control | All_Treat | Lek_Treat | Nest_Treat | LekNest_Treat | Pre_Treat | Post_Treat |
| Stable Age Distribution | | | | | | | | | |
| Node 1 | 1st year | 0.747 | 0.589 | 0.774 | 0.565 | 0.557 | 0.616 | 0.755 | 0.758 |
| Node 2 (2Y) | 2nd year[b] | 0.037 | 0.025 | 0.041 | 0.034 | 0.018 | 0.037 | 0.035 | 0.044 |
| Node 3 (2N) | 2nd year[c] | 0.015 | 0.054 | 0.014 | 0.083 | 0.047 | 0.066 | 0.016 | 0.019 |
| Node 4 (AY) | Adult[b] | 0.151 | 0.123 | 0.155 | 0.109 | 0.123 | 0.118 | 0.155 | 0.148 |
| Node 5 (AN) | Adult[c] | 0.050 | 0.208 | 0.016 | 0.209 | 0.256 | 0.163 | 0.038 | 0.032 |

[a] Reference Figure 9.

[b] Nesting or brood-rearing females.

[c] Non-nesting or barren females.

Table 14. Population growth rate estimates (λ) and treatment effect (life table response experiment; Caswell 1989, 1996) for matrix population growth models analyzing demographic information collected from female greater sage-grouse in southwestern Wyoming, 1998-2004. Individual female separation based on potential gas field development impacts (Group Comparison as defined in Statistical Methods section; Table 1); individuals potentially impacted by gas development designated treatments, non-impacted individuals designated controls. Note that natural gas development had a consistently negative effect on population growth (Treatment Effect).

| Group Comparison | Treatment λ | Control λ | Treatment Effect |
|---|---|---|---|
| All_Treat vs. All_Control | 0.7874 | 0.8659 | -0.0785 |
| Lek_Treat vs. Nest_Control | 0.8031 | 1.0140 | -0.2109 |
| Nest_Treat vs. Nest_Control | 0.9277 | 1.0140 | -0.0863 |
| LekNest_Treat vs. Nest Control | 0.9066 | 1.0140 | -0.1074 |
| Pre_Treat vs. Post_Treat | 0.7207 | 0.9317 | -0.2110 |

Table 15. Mean extinction time (years) and estimated change in population growth (λ) with the addition of stochasticity[a] to demographic information[b] collected from female greater sage-grouse in southwestern Wyoming, 1998-2004. Individual female separation based on potential gas field development impacts (Group Designation as defined in Statistical Methods section; Table 1). Note the change in λ values; relatively large values suggest increased variation was present in vital rate estimates.

| Group Designation | Runs Resulting in Extinction (of 1000) | Mean Extinction Time (95% CI) | Change in λ |
|---|---|---|---|
| All_Control | 1000 | 94 (96.3, 91.7) | 1.407% |
| Nest_Control | 86 | 826 (917.1, 734.9) | 0.559% |
| All_Treat | 1000 | 55 (55.6, 54.4) | 0.363% |
| Lek_Treat | 1000 | 49 (49.9, 48.1) | 5.549% |
| Nest_Treat | 1000 | 121 (123.2, 118.8) | 0.075% |
| LekNest_Treat | 1000 | 114 (116.3, 111.7) | 1.985% |
| Pre_Treat | 1000 | 219 (226.1, 211.9) | 0.063% |
| Post_Treat | 1000 | 40 (40.6, 39.4) | 0.878% |

[a] Stochasticity added to 1000 iterations, starting population size for each simulation was 1,000,000 individuals; each simulation followed for 2000 years.

[b] The mean and standard error of each vital rate for each population were used to establish beta distributions; for each of 1000 iterations, vital rate values were selected from these distributions and used in matrix building procedures.

Figure 1. Greater sage-grouse study location in southwestern Wyoming, 1998-2004. General outlines of the Pinedale Anticline Project Area (PAPA) and the Jonah II natural gas field (gas field boundaries adapted from Bureau of Land Management 2000), and general study lek ($n$ = 21) locations are provided for reference.

Figure 1

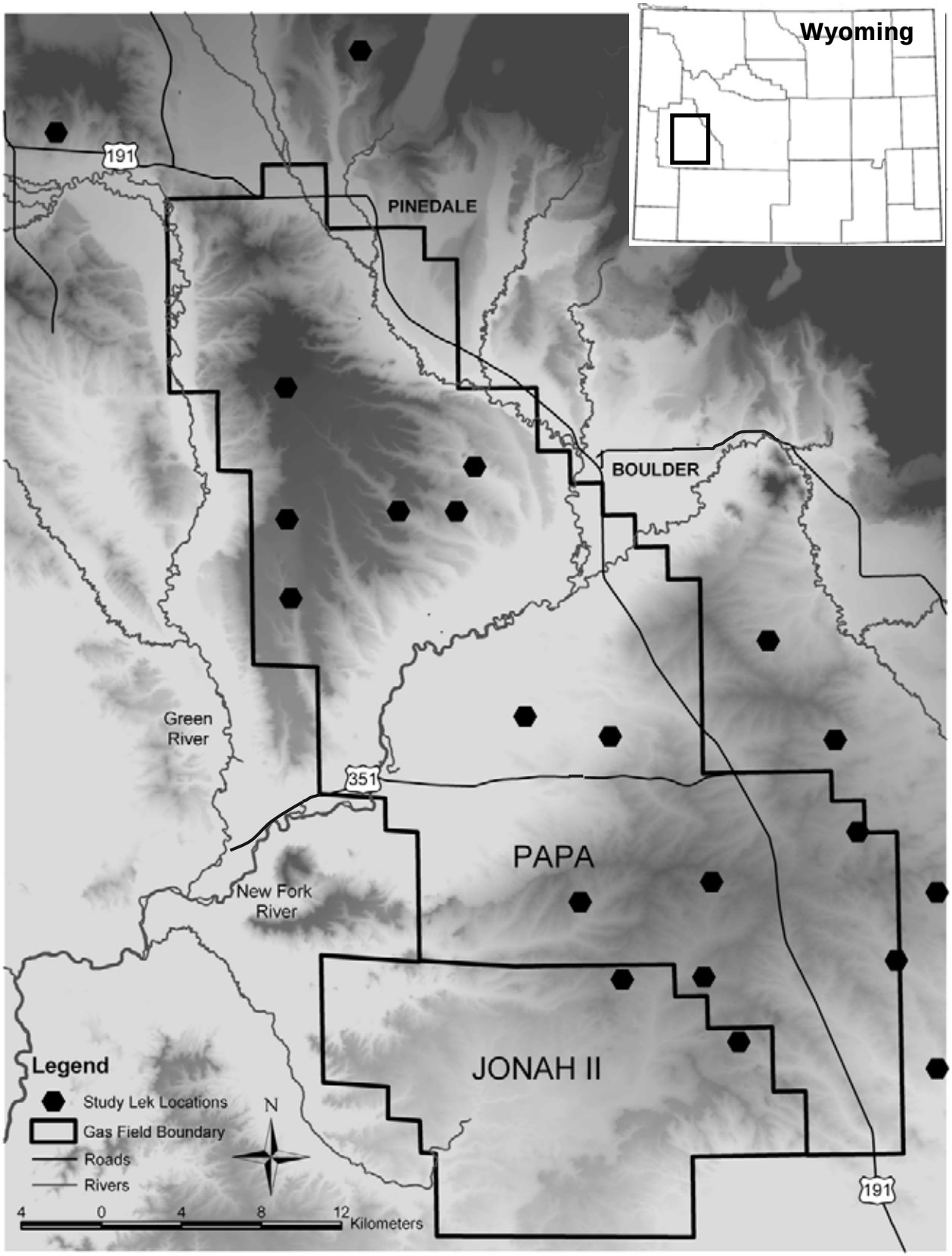

Wyoming
191
PINEDALE
BOULDER
Green
River
351
PAPA
New Fork
River
JONAH II
191
Legend
Study Lek Locations
Gas Field Boundary
Roads
Rivers
N
4 0 4 8 12 Kilometers

Figure 2. Greater sage-grouse study location in southwestern Wyoming, 1998-2004 (reference Figure 1). This figure illustrates the level of natural gas development that occurred during the duration of the study (1998-2004), and additionally illustrates lek locations in relation to natural gas field infrastructure. The road network represents natural gas field related roads within 10 km of study leks and state highways. Well locations were obtained from the Wyoming Oil and Gas Conservation Commission (Casper, WY, USA), and road locations were provided by the Bureau of Land Management (Pinedale Field Office, Pinedale, WY, USA).

Figure 2

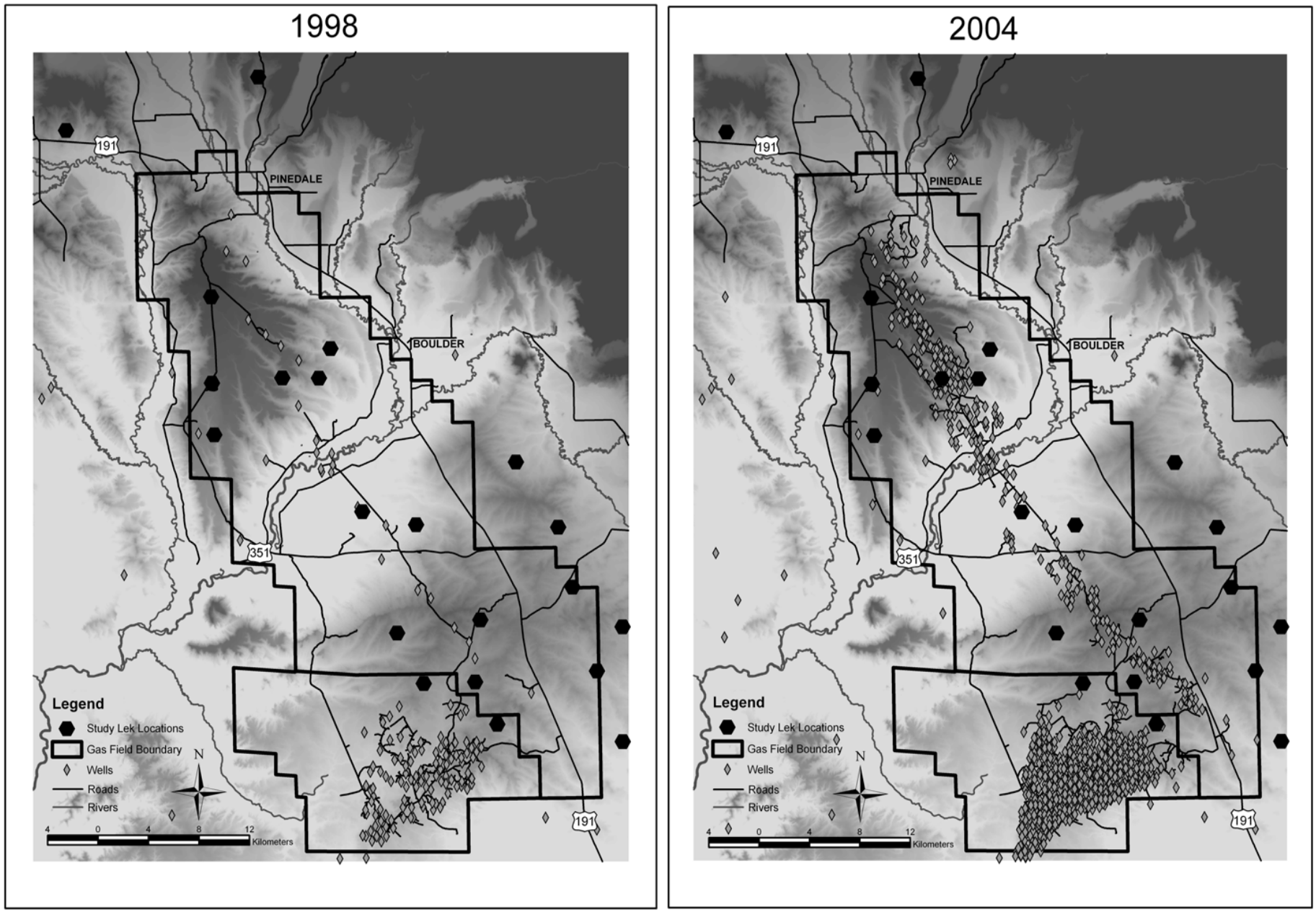

1998
2004
191
PINEDALE
BOULDER
351
Legend
Study Lek Locations
Gas Field Boundary
Wells
Roads
Rivers
N
4 0 4 8 12
Kilometers

Figure 3. Greater sage-grouse study location in southwestern Wyoming, 1998-2004 (reference Figure 1). The dashed lines are 5 km buffers around known leks located within 3.2 km of the Pinedale Anticline crest, and represent the spatial area used for nesting and early brood-rearing habitat selection. This figure illustrates the level of natural gas development that occurred during the female habitat selection portion of the study (2000-2004). The road network represents natural gas field related roads within 10 km of study leks and state highways. Well locations were obtained from the Wyoming Oil and Gas Conservation Commission (Casper, WY, USA), and road locations were provided by the Bureau of Land Management (Pinedale Field Office, Pinedale, WY, USA).

Figure 3

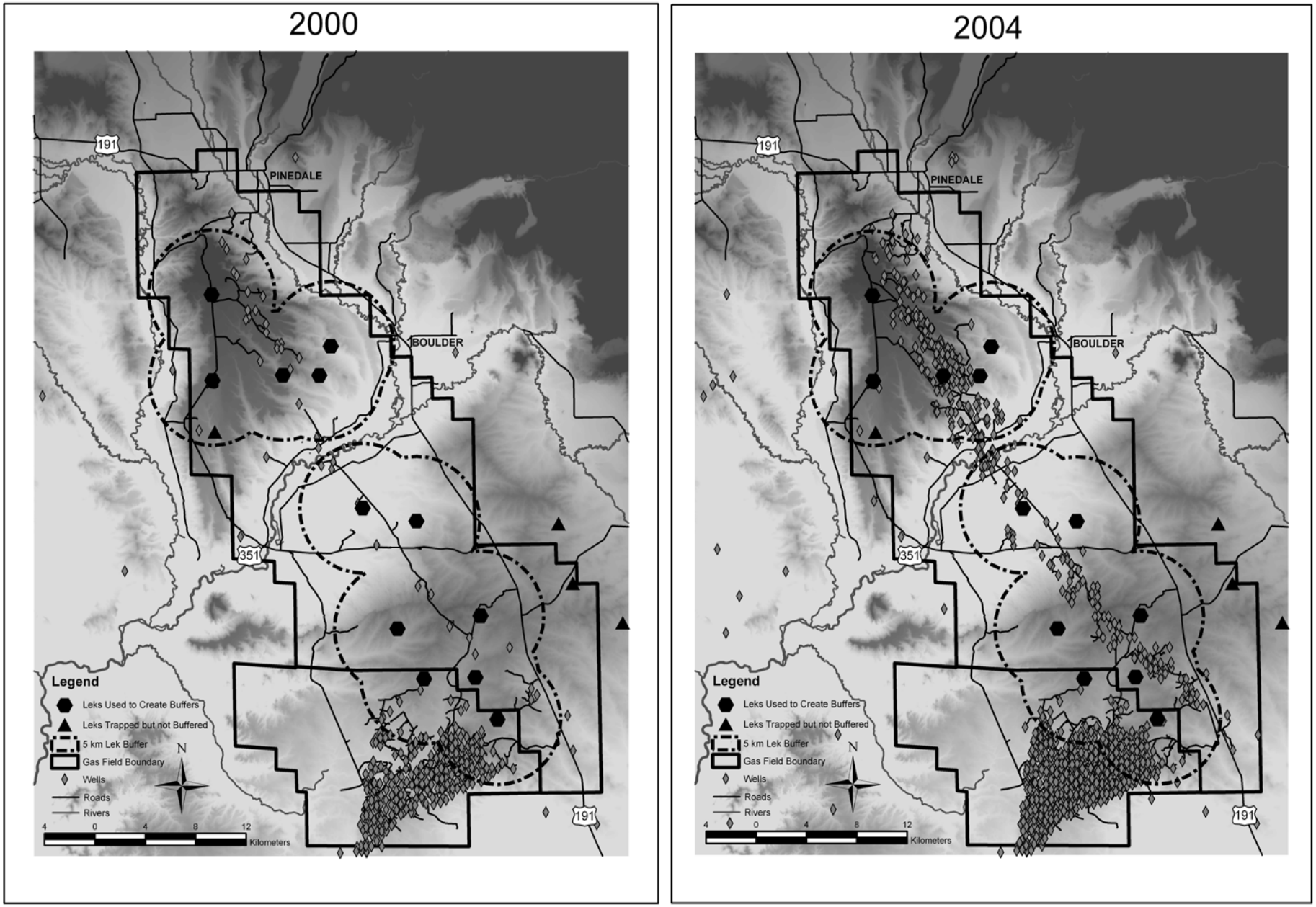

2000
2004
191
PINEDALE
BOULDER
351
Legend
Leks Used to Create Buffers
Leks Trapped but not Buffered
5 km Lek Buffer
Gas Field Boundary
Wells
Roads
Rivers
N
4 0 4 8 12
Kilometers

Figure 4. Regression relationship between overall change (%) in the number of greater sage-grouse males attending leks in southwestern Wyoming, 1998-2004 and principal component 1 scores. Principal component 1 included: average annual distance (km) from leks to closest drilling rig active during the breeding season, distance (km) to closest producing gas well, and distance (km) to closest point on a main haul road; the total number of quadrats (categorized by the cardinal directions) occupied by a producing well within 5 km of leks; and the total length (km) of main haul road within 3 km of leks. Note that the relationship suggests that as natural gas development levels increase relatively near a greater sage-grouse lek, male lek attendance approaches 100% decline (i.e., lek inactivity; notice Y-axis scale).

Figure 4

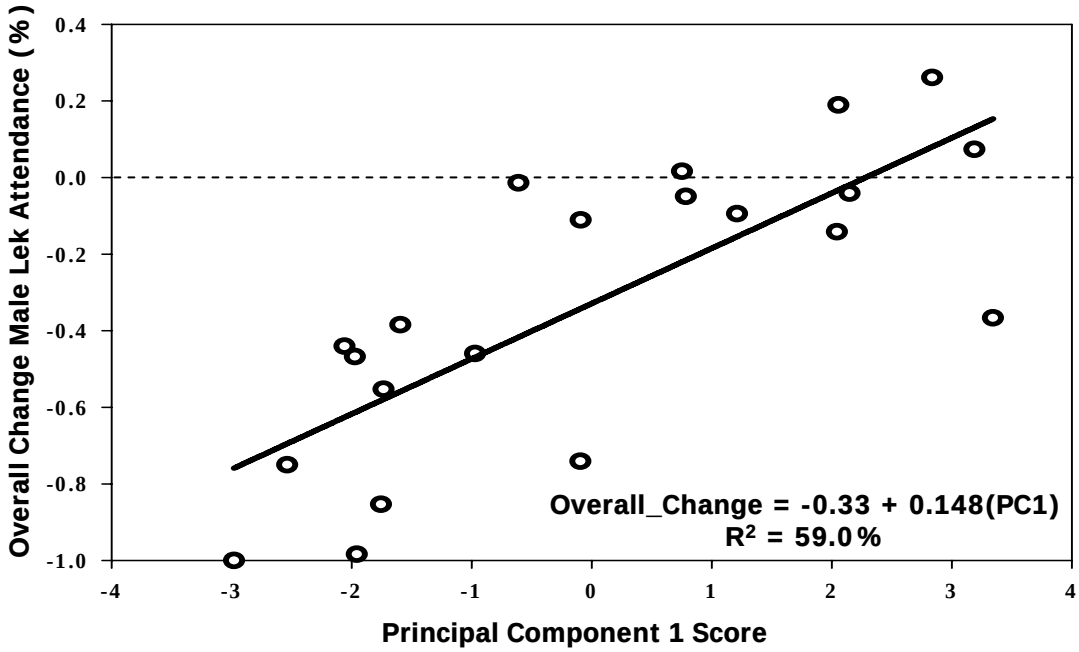

Overall Change Male Lek Attendance (%)
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-4
-3
-2
-1
0
1
2
3
4
Principal Component 1 Score
Overall_Change = -0.33 + 0.148(PC1)
R² = 59.0 %

Figure 5. Regression relationships between overall change (%) in the number of greater sage-grouse males attending leks in southwestern Wyoming, 1998-2004 and average annual distance from leks to closest drilling rig active during the breeding season, closest producing natural gas well, and closest point on a main haul road. Notice scale differences on X-axes. Note that the curvilinear relationships suggest a distance-effect to greater sage-grouse male lek attendance relative to natural gas field-related structures.

Figure 5

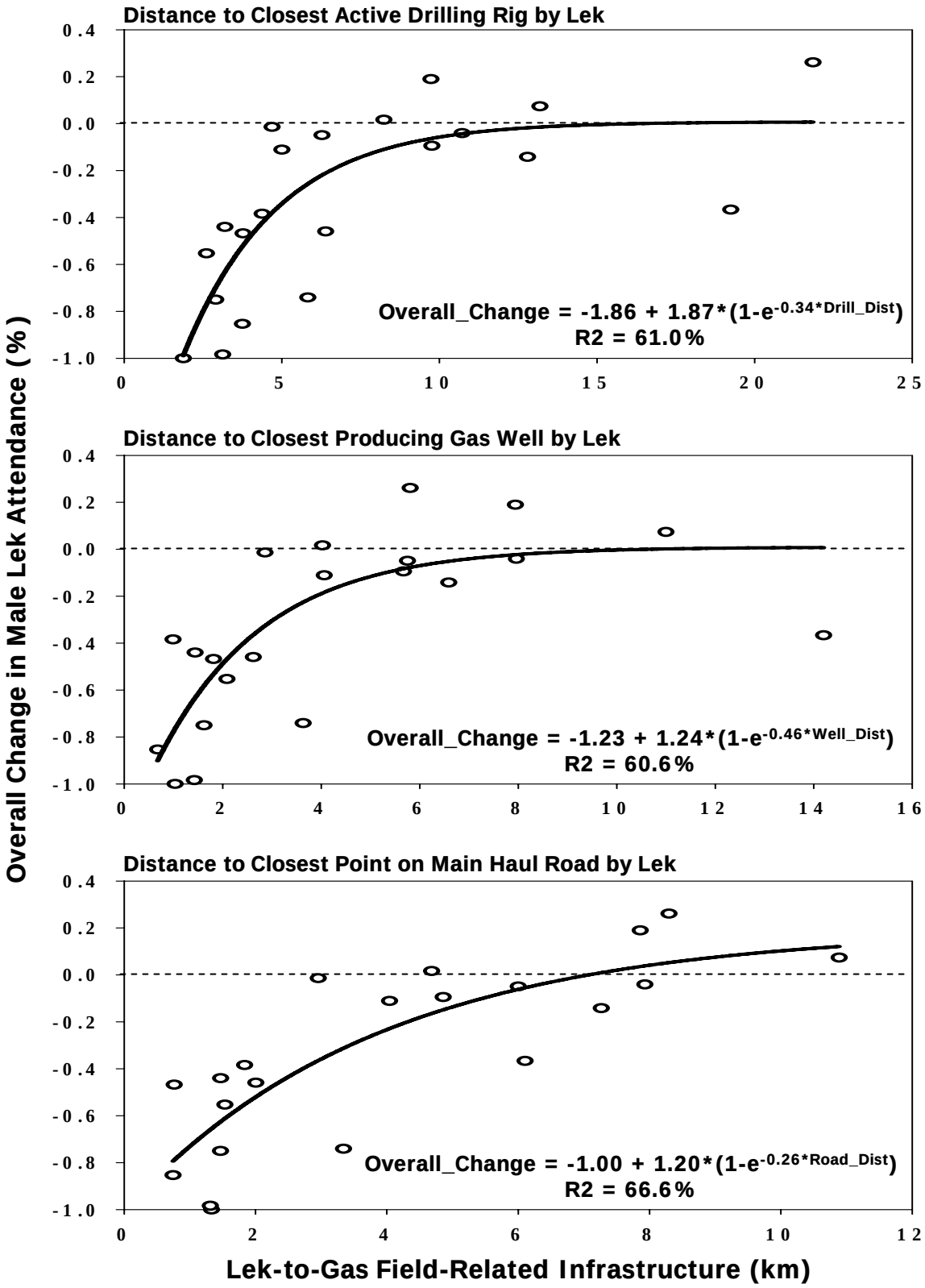

Distance to Closest Active Drilling Rig by Lek
Overall_Change = -1.86 + 1.87*(1-e-0.34*Drill_Dist)
R2 = 61.0%
Distance to Closest Producing Gas Well by Lek
Overall_Change = -1.23 + 1.24*(1-e-0.46*Well_Dist)
R2 = 60.6%
Distance to Closest Point on Main Haul Road by Lek
Overall_Change = -1.00 + 1.20*(1-e-0.26*Road_Dist)
R2 = 66.6%
Overall Change in Male Lek Attendance (%)
Lek-to-Gas Field-Related Infrastructure (km)

Figure 6. Mean annual change (%) in the number of greater sage-grouse males attending leks in southwestern Wyoming, 1998-2004 by lek-to-closest drilling rig active during the breeding season distance categories, lek-to-closest producing natural gas well distance categories, and lek-to-closest point on a main haul road distance categories. Solid bars differed significantly from controls (separate variance, 2-sample *t*-tests; $p \leq 0.05$). Error bars represent 95% confidence intervals. Control distances were determined from curvilinear regression relationships (Figure 3) using geostatistical methods (Royle et al. 1980). Note that drilling rigs within 5 km, producing wells within 3 km, and main haul roads within 3 km of a lek negatively influenced greater sage-grouse male lek attendance.

Figure 6

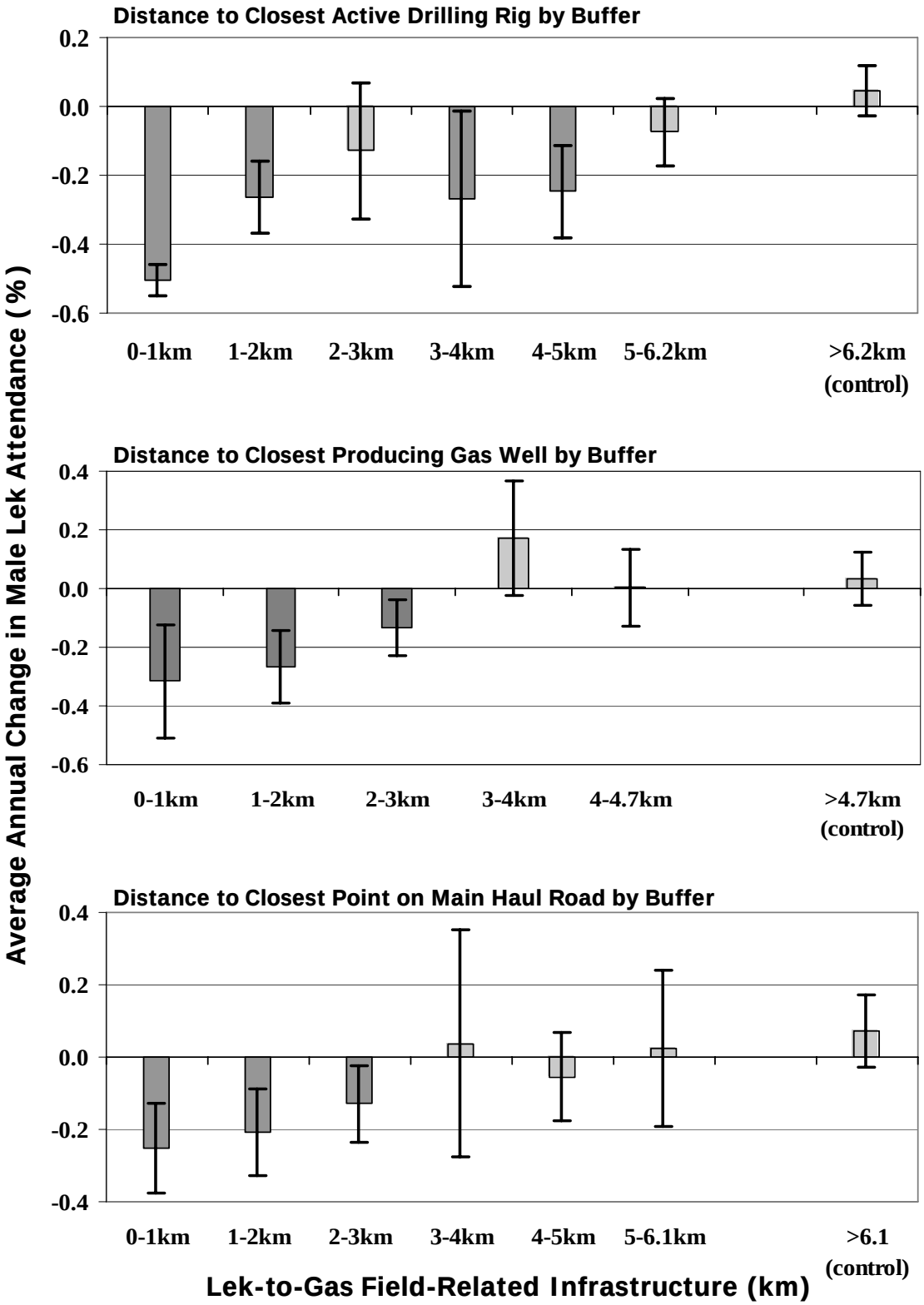

Distance to Closest Active Drilling Rig by Buffer
0.2
0.0
-0.2
-0.4
-0.6
0-1km
1-2km
2-3km
3-4km
4-5km
5-6.2km
>6.2km (control)
Distance to Closest Producing Gas Well by Buffer
0.4
0.2
0.0
-0.2
-0.4
-0.6
0-1km
1-2km
2-3km
3-4km
4-4.7km
>4.7km (control)
Distance to Closest Point on Main Haul Road by Buffer
0.4
0.2
0.0
-0.2
-0.4
0-1km
1-2km
2-3km
3-4km
4-5km
5-6.1km
>6.1 (control)
Average Annual Change in Male Lek Attendance (%)
Lek-to-Gas Field-Related Infrastructure (km)

Figure 7. Nest probabilities relative to natural gas development levels generated from an $AIC_c$ weighted logistic regression model comparing selected nesting sites ($n$ = 112) and random locations ($n$ = 112) for greater sage-grouse nesting within 5 km of leks located within 3.2 km of the Pinedale Anticline crest (Bureau of Land Management 2000) in southwestern Wyoming, 2000-2004. Independent variables included: distance to closest active drill rig (Drill_Dist), distance to closest producing gas well (Well_Dist), distance to closest point on a main haul road (Road_Dist), total number of producing gas wells within 1480m (Total_Well1480) and total linear distance of main haul road within 1480m (Total_Road1480). Variables were measured for gas related factor active during the nest initiation period (Apr 15 through May 15). Average $AIC_c$ weighted logistic regression model used to estimate probabilities: Nest probability = e^[0.364 – 0.001(Drill_Dist) – 0.073(Well_Dist) – 0.023(Road_Dist) – 0.063(Total_Well1480) – 0.025(Total_Road1480)]. Levels of gas field development (X-axis) represent the range of values witnessed for nesting females, and ranged between: 0.7 – 38.0 km for Drill_Dist, 0.1 – 9.2 km for Well_Dist, 0.01 – 6.2 for Road_Dist, 0 – 21 wells for Total_Well1480, and 0 – 7.1 km for Total_Road1480.

Figure 7

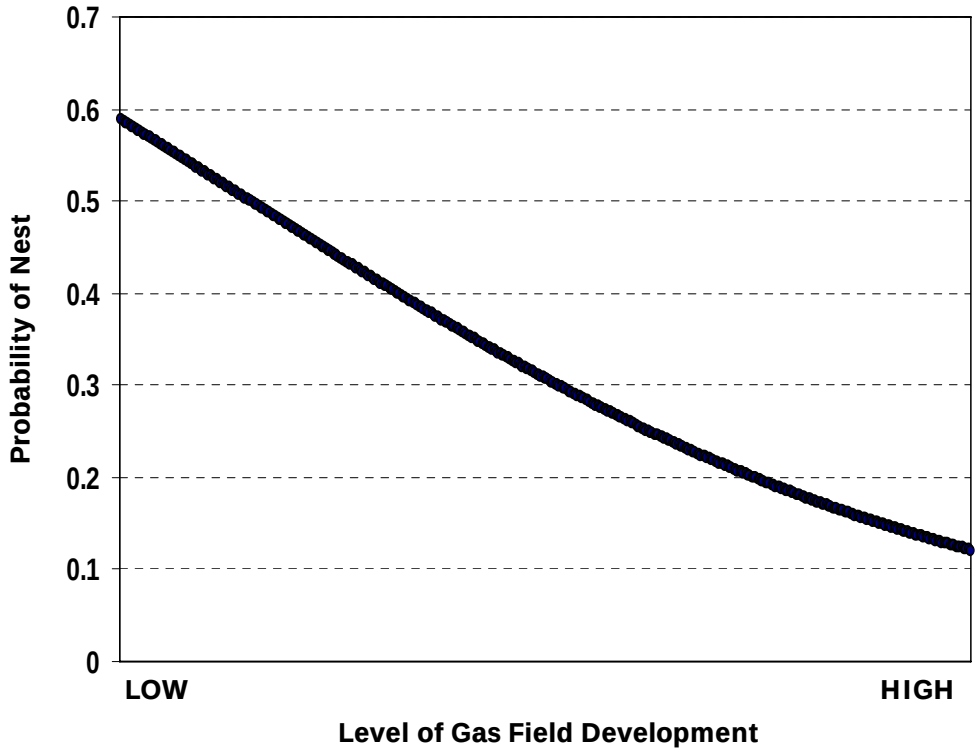

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Probability of Nest
LOW
HIGH
Level of Gas Field Development

Figure 8. Annual sample size and percent normal precipitation for female greater sage-grouse in southwestern Wyoming, 1998-2004. Pre_Treat and Post_Treat groups (defined in Statistical Methods section) compared. Note sample sizes in 2001 and 2002, suggesting that population growth differences pre- versus post-treatment were not unduly confounded by drought conditions.

Figure 8

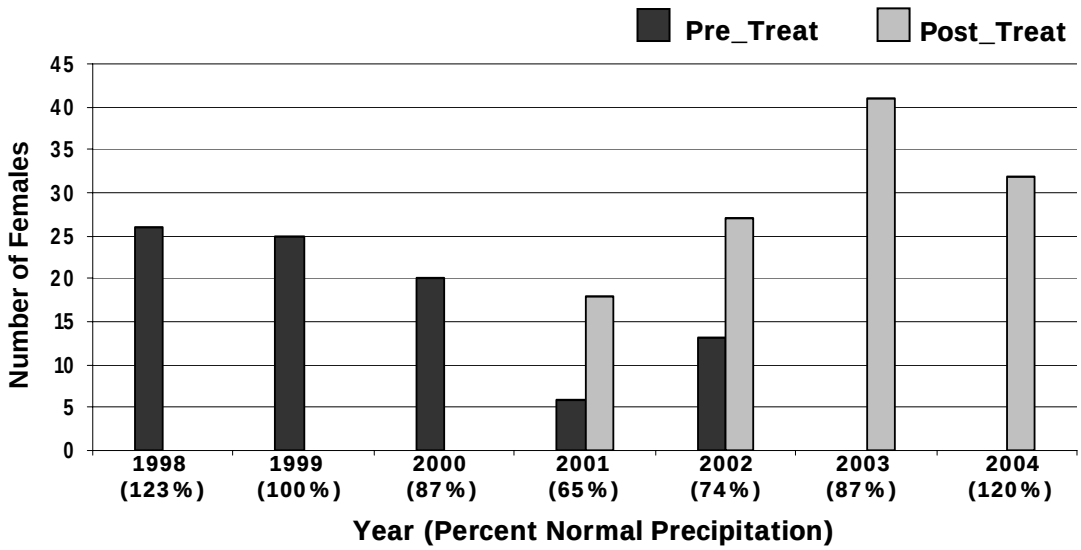
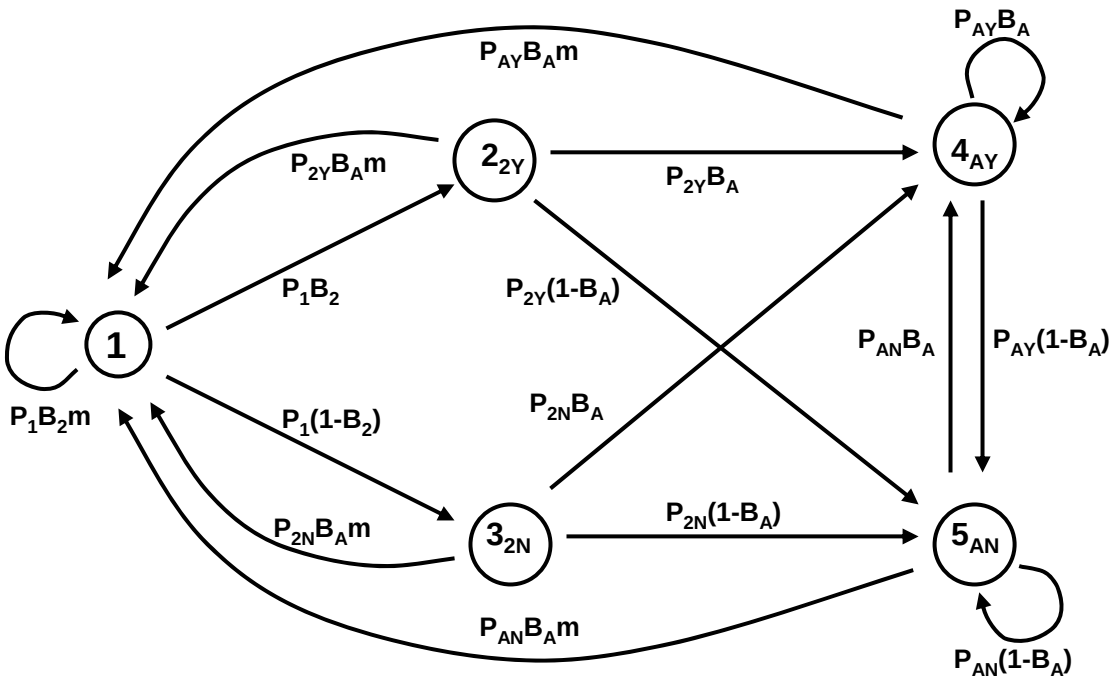

Pre_Treat
Post_Treat
Number of Females
45
40
35
30
25
20
15
10
5
0
1998 (123%)
1999 (100%)
2000 (87%)
2001 (65%)
2002 (74%)
2003 (87%)
2004 (120%)
Year (Percent Normal Precipitation)

Figure 9. Life-cycle diagram and matrix for a 5 stage population growth model of female greater sage-grouse in southwestern Wyoming, 1998-2004. Notations for matrix entries defined in Statistical Methods section and Table 12. Separation into stages based on differential survival estimated using program MARK (White and Burnham 1999; Table 8).

Figure 9




$$A = \begin{pmatrix} P_1B_2m & P_{2Y}B_Am & P_{2N}B_Am & P_{AY}B_Am & P_{AN}B_Am \\ P_1B_2 & & & & \\ P_1(1-B_2) & & & & \\ & P_{2Y}B_A & P_{2N}B_A & P_{AY}B_A & P_{AN}B_A \\ & P_{2Y}(1-B_A) & P_{2N}(1-B_A) & P_{AY}(1-B_A) & P_{AN}(1-B_A) \end{pmatrix}$$

Figure 10. Life table response experiment (Caswell 1989, 1996) results from population growth models analyzing demographic information collected from female greater sage-grouse in southwestern Wyoming, 1998-2004. Bars indicate the contribution of vital rates to the difference in population growth between treatment and control populations. Vital rates include: yearling and adult nesting propensity [NP(y) and NP(a) respectively], the number of female eggs per clutch (#Eggs), nest success probability (NS), brood survival probability (BS), Chick summer (CS) and winter (CW) survival, nesting yearling and adult female annual survival [P2y and Pay respectively], and non-nesting yearling and adult annual survival [P2n and Pan respectively]. Groups considering all individuals (as defined in Statistical Methods section) are presented. Note that lower annual survival of nesting and non-nesting adult treatment females was primarily responsible for differences in population growth (Table 14).

Figure 10

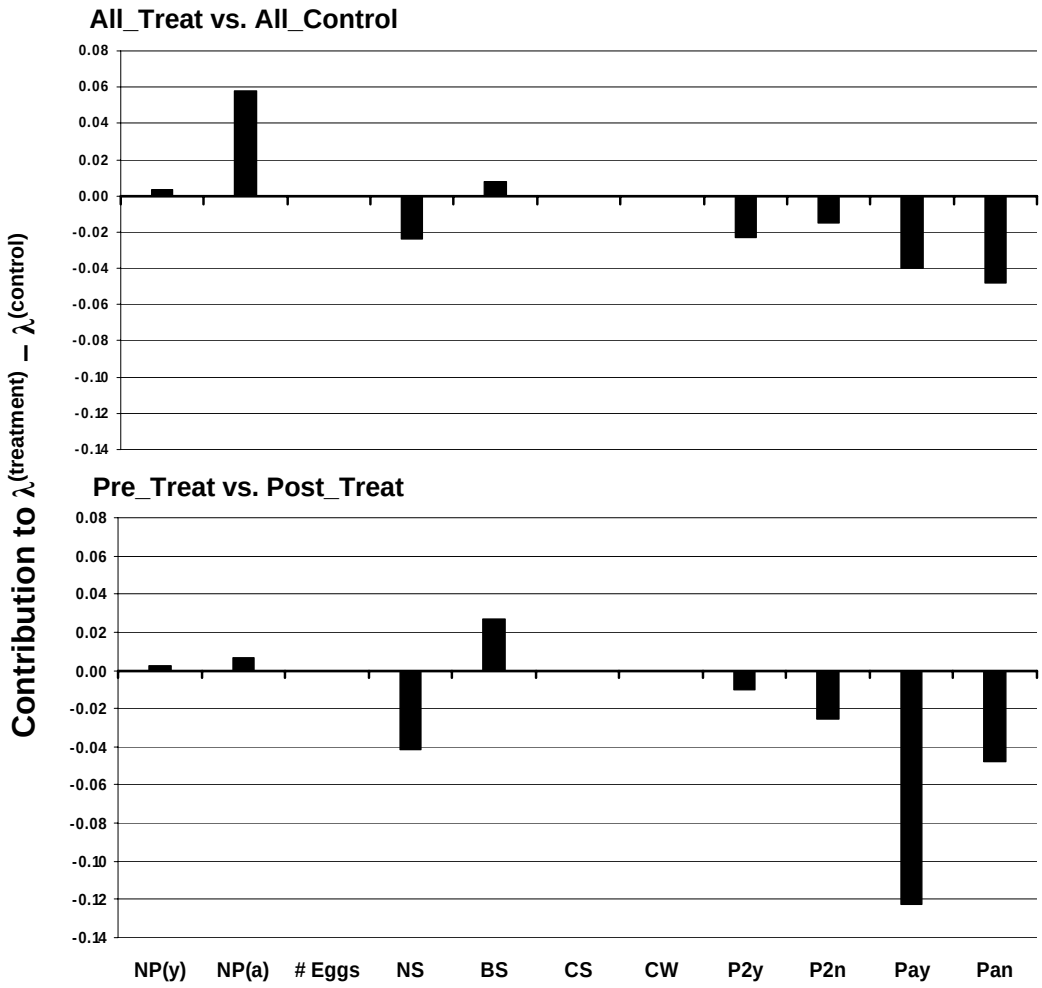
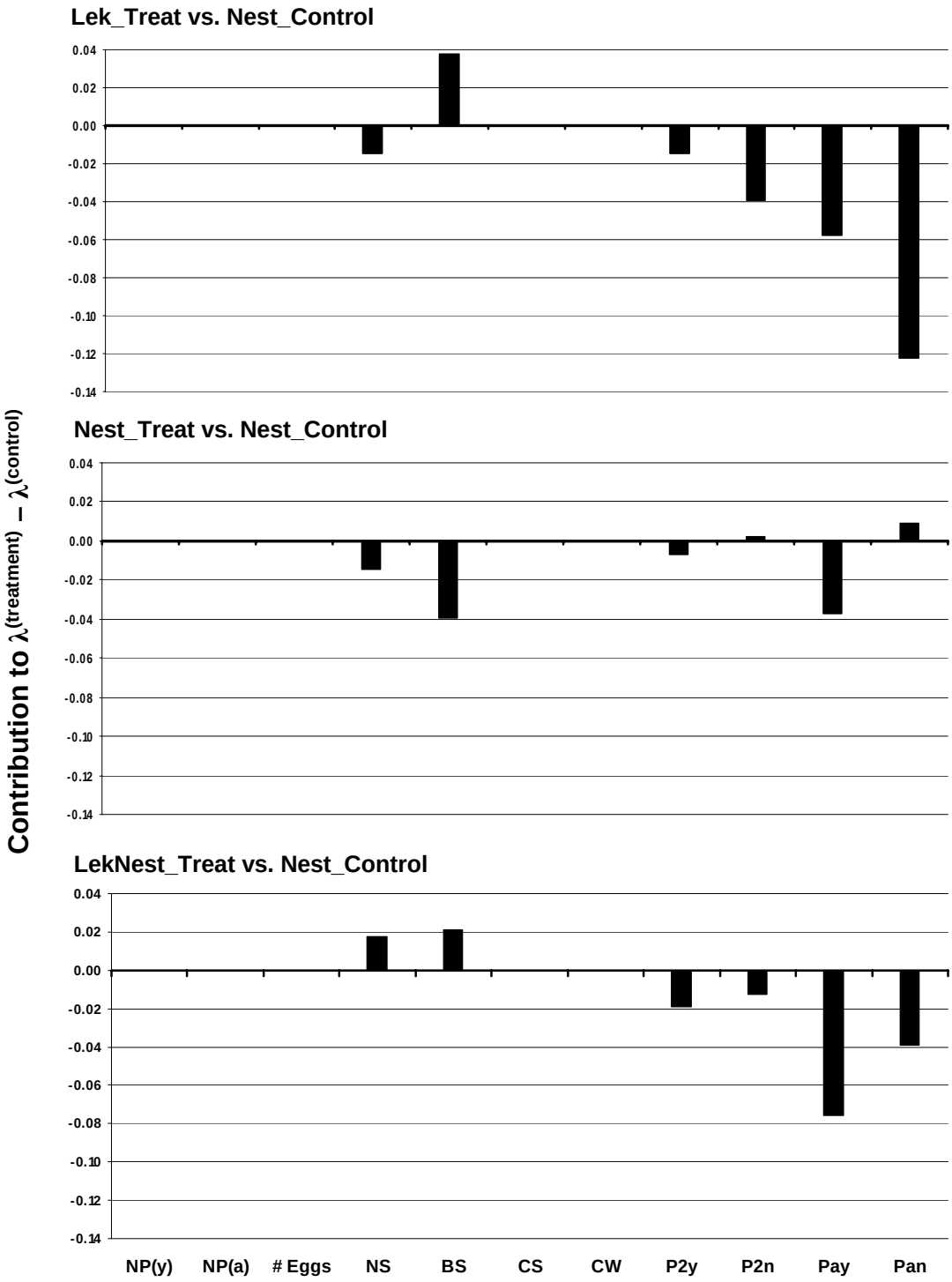

All_Treat vs. All_Control
Pre_Treat vs. Post_Treat
Contribution to λ(treatment) – λ(control)
0.08
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.12
-0.14
NP(y)
NP(a)
# Eggs
NS
BS
CS
CW
P2y
P2n
Pay
Pan

Figure 11. Life table response experiment (Caswell 1989, 1996) results from population growth models analyzing demographic information collected from female greater sage-grouse in southwestern Wyoming, 1998-2004. Bars indicate the contribution of vital rates to the difference in population growth between treatment and control populations. Vital rates include: yearling and adult nesting propensity [NP(y) and NP(a) respectively], the number of female eggs per clutch (#Eggs), nest success probability (NS), brood survival probability (BS), Chick summer (CS) and winter (CW) survival, nesting yearling and adult female annual survival [P2y and Pay respectively], and non-nesting yearling and adult annual survival [P2n and Pan respectively]. Groups considering nesting individuals (as defined in Statistical Methods section) are presented. Note that lower annual survival of nesting and non-nesting adult treatment females and lower brood survival (Nest_Treat vs. Nest_Control) were primarily responsible for differences in population growth (Table 14).

Figure 11


Lek_Treat vs. Nest_Control
Nest_Treat vs. Nest_Control
LekNest_Treat vs. Nest_Control
Contribution to λ(treatment) – λ(control)
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.12
-0.14
NP(y)
NP(a)
# Eggs
NS
BS
CS
CW
P2y
P2n
Pay
Pan

# CHAPTER 3

# NATURAL GAS DEVELOPMENT IMPACTS TO GREATER SAGE-GROUSE POPULATIONS: A SUMMARY OF RESEARCH CONDUCTED IN WESTERN WYOMING WITH THOUGHTS ON MANAGEMENT AND FUTURE RESEARCH OPTIONS.

Natural gas development in western North America has been escalating since the 1960s (Braun et al. 2002, Connelly et al. 2004), and the current U.S. political climate suggests that development of domestic fossil fuels reserves will continue to expand through the first half of the 21st century. Given that reducing the U.S. dependence on foreign sources of petroleum, the use of natural gas (versus oil or coal) as an energy source has air quality benefits, and the protection of natural ecosystems and the wildlife that depend on these habitats are of equivalent importance to the future of the country, it behooves us to develop extractive techniques that minimize extraneous consequences. This study concentrated on natural gas development impacts to a single species, but the results imply potential responses of an array of wildlife populations dependent on sagebrush-dominated landscapes.

Scientific and anecdotal evidence suggest that sage-grouse (*Centrocercus* spp.) leks situated within a developing natural resource field become unoccupied over a relatively short period of time (Braun et al. 2002, Aldridge and Brigham 2003); however, the specific components of a developing field that result in declines, as well as the root causes of lek abandonment, remain unidentified. Remington and Braun (1991) studied the effects of coal mining on breeding greater sage-grouse (*Centrocercus urophasianus*) in North Park, Colorado, and theorized that regional distributions were altered by this disturbance. This displacement theory is supported by several other studies. In Wyoming, Lyon and Anderson (2003) reported that female greater sage-grouse disturbed on a lek by road-related activity in natural gas fields moved farther from leks to nest compared to undisturbed females. Greater sage-grouse in Canada avoided nesting in areas with increased levels of human development and brooding females avoided areas with increased levels of visible oil wells (Aldridge 2005). Lesser prairie-chickens (*Tympanuchus pallidicinctus*) in Kansas selected habitats removed from anthropogenic features (Hagen 2003), and patch occupancy probabilities of Gunnison sage-grouse (*Centrocercus minimus*) in Colorado have been positively correlated with distance to roads (Oyler-McCance 1999). There is also evidence to suggest negative effects at the population scale. Female greater sage-grouse disturbed by natural gas development during the breeding season had lower nest initiation rates compared to undisturbed females in Wyoming (Lyon and Anderson 2003), and chick survival decreased as oil well densities within 1 km of brooding locations increased in Canada (Aldridge 2005). Hagen (2003) reported that a lesser prairie chicken population subjected to

anthropogenic activity in Kansas had population growth rates 21% lower than an undisturbed population, and suggested that the difference was primarily due to decreased nest success and female survival in the disturbed area.

I investigated potential impacts of development of natural gas fields to greater sage-grouse populations in the upper Green River Basin of western Wyoming. The populations and habitats within this area are currently considered internationally significant strongholds for the species (Connelly et al. 2004). Natural gas development throughout the Intermountain West is occurring primarily within the sagebrush-dominated landscapes important for sage-grouse survival (Knick et al. 2003). Our objectives were to investigate several increasingly specific questions: Are breeding greater sage-grouse populations impacted by natural gas development? What aspects of developing fields are influencing breeding populations? Are individuals dispersing from natural gas development or are population sizes declining? Additionally, land management agencies stipulate restrictions on some types of development during breeding and nesting seasons to protect sage-grouse; so I addressed the adequacy of these stipulations. I investigated population and individual bird response to natural gas drilling rigs, producing wells, and main haul roads (i.e., roads accessing at least 5 producing natural gas wells).

I assessed temporal changes in the number of displaying males with respect to distance and direction from leks to drilling rigs, producing wells, and main haul roads, producing well and main haul road densities, and traffic activity levels and timing. I also investigated male survival probabilities, lek tenacity, and habitat selection during the breeding season relative to cumulative levels of gas field development surrounding leks. My investigation of female habitat selection response to energy development concentrated on 2 demographic stages, nesting and early brood-rearing (hatch through 2 weeks post-hatch). I examined distances moved between nests in consecutive years, used versus available nesting and early brood-rearing habitats, and successful (i.e., hatched or survived) versus unsuccessful nests and broods with respect to differing levels of gas field development. Finally, I used matrix population modeling and life-table-response procedures (Caswell 1989, 1996) to investigate the effects of natural gas development on female greater sage-grouse population growth. I compared populations potentially impacted by natural gas infrastructure during the breeding or nesting season to non-impacted populations.

**Results**

Investigating changes in the number of male greater sage-grouse occupying a lek relative to cumulative gas field development levels using principal components analysis suggested that as the distance from leks to drilling rigs, producing wells, and main haul roads decreased, and as main haul

road densities within 3 km and the number of directions to producing wells within 5 km (i.e., the lek became more centrally located within the developing field) increased, lek attendance by males approached zero. The number of males occupying leks within 5 km of drilling rigs declined relative to non-impacted leks. There did not appear to be visual effects of drilling rigs on lek attendance by males, but the number of males declined on leks east of drilling rigs (i.e., generally downwind based on prevailing wind direction). The number of males occupying leks within 3 km of producing wells also declined. Male lek attendance declined if well densities within 3 km of the lek exceeded approximately 5 wells and if producing wells within 5 km occurred in over half of the directions from leks. Male lek occupancy also declined on leks within 3 km of main haul roads. Rates of decline increased as traffic volumes increased, and vehicle activity on roads during the daily strutting period (i.e., early morning) had a greater influence on attendance compared to roads with no vehicle activity during early morning.

Probabilities of adult male desertion (i.e., males captured from a particular lek and not documented on that lek following capture) were higher from leks impacted by at least 1 gas-field-related factor compared to non-impacted leks, and male breeding season survival probabilities were lower for lightly impacted (i.e., leks impacted by 1 or 2 factors) compared to heavily impacted leks (i.e., leks impacted by more than 2 factors). Additionally, impacted leks had fewer yearling males trapped and earlier peak attendance dates compared to non-impacted leks.

Greater sage-grouse nesting sites were close to wells in areas with low well densities compared to available sites. Temporally, nests were located farther from drilling rigs and gas wells in 2004 compared to available sites, whereas nests were closer to these structures in 2000-2003. Adult females nested within previously selected nesting areas regardless of changes in gas development levels within those areas, but nesting yearlings avoided road-related disturbances. Brooding females avoided producing wells during the early brood-rearing period. The effect of natural gas development on female population growth was generally negative. There were relatively consistent negative contributions to population growth from adult and yearling female annual survival, whereas productivity contributions were generally positive. This suggests that reduced population growth was attributable to decreased annual survival of both adult and yearling females.

**Discussion**

The evidence suggests that current natural gas development techniques lead to greater sage-grouse population declines. Male lek attendance declined as the distance from leks to drilling rigs, producing wells, and main haul roads decreased and as densities of these features increased. Lek attendance also declined as traffic volumes and potential for greater noise increased, and when well

densities exceeded 1 well per 283 ha within 3 km of leks. Developing natural gas fields simultaneously consists of all the disturbance factors considered plus others not investigated (i.e., well completion activity, compressor stations). Greater sage-grouse breeding populations were probably reacting to a combination of these factors' effects.

Adult male displacement and low juvenile male recruitment appear to contribute to declines in the number of breeding males on impacted leks. Additionally, avoidance of gas field development by predators could be responsible for decreased male survival probabilities on leks situated near the edges of developing fields (i.e., lightly impacted leks). Although site-tenacious adult females did not engage in breeding dispersal in response to increased levels of gas development, subsequent generations avoided gas fields, as suggested by the temporal shift in nesting habitat selection and differences in habitat selection by yearling and adult females. This suggests that the nesting population response is delayed avoidance of natural gas development. The results suggest that male and female greater sage-grouse displacement from developing natural gas fields contributes to breeding population declines.

Population growth differences between impacted and non-impacted populations suggest that natural gas development negatively impacts population growth of females. Most of the variability in population growth was explained by lower annual survival buffered to some extent by higher productivity in impacted populations. Development effect was especially noticeable on annual survival of nesting adults. Seasonal survival differences suggested a lag period between when an individual was impacted by disturbance and when survival probabilities were influenced. Individuals were influenced by natural gas development primarily during the breeding and nesting periods, while differential survival occurred primarily during the early brooding and summer periods. Impacted and non-impacted populations summered in the same general areas, and predators were responsible for most summer mortalities. Increased predation probabilities during the summer suggest increased exposure, possibly through a change in foraging behavior (i.e., spending more time feeding), habitat selection (i.e., selecting areas with greater food resources and reduced cover), or self-preservation behavior (i.e., reduced alertness).

The evidence suggests that breeding population declines and eventual extirpation of leks near disturbances resulted from both displacement and decreased survival. Regional greater sage-grouse population levels as well as population distributions are likely to be influenced negatively by development of natural gas fields.

**Management Considerations**

To protect breeding greater sage-grouse, the Bureau of Land Management (2000) stipulates the following restrictions to development: (1) no surface disturbance with 0.4 km of a lek; (2) no activity within a 0.8-km radius of active leks between 0000 and 0900 hrs during the breeding season; (3) no construction or drilling activities during the breeding season within 1.6 km of active leks. To protect nesting and brooding females, the Bureau of Land Management (2000) stipulates that gas field related construction activities will be restricted during the breeding and nesting seasons in suitable nesting habitat within 3.2 km of active leks; a suitable habitat designation requires that an active nest be located during an on-site review of the proposed development area. This study suggests that current stipulations are inadequate to maintain greater sage-grouse breeding populations within natural gas fields. The effect-distance from disturbance sources to leks during the breeding season could be conservatively estimated at 3-5 km, especially if that source was located where sound propagation towards a lek was intensified by environmental factors (i.e., prevailing wind direction). Therefore, sound muffling devices installed on noisy gas field structures could reduce the negative consequences on breeding grouse. Declines in lek attendance were positively correlated with traffic levels and vehicular activity during the daily strutting period. Reducing overall traffic volumes (i.e., offsite condensate collection facilities, car-pooling) and isolating the timing and location of traffic disturbance (i.e., restricting travel to and from the gas field to 1 major artery, enforcing daily travel timing restrictions) within gas fields could reduce road effects.

Barring direct disturbance resulting in nest abandonment, the stipulation (Bureau of Land Management 2000) aimed at protecting nesting females protects only philopatric individuals. Basing designations on habitat conditions rather than habitat occupancy could assist in maintaining nesting areas. Although adequate buffer distances are unknown, our findings suggest that areas designated as suitable breeding habitats (Connelly et al. 2000) within 5 km of known leks (Holloran and Anderson 2005) need to be protected and buffered from gas field development. Additionally, nesting females avoided areas with high well densities. Although actual densities resulting in avoidance are unknown, this result suggests that 16 ha well-spacing excludes nesting females. Because a developing natural gas field consists of multiple disturbance sources, all of which potentially influence greater sage-grouse leks and nests, managers need to ensure that all potential factors are addressed concomitantly.

Our results suggest that protection and enhancement of greater sage-grouse populations inhabiting areas adjacent to natural gas fields could be required to maintain regional population levels. Off-site mitigation measures aimed at minimizing the negative consequences of natural gas development on regional populations imply the need for a refugia approach to species conservation. By

protecting and enhancing reservoir populations surrounding developing gas fields, greater sage-grouse could be present to re-colonize the field following reclamation. However, managers need to ensure that these reservoir populations are protected through the life-expectancy of the developing field (minimum life-expectancy of the Pinedale Anticline natural gas field has been estimated at 59 years; Bureau of Land Management 2000). We suggest delaying development of natural gas fields surrounding the original field until populations within the original field following reclamation are substantial enough to re-colonize subsequently developed fields. The staggered development of gas fields across a landscape could not only ensure refugia for wildlife, but could ensure long-term financial stability for states dependent on fossil fuels generated revenue (at least until alternatives to fossil fuels are developed).

**Research Needs**

Results from this study identified several questions for future research. Of utmost importance is determining natural gas development options that reduce detrimental consequences to greater sage-grouse populations. An investigation of greater sage-grouse population and individual response to differing development strategies in an experimental context is required for accurate conclusions. The study design would need to ensure both adequate pre-treatment data for development threshold identification and spatial independence to guard against potential dispersal consequences. Investigating potential development options in this manner will require substantial cooperation between researchers, land managers, and operators.

Research investigating yearling responses to a developing gas field would improve our understanding of regional consequences. For example: what proportion of the yearling male population does not breed? What is the spatial extent of the area searched by disturbed yearling males prior to establishing a territory on a lek (spatial extent of gas field influence)? Is territorial establishment timing and survival of yearling males influenced by displacement? Future research should further address potential impacts to the yearling female cohort. In addition to the questions asked concerning yearling males, information relative to female seasonal habitat selection and productivity is needed. What is the proportion of the yearling female population displaced from their natal nesting or natal brooding areas? Are vital rates (i.e., survival, nesting initiation and success probabilities, and chick productivity rates) of the yearling females displaced from their natal lek, nesting, or brooding areas negatively influenced?

Research investigating the consequences of dispersal is also needed. If the majority of displaced adult and recruited yearling males are establishing on non-impacted leks surrounding the developing gas field, and the eventual nesting population response is avoidance of natural gas development,

populations surrounding the gas field may be artificially high. Are density-dependant processes occurring that affect greater sage-grouse survival, breeding potential, and productivity in sagebrush habitats with potentially artificially high populations adjacent to natural gas fields (LaMontagne et al. 2002)? And do these processes influence the ability to conduct off-site mitigation for natural gas development?

Finally, investigating long-term impacts of natural gas development is warranted. Do breeding populations reoccupy abandoned leks after development stages are completed and the field enters primarily production phases (i.e., determination of a gas field's temporal extent of influence)? Braun et al. (2002) reported that 2 leks in Canada remained inactive for ≥10 years after gas or oil well site reclamation; however, Remington and Braun (1991) suggested that 2 leks where coal mining activity potentially caused substantial male lek attendance declines in the early 1980s recovered to some extent over a 5-year period following the reduction in mining activity in 1985. Research investigating potential cumulative effects (i.e., influence of gas development on predator core-area use patterns, produced water and West Nile Virus prevalence [Naugle et al. 2004]) of natural gas field development is additionally needed. These studies are required to accurately evaluate mitigation options.

**Literature Cited**

Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. PhD Dissertation, University of Alberta, Edmonton, Alberta, Canada.

Aldridge, C. L., and R. M. Brigham. 2003. Distribution, abundance, and status of the greater sage-grouse, *Centrocercus urophasianus*, in Canada. Canadian Field-Naturalist 117:25-34.

Braun, C. E., O. O. Oedekoven, and C. L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage grouse. Transactions North American Wildlife and Natural Resources Conference 67:337-349.

Bureau of Land Management. 2000. Record of decision, environmental impact statement for the Pinedale anticline oil and gas exploration and development project Sublette County, Wyoming. United States Bureau of Land Management, Pinedale, WY, USA.

Caswell, H. 1989. Analysis of life table response experiments I. decomposition of effects on population growth rate. Ecological Modelling 46:221-237.

Caswell, H. 1996. Analysis of life table response experiments II. alternative parameterizations fro size- and stage-structured models. Ecological Modelling 88:73-82.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of Greater Sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, WY, USA.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Hagen, C. A. 2003. A demographic analysis of Lesser Prairie-Chicken populations in southwestern Kansas: survival, population viability, and habitat use. PhD Dissertation, Kansas State University, Manhattan, KS, USA.

Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742-752.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634.

LaMontagne, J. M., R. L. Irvine, and E. E. Crone. 2002. Spatial patterns of population regulation in sage grouse (*Centrocercus* spp.) population viability analysis. Journal Animal Ecology 71:672-682.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486-491.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Dato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: pending crisis for greater sage-grouse. Ecology Letters 7:704-713.

Oyler-McCance, S. J. 1999. Genetic and habitat factors underlying conservation strategies for Gunnison sage-grouse. PhD Dissertation, Colorado State University, Fort Collins, CO, USA.

Remington, T. E. and C. E. Braun. 1991. How surface coal mining affects sage grouse, North Park, Colorado. Proceedings, Issues and Technology in the Management of Impacted Western Wildlife. Thorne Ecological Institute 5:128-132.

APPENDIX A

*Abridged Title.* Greater Sage-Grouse Nest Distribution

# SPATIAL DISTRIBUTION OF GREATER SAGE-GROUSE NESTS IN RELATIVELY CONTIGUOUS SAGEBRUSH HABITATS

MATTHEW J. HOLLORAN, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Department 3166, Laramie, WY 82071. 307 766 2091 (voice); 307 766 5400 (fax); holloran@uwyo.edu (e-mail).

STANLEY H. ANDERSON, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Department 3166, Laramie, WY 82071.

*Abstract.* Degradation of nesting habitat has been proposed as a factor contributing to Greater Sage-Grouse (*Centrocercus urophasianus*) population declines throughout North America. Delineating suitable nesting habitat across landscapes with relatively contiguous sagebrush cover is difficult but important to identify areas for protection. We used radio-telemetry to locate Greater Sage-Grouse nests in relatively contiguous sagebrush habitats in Wyoming to investigate the spatial arrangement of nests relative to lek and other nest locations. Nest distributions were spatially related to lek location within 3 and 5 km of a lek, and a 5-km buffer included 64% of the nests. There was no relationship between lek size and lek-to-nest distance, suggesting that accurate population trend evaluation might require lek surveys in addition to lek counts. Closest known lek-to-nest distance was greater for successfully hatched compared to destroyed nests, and closely spaced nests tended to experience lower success and have higher probabilities of both nests experiencing the same fate compared to isolated nests, suggesting that a mechanism of enhanced prey detection occurred at higher nest densities. A low probability that a given individual's consecutive-year nest spacing occurred randomly suggested nesting site-area fidelity. Although a grouped pattern of nests occurred within 5 km of a lek, the proportion of nesting females located farther than 5 km could be important for population viability. Managers should limit strategies that negatively influence nesting habitat regardless of lek locations, and preserve adequate amounts of unaltered nesting habitat within treatment boundaries to maintain nest dispersion and provide sites for philopatric individuals.

*Key words:* Centrocercus urophasianus, *fidelity*, *lek-to-nest distance*, *nest distribution*, *nest spacing*, *Greater Sage-Grouse*, *Wyoming*.

## INTRODUCTION

Shrubland and grassland bird species are declining faster than any other group of species in North America, primarily due to human caused destruction and degradation of their habitats (i.e., livestock grazing, land conversion, natural resource development, habitat treatment; Knick et al. 2003). However, because of the perceived uniformity of relatively contiguous sagebrush dominated and grassland ecosystems, accurate delineation of areas supporting habitat conditions seasonally required by obligate bird species across landscapes is difficult. Greater Sage-Grouse (*Centrocercus urophasianus*) currently occupy 56% of their pre-European settlement distribution (Schroeder et al. 2004), and breeding populations throughout North America are two to three times lower than those during the late 1960s (Connelly et al. 2004); the loss of suitable nesting habitat may be contributing to these declines (Crawford et al. 2004). Because recognizing suitable nesting areas based on habitat structural cues throughout the core of the species' range is often difficult, managers have long used leks to identify nesting habitats. The 1977 Sage-Grouse habitat management guidelines (Braun et al. 1977) recommend protecting all areas within 3 km of a lek as potential nesting habitat. The current management guidelines (Connelly et al. 2000) suggest using leks as focal points for nesting habitat management efforts, and recommend protecting the sagebrush (*Artemisia* spp.) overstory and herbaceous understory within 3.2 km of occupied leks in areas with uniformly distributed habitats. In non-uniformly distributed habitats, the current guidelines (Connelly et al. 2000) recommend protecting the area within 5 km of a lek.

The spatial dependence between an organism and a suspected influential component of its environment is a fundamental question in ecology (Rossi et al. 1992). The development of theories on spatial organization revolves around the discovery of patterns (Levin 1992), and because patterns change as a function of spatial resolution, the scale of observation can alter the description of species distributions (Trani 2002). Although Wakkinen et al. (1992a) concluded that the distribution of Greater Sage-Grouse nests was random with respect to lek location because of no statistical differences between closest known lek-to-nest and lek-to-random point distances in Idaho, the spatial scale of interest was restricted to the study area. If the area of interest was expanded, at some spatial scale a non-random distribution of nests relative to lek location should have become discernable. The spatial scale at which a discernable pattern exists (where the distribution of nests become non-random with respect to lek location) could be used to quantify the area surrounding an occupied lek where female Greater Sage-

Grouse are likely to select a nesting site; this could be used by land managers as a preliminary designation of potential nesting habitat in areas where differentiating habitats is difficult.

Several theories exist concerning the relationship between the probability of hatching success and nest placement relative to the location of the lek, another individual's nest, and an individual's previous nesting location. Bergerud (1988) suggested that, to lower nest depredation probabilities, nesting females should avoid leks to minimize disturbance by males and evade increased predator activity associated with leks. Mean lek-to-nest distance was greater for successful compared to unsuccessful Greater Sage-Grouse nests in California (Popham and Gutierrez 2003). In vulnerable species, the optimal dispersion pattern for avoiding detection in continuous habitats should be towards well-spaced, solitary individuals (Taylor 1976, Andersson and Wiklund 1978, Bergerud and Gratson 1988). Niemuth and Boyce (1995) suggested that nest detection by predators was greater at high-density compared to low-density artificial Greater Sage-Grouse nest situations in Wyoming. Fidelity to nesting areas could have potential advantages, including increased familiarity with a site and its predators and competitors and reduced dispersal costs (Bergerud and Gratson 1988). Fischer et al. (1993), in Idaho, reported that distances between Greater Sage-Grouse nests in consecutive years represented 3.5% of median annual movements, suggesting fidelity for specific nesting areas.

Because of Greater Sage-Grouse population declines (Connelly et al. 2004, Schroeder et al. 2004) and the numerous potential deleterious impacts occurring to nesting habitats (Braun 1998), identifying potential nesting areas and characteristics favorable for increased productivity could be important for population sustainability. We used Greater Sage-Grouse nest sites located in relatively contiguous sagebrush habitats in central and western Wyoming to investigate the spatial arrangement of nests relative to lek and other nest locations. Our primary objective was to determine the spatial scale at which nests become non-randomly distributed around leks. As predicted by the optimal nest dispersion pattern theory (Taylor 1976, Andersson and Wiklund 1978, Bergerud and Gratson 1988), we hypothesized that lek-to-nest distances, and thus the distance from a lek where a non-random nest distribution pattern was detected, would be positively correlated with lek size. We further hypothesized that hatching success probabilities would be positively correlated with lek-to-nest distances, that isolated nests would experience higher rates of success than closely-spaced nests, and that females would exhibit fidelity to specific nesting-areas.

## METHODS

### STUDY AREA

We studied Greater Sage-Grouse at seven sites located in central and southwestern Wyoming in 1994-2003 (detailed description in Holloran et al. *in press*). Although habitat manipulations (i.e., fire, herbicide application) and livestock grazing occurred in the areas (Holloran 1999, Lyon 2000, Slater 2003, Kuipers 2004), large scale habitat conversions (i.e., cropland, human dwellings) were not present, and the areas were dominated by uniformly distributed sagebrush habitats. Areas fragmented by natural gas development were removed from consideration. Vegetation was dominated by Wyoming big sagebrush (*A. tridentata wyomingensis*). Black sagebrush (*A. nova*) and low sagebrush (*A. arbuscula*) were located on relatively flat terrain in shallow soils, basin big sagebrush (*A. t. tridentata*) and silver sagebrush (*A. cana*) were located in deeper soils, and mountain big sagebrush (*A. t. vaseyana*) was found in mixed stands with Wyoming big sagebrush at higher elevations. Rabbitbrush (*Chrysothamnus* spp.), black greasewood (*Sarcobatus vermiculatus*), antelope bitterbrush (*Purshia tridentata*), snowberry (*Symphoricarpos* spp.), and serviceberry (*Amelanchier alnifolia*) were interspersed throughout study areas. Dominant grasses included bluebunch wheatgrass (*Pseudoroegneria spicata*), western wheatgrass (*Agropyron smithii*), junegrass (*Koeleria pyramidata*), needlegrasses (*Stipa* spp.), bluegrasses (*Poa* spp.), Indian ricegrass (*Oryzopsis hymenoides*), Idaho fescue (*Festuca idahoensis*), and cheatgrass (*Bromus tectorum*). Common understory forbs included lupine (*Lupinus* spp.), phlox (*Phlox* spp.), buckwheat (*Eriogonum* spp.), common dandelion (*Taraxacum officinale*), milkvetch (*Astragalus bisulcatus*), sandwort (*Arenaria capillaris*), and several species of Asteraceae.

### FIELD TECHNIQUES

Female Greater Sage-Grouse were captured on and near leks each year from mid-March through April by spot-lighting and hoop-netting (Giesen et al. 1982, Wakkinen et al. 1992b). Each captured female was classified as a juvenile (first breeding season) or adult (≥ second breeding season) based on the shape of the outermost wing primaries (Eng 1955). Radio transmitters were secured to females with a PVC-covered wire necklace (Advanced Telemetry Systems Inc. [ATS], Isanti, MN). Transmitters used between 1994 and 1997 weighed 12 g and had a battery life expectancy of 305 days. In 1998, transmitters weighing 25 g with a battery life expectancy of 610 days were developed by ATS and used between 1998 and 2003.

Hand-held receivers and Yagi antennas were used to monitor radio-marked females at least twice weekly through pre-laying (April) and nesting (May-June). Nests of radio-marked birds were located by circling the signal source until females could be directly observed. Nest locations were

recorded in Universal Transverse Mercator (UTM) coordinates using a hand-held 12 channel Global Positioning System (GPS; Garmin 12; Garmin International, Olathe, KS) or 7.5 minute topographic maps (US Geological Survey, Denver, CO). We wore rubber boots while confirming nest locations to reduce human scent, and monitored incubating females after nest identification from a distance of >60 m to minimize the chance of human-induced nest predation or nest abandonment. Nest fate (successful or unsuccessful) was recorded when radio monitoring indicated the female had left the area. Nests were considered successful if at least one egg hatched, indicated by presence of detached eggshell membranes (Wallestad and Pyrah 1974). Unsuccessful hens were monitored twice-weekly to detect renesting attempts.

## STATISTICAL ANALYSES

The spatial scale at which nests became associated with lek location was assessed using Chi-square tests with continuity corrections (due to sample sizes <25 in certain instances; Dowdy and Wearden 1991). We compared the number of nests (observed locations) to the number of expected points (assuming a uniform distribution) occurring within 0.5-km bands radiating from the lek. Lek-to-nest distance was estimated from the lek-of-capture. Because repeated anthropogenic disturbance near a lek during the breeding season may influence how far a female moves from the lek to nest (Lyon and Anderson 2003), we excluded any female captured on a lek ≤500 m from a maintained road or other anthropogenic disturbance source (e.g., natural gas wells; $n$ = 9 leks). Due to a potential lack of independence, all re-nests ($n$ = 19) and nests from the same individual in years following her first identified nest ($n$ = 78) were omitted from the lek association analysis. Because each successive 0.5-km band radiating from the lek encompasses more total area (e.g., 0 to 0.5 km band = 79 ha, 0.5 to 1 km band = 236 ha, 1 to 1.5 km band = 393 ha), the number of expected nests per 0.5-km band will increase proportionally to the amount of area included in each band. Therefore, using the spatial scale required to encompass all nests could result in an expected distribution biased away from the lek. We calculated the total spatial area to consider for the analysis using the upper limit of the 90% confidence interval around the mean number of nests within each 0.5-km band. We truncated the spatial area of interest at the point where all successive bands contained fewer nests than designated by this upper limit (hereafter referred to as the truncated area). Nests situated outside the truncated area ($n$ = 59) were removed from the analysis. Expected numbers of nests within 0.5-km bands were estimated assuming a uniform distribution within the truncated area. Given our trapping protocol, nesting (versus breeding) females could have been radio-tagged (especially those individuals captured later in the breeding season) which could result in nest distributional estimations biased towards the lek. To test

for this possibility, we removed all individuals radio-tagged later than the median annual date-of-capture and compared proportional nest numbers per 0.5-km band between this reduced and the full data sets.

Linear regression was used to evaluate the relationship between lek-to-nest distances and lek size. Annual median and mean lek-to-nest distance by lek (independent variable) were calculated using all nests of females captured from a given lek during a given year. To ensure a relatively accurate mean lek-to-nest distance estimate, only lek years with ≥5 identified nests were used ($n$ = 26). Lek size (dependent variable) was estimated as the maximum number of males counted during the breeding period and lek-to-nest distance was estimated from the lek-of-capture. Lek counts were conducted by researchers according to standardized methods outlined by the Wyoming Game and Fish Department's (WGFD) Sage-Grouse technical committee (WGFD, Cheyenne, WY; Connelly et al. 2003).

Separate-variance, two-sample $t$-tests (Dowdy and Wearden 1991) were used to compare mean lek-to-nest distance differences between successful and unsuccessful nests. In contiguous habitats, females may nest closer to a lek other than where bred (i.e., lek-of-captured; Wakkinen et al. 1992a) and success probabilities may be influenced by the proximate lek; therefore, lek-to-nest distance was estimated from the closest known lek (versus the lek-of-capture) for this analysis. Radio-marked individual females dispersing long distances from the lek-of-capture could be difficult to locate, and thus located late during incubation stages. Because nests located later in the nesting cycle have fewer days at risk of nest failure (Nur et al. 2004), apparent nest success probabilities could be biased by distance. To investigate the possibility of distance-biased apparent success probabilities, we compared the total number of days successfully nesting females were documented incubating (i.e., number of days between nest identification and hatch) and closest known lek-to-nest distances using Pearson's correlation coefficients ($r$).

The influence of nest density on the probability of nest success was evaluated using nest spacing distances (i.e., known nest-to-nest distances). To ensure relatively representative nest-to-nest distance estimations, we included only those nests located within the truncated area, and used lek years with ≥10 individual identified nests ($n$ = 9 lek years; mean female sample by lek = 13 [range 10 to 20 females]). Individual nests ($n$ = 114) and nest pairs ($n$ = 86) were classified into 0.5-km categories based on distance to closest known nest and distance between nest pair, respectively (i.e., nest-to-nest distance 0 to 500 m, 501 to 1000 m). Expected probabilities of nest success were estimated using overall nest success probabilities (all nests) and expected probabilities of nest pairs experiencing the same fate were estimated as chance (50%); apparent nest success probabilities (observed probabilities) were compared to expected probabilities by category and inclusively using Chi-square tests with continuity corrections

(Dowdy and Weardon 1991). Because our nest density estimates could have been influenced by lek size or trapping effort, we investigated relationships between mean nest-to-nest distances and maximum number of males and total number of identified nests by lek year using Pearson's correlation coefficients.

To examine female fidelity to specific nesting areas, we compared distances between consecutive-years' nests to distances expected given random between-year nest placements within the truncated area. We generated a uniform distribution of random points (numerically equal to the number of nests; $n = 78$) within the truncated area using Animal Movement (Hooge and Eichenlaub 1997) in ArcGIS 9 (Environmental Systems Research Institute, Redlands, CA) and calculated the distance between each point and a randomly chosen additional point. The point-to-point distances were binned into 0.5-km categories and a probability distribution was produced based on the cumulative number of point-to-point distances occurring within each 0.5-km band radiating to the maximum possible distance between two points (i.e., diameter of the truncated area). We used this random point spacing probability distribution to assess the probability that mean and median consecutive-year nest-to-nest distances were random. Additionally, Mann-Whitney *U*-tests (Sokal and Rohlf 1995) were used to investigate median consecutive-year movement differences between adult and yearling, and both 1st and 2nd year successful and unsuccessful females. Values reported in the results section are medians and means (± standard error). All statistical procedures were performed with MINITAB 13.1 (Minitab Inc., State College, PA). Statistical significance was assumed at $\alpha \leq 0.05$, and tendencies were assumed at $\alpha \leq 0.10$.

## RESULTS

Between 1994 and 2003, we located 437 Greater Sage-Grouse nests of females captured from 30 relatively undisturbed leks throughout central and western Wyoming. Median and mean lek-of-capture to nest distance for all nests was 3506 and 4700 m (± 204 m), respectively (range 282 m to 27.4 km). Mean number of nests per 0.5-km band was 6.2 (± 1.2), and suggested that the area of interest should be truncated at 8.5 km (Fig. 1). Twenty-six leks ranging in size from 9 to 102 males were used for the spatial distribution relative to lek size analysis. After removing all nests of unknown fate and abandoned nests, 415 total nests (187 successful; 228 unsuccessful) and 384 nests within 8.5 km of the closest known lek (168 successful; 216 unsuccessful) were used for the nest fate analysis. We used 78 consecutive-year pairs of nests for the nesting-area fidelity analysis.

Significantly greater numbers of nests than expected occurred in all 0.5-km bands ≤3 km of the lek ($\chi^2_1 \geq 7.6$; $P < 0.01$); in all bands between 3 and 5 km of the lek, the number of nests did not differ

from expected ($\chi^2_1 \leq 1.8$; $P > 0.17$); and there were significantly fewer nests than expected ($\chi^2_1 \geq 4.0$; $P < 0.05$) within all bands between 5 and 8.5 km of the lek (Fig. 1). Forty-five and 64% of all nests ($n$ = 437) were within 3 and 5 km of the lek, respectively. After removing all nests of individuals radio-tagged later than the median annual date-of-capture, we found that proportional differences were ≤2% except the 1 to 1.5-km band, where proportional nest numbers were 5% lower for the reduced compared to full data set. However, the reduced number of nests within the 1 to 1.5-km band was still greater than expected given a uniform distribution ($\chi^2_1 = 12.3$; $P < 0.01$). There was no relationship between lek size and median ($R^2 = 1.0\%$) or mean ($R^2 = 0.2\%$) lek-to-nest distance.

Closest known lek-to-nest distance was not highly correlated with the number of days females were documented incubating ($r = 0.22$), suggesting no distance-bias associated with apparent success probability estimates; therefore, apparent nest success probabilities were used for fate analyses. For all nests, mean closest known lek-to-nest distance was significantly greater for successful (3978 m) compared to unsuccessful (3338 m) nests ($t_{334} = 2.0$; $P = 0.04$). However, comparing successful and unsuccessful nests within 8.5 km of a lek indicated no differences in mean lek-to-nest distances (successful 3087 m; unsuccessful 2952 m; $t_{358} = 0.6$; $P = 0.53$). We additionally investigated hatching success probabilities for nests within 5 km of a lek post-hoc, and found no differences in mean lek-to-nest distances between successful (2183 m; $n$ = 133) and unsuccessful (2092 m; $n$ = 174) nests ($t_{284} = 0.6$; $P = 0.52$).

Inclusively, nest success probabilities for nests categorized by distance to another known nest did not differ from success probabilities expected by overall nest success rates (45%; $\chi^2_4 = 5.9$; $P = 0.21$). Additionally, inclusive probabilities of both nests experiencing the same fate did not differ from probabilities expected by chance (50%; $\chi^2_4 = 4.7$; $P = 0.32$). However, nests located ≤1 km from another known nest ($n$ = 58) tended to have lower than expected probability of success (cumulative 28%; $\chi^2_1 = 3.5$; $P = 0.06$), and the probability of both nests ($n$ = 38 pairs) experiencing the same fate (cumulative 71%) tended to be greater than expected by chance ($\chi^2_1 = 3.0$; $P = 0.08$). Nest success probabilities (cumulative 41%) for nests >1 km from another known nest ($n$ = 56) did not differ from overall nest success probabilities ($\chi^2_1 = 0.1$; $P = 0.73$), and paired fate for nests >1 km (cumulative 56%; $n$ = 48 pairs) did not differ from chance ($\chi^2_1 = 0.4$; $P = 0.61$). Mean nest-to-nest distances by lek year were not highly correlated with lek size ($r = 0.37$), but were highly correlated with female sample size ($r = 0.75$). The relationship between mean nest-to-nest distance and female sample size was positive (i.e., longer mean nest-to-nest distances for leks with larger sample sizes). There was low correlation between lek size and sample size ($r = 0.27$).

Median and mean distance between consecutive-year nests for all females was 415 and 740 m (± 97 m), respectively (range 40 to 4966 m). Based on the cumulative probability distribution assuming random annual nest placement within the truncated area, the probability that a female selected a nest site within 0.5 km from the previous year's nest was 1.2% (median distance probability); the probability that between year nest movements were ≤1 km was 2.6% (mean distance probability). Median distances moved between consecutive-year nests by adults (391 m; $n = 50$) and yearlings (540 m; $n = 28$) were similar ($U = 832$; $P = 0.17$). Females moved significantly farther ($U = 825$; $P < 0.01$) to subsequent-year nests following an unsuccessful nesting attempt (median = 512 m; $n = 40$) compared to movements following a successful nesting attempt (median = 283 m; $n = 28$). However, there was no relationship between distance moved and subsequent-year nest success for all nests ($2^{nd}$ year successful median = 382 m, $n = 27$; $2^{nd}$ year unsuccessful median = 415 m, $n = 41$; $U = 625$; $P = 0.37$) or for females whose first documented nest was unsuccessful ($2^{nd}$ year successful median = 497 m, $n = 15$; $2^{nd}$ year unsuccessful median = 532 m, $n = 25$; $U = 208$; $P = 0.58$).

## DISCUSSION

Protection of Greater Sage-Grouse nesting habitat within 3.2 km of occupied leks has been a standard management recommendation since the 1970s (Braun et al. 1977, Connelly et al. 2000). However, research in fragmented (Schroeder et al. 1999, Aldridge and Brigham 2001) and contiguous (Bradbury et al. 1989, Wakkinen et al. 1992a) habitats suggest these recommendations offer limited or unsubstantiated protection to nesting areas. Bradbury et al. (1989) and Wakkinen et al. (1992a) argue that females select nest sites independent of lek location. However, as the spatial resolution of interest expands from a lek, a point should be reached where a discernable pattern of nest placement relative to lek location becomes apparent.

Greater Sage-Grouse nest distributions were grouped relative to lek location at multiple spatial scales. The question thus becomes, which distance (3 or 5 km) represents the spatial scale that effectively delineates the amount of area surrounding a lek that encompasses the proportion of nesting individuals required for population viability? The proportion of nests located within 3 versus 5 km (45 vs. 64%, respectively) suggested that a 5-km buffer around a lek was required to encompass a relative majority of nests. Additionally, nests located within 1 km of another known nest tended to have lower success probabilities, suggesting that increased nest densities could negatively influence the probability of a successful hatch. Given the number of nests relative to the amount of area within 0 to 3 km (2827 ha) versus 3 to 5 km (5027 ha) from a lek (Fig. 1), nest densities decreased as lek-to-nest distance

increased. This further indicates that a 5-km buffer could be required, and suggests that the area between the 3 and 5-km buffers could be especially important.

Although the observed distribution of nests relative to a uniform distribution surrounding a lek indicated that a pattern of landscape scale spatial association of nests relative to lek location occurred at 5 km, only 64% of the nests were located within this buffer distance. Additionally, lek-to-nest distance and hatching success probabilities were not related for nests within 5 km, but were positively correlated for all nests, suggesting increased success probabilities for individuals nesting far from a known lek. Survival of nests located far from a lek may be influenced by factors other than lek proximity (Moynahan 2004). However, regardless of the mechanism responsible for increased success probabilities, the segment of the population nesting beyond the 5-km distance may be important for population sustainability. Our results suggested that 5-km buffers around leks located within relatively contiguous habitats could be used by land managers as a preliminary designation of potential nesting areas. Additionally, nesting habitats located beyond 5 km from a lek may be important for population viability, suggesting protection (Connelly et al. 2000) should also be afforded to these areas.

Our trapping protocol potentially resulted in the capture of nesting (versus breeding) females within approximately 1 to 2 km (typical area trapped) of the lek. Although statistical results were not influenced, this potential bias suggested nest numbers within 0 to 3 km were overestimated. The lack of a relationship between lek-to-nest distances and documented incubation duration suggested that there was no distance bias associated with our fate analyses. Mean nest-to-nest distance correlations by lek year suggested no nest density estimate bias associated with lek size, but a potential bias associated with female sample size. However, the relationship between nest spacing and sample size was positive, opposite of the relationship expected if trapping effort influenced nest density estimates.

The mutual avoidance hypothesis (Taylor 1976, Andersson and Wiklund 1978, Bergerud and Gratson 1988) predicts that females should disperse nests to decrease detection probabilities. Our results suggest that Greater Sage-Grouse nests located relatively near (within 1 km) another known nest tended to be less likely to successfully hatch, supporting this hypothesis. Additionally, lek-to-nest distances were not related to lek size, suggesting a negative correlation between nest spacing and the number of females breeding on a lek. Theoretically, nest densities would eventually reach a threshold, suggesting that the spatial association between nest and lek location could be a mechanism restraining maximum lek size and leading to range expansion during population increases. Research in Minnesota suggested that, during a population increase, nest-spacing tendencies of greater prairie chickens (*Tympanuchus cupido pinnatus*) resulted in formation of new leks rather than changes in mean number of males per lek (Bergerud and Gratson 1988). Given that maximum lek size could be constrained by

female nest spacing tendencies, the number of males using a lek may be influenced by parameters other than population size, and new or historical (unoccupied) leks could become active during population increases. The current Sage-Grouse management guidelines recommend using annual lek counts to assess numerical trends in breeding population levels (Connelly et al. 2000). Our results suggest that surveys for new leks and monitoring of historical (unoccupied) leks in addition to annual lek counts could be important for accurate population trend evaluation.

Bergerud (1988) hypothesized that leks act as predator attractants and nesting females should avoid leks to improve hatching probabilities, an idea supported by research in California (Popham and Gutierrez 2003). Although closest known lek-to-nest distances did not influence hatching success for Greater Sage-Grouse nests within 8.5 km, there was a positive correlation between distance and success probabilities for all nests, suggesting increased success rates for nests >8.5 km from a lek (61% success >8.5 km, 44% success ≤8.5 km). It is probably unreasonable to assume that leks acted as predator attractants out to 8.5 km, and that decreased nesting success probabilities were being caused by increased predator numbers within this area. However, the development of prey detection enhancing behaviors by those predatory individuals residing within the truncated region could be possible. Locally increased predation could be explained through the development of a search image (Pietrewicz and Kamil 1981, Allen 1989) or reduced search rate (i.e., predators enhance cryptic prey detection probabilities by spending more time searching a particular area; Guilford and Dawkins 1987). Pairs of nests spaced relatively closely within 8.5 km of a lek tended to experience the same fate more frequently than was expected by chance, suggesting area-concentrated search and enhanced prey detection (Niemuth and Boyce 1995) and supporting the idea of behavioral changes by predators. Our results suggest that a mechanism of enhanced prey detection occurs at higher nest concentrations, and that increased nest densities could result in increased nest depredation probabilities.

Quantifying fidelity to a specific nesting area is difficult (Greenwood and Harvey 1982), given that female Greater Sage-Grouse are probably not territorial (Schroeder et al. 1999) and do not select the same shrub for nesting in consecutive years (i.e., Fischer et al. 1993 and this study). Fischer et al. (1993) used a comparison between consecutive-year nest and annual straight-line movement distances to suggest that females in Idaho exhibited fidelity for specific nesting areas. However, seasonal movements are generally in response to changing habitat requirements (Patterson 1952), which in our study sites resulted in movements between distinct areas that provided resources. Thus, movements between seasonal ranges might not accurately reflect expected movements within a specific habitat type in Wyoming. We chose to investigate the question of nesting-area fidelity by creating a probability distribution with the assumption of random between year nest placement within 8.5 km of a lek. The

probability that observed consecutive-year nest spacing occurred randomly was between 1.2 and 2.6%, strongly suggesting nesting site-area fidelity. Reasons for site-attachment could include familiarity with food and cover (refuges from predators) resources, allowing individuals to exploit the area more efficiently (Greenwood and Harvey 1982).

Our data additionally support Bergerud and Gratson's (1988) hypothesis that females should shift nesting areas following an unsuccessful nesting attempt. Unsuccessful females moved farther between consecutive-year nests in Washington (Schroeder and Robb 2003). Additionally, females moved 85% farther in Idaho (Fischer et al. 1993) and 81% farther in Colorado (Hausleitner 2003) following an unsuccessful compared to a successful nesting attempt. However, the relatively long movements in Wyoming following an unsuccessful nesting attempt did not influence subsequent-year nesting success probabilities, results similar to those reported from Washington (Schroeder and Robb 2003). The lack of a positive response following a shift in nesting sites could be related to an individual's initial unfamiliarity with the new area and the inability to optimally exploit the area's resources. However, the consistency of the shifting behavior following an unsuccessful breeding attempt implies that such breeding dispersal may be advantageous in the long term (Greenwood and Harvey 1982).

Implicit in the recommendation to use leks as focal points for identifying potential Greater Sage-Grouse nesting habitat (Connelly et al. 2000) is that nest distributions are related to lek location, which at some spatial scale will be inherently true. Nest distributions exhibited a grouped pattern across relatively contiguous sagebrush landscapes within 5 km of a lek; however, the substantial number of females nesting farther than 5 km from a lek could be important for population viability. Nest distribution patterns may change as a result of habitat alteration and fragmentation (Schroeder and Robb 2003), thus a 5-km buffer should be considered relevant only within contiguous sagebrush habitats. To protect and maintain Greater Sage-Grouse populations residing in relatively contiguous habitats, our results imply that managers should initially minimize or halt actions that reduce suitability of nesting habitats within 5 km of a lek. Managers should additionally identify all potential nesting areas, regardless of proximity to a lek, and consider those for protection. Further, if sagebrush manipulating proactive treatments are prescribed within potential nesting habitats, treated blocks need to be relatively small (i.e., less than 54 to 172 ha based on consecutive-year nest movements) and widely dispersed to provide suitable sites for philopatric individuals and maintain nest spacing.

ACKNOWLEDGMENTS

The Bureau of Land Management, Wyoming Game and Fish Department, U.S. Department of Energy, Ultra Petroleum, Animal Damage Management Board, Yellowstone-to-Yukon Initiative, EnCana Oil & Gas Inc., and Cowboy 3-Shot Sage-Grouse Foundation provided financial support for this study. We thank the following landowners for access: Bates Creek Cattle Company; Bousman Ranch; Carney Ranch; Ferris Mountain Ranch; Garrott Ranch; Julian Sheep Company; Little Sandy Grazing Association; Luther Ranch; Miles Cattle Company; Miller Estate; Red Bluff Ranch; Ruby Ranch; Sealy/Sawyer Ranch; Sommers Ranch; Stone Ranch; and the Three-quarter Circle Ranch. Additional lek count and nest location data were supplied by B. J. Heath, J. L. Kuipers, A. G. Lyon, and S. J. Slater. Field assistance was provided by K. D. Downs, M. B. Hicks, R. A. Holloran, B. K. Holtby, M. A. Kaeminglk, Mr. and Mrs. T. W. Malmberg, T. E. McCollum, R. C. Powell, C. M. Sazama, M. S. Stotts, C. G. Taber, Mr. and Mrs. N. A. Tratnik, C. T. Weibel, G. L. Wilson, and J. A. Wyllie. Cheney Flying Service (Casper, WY), France Flying Service (Rawlins, WY), and Mountain Air Research (Driggs, ID) flew telemetry flights and lek surveys. P. T. McLean (University of Wyoming, Laramie, WY) provided the abstract translation. D. S. Dobkin, F. G. Lindzey, M. C. Quist, T. E. Rinkes, S. J. Slater, K. M. Thompson, and 2 anonymous reviewers improved the manuscript greatly.

LITERATURE CITED

Aldridge, C. L., and R. M. Brigham. 2001. Nesting and reproductive activities of Greater Sage-Grouse in a declining northern fringe population. Condor 103:537-543.

Allen, J. A. 1989. Searching for search image. Trends in Ecology and Evolution 4:361.

Andersson, M., and C. G. Wiklund. 1978. Clumping versus spacing out: experiments on nest predation in Fieldfares (*Turdus pilaris*). Animal Behaviour 26:1207-1212.

Bergerud, A. T. 1988. Increasing the numbers of grouse, p. 686-731. *In* A. T. Bergerud and M. W. Gratson [eds.], Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis, MN.

Bergerud, A. T., and M. W. Gratson. 1988. Survival and breeding strategies of grouse, p. 473-577. *In* A. T. Bergerud and M. W. Gratson [eds.], Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis, MN.

Bradbury, J. W., R. M. Gibson, C. E. McCarthy, and S. L. Vehrencamp. 1989. Dispersion of displaying male Sage Grouse II: the role of female dispersion. Behavioral Ecology and Sociobiology 24:15-24.

Braun, C. E. 1998. Sage Grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139-156.

Braun, C. E., T. Britt, and R. O. Wallestad. 1977. Guidelines for maintenance of Sage Grouse habitats. Wildlife Society Bulletin 5:99-106.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Unpublished Report, Cheyenne, WY.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of Greater Sage-Grouse habitats and populations. College of Natural Resources Experiment Station publication No. 979, University of Idaho, Moscow, ID.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage Sage Grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Witson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of Sage-Grouse and Sage-Grouse habitat. Journal of Range Management 57:2-19.

Dowdy, S. M., and S. Wearden. 1991. Statistics for research. Second edition. John Wiley & Sons, Inc., New York, NY.

Eng, R. L. 1955. A method for obtaining Sage Grouse age and sex ratios from wings. Journal of Wildlife Management 19:267-272.

Fischer, R. A., A. D. Apa, W. L. Wakkinen, and K. P. Reese. 1993. Nesting-area fidelity of Sage Grouse in southeastern Idaho. Condor 95:1038-1041.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping Sage Grouse in Colorado. Wildlife Society Bulletin 10:224-231.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13:1-21.

Guilford, T., and M. S. Dawkins. 1987. Search images not proven: a reappraisal of recent evidence. Animal Behaviour 35:1838-1845.

Hausleitner, D. 2003. Population dynamics, habitat use and movements of Greater Sage-Grouse in Moffat County, Colorado. M.S. thesis, University of Idaho, Moscow, ID.

Holloran, M. J. 1999. Sage Grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. M.S. thesis, University of Wyoming, Laramie, WY.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. *In press*. Greater Sage-Grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 00:000-000.

Hooge, P. N., and B. Eichenlaub. 1997. Animal movement extension to ArcView Version 1.1. Alaska Science Center, Biological Science Office, U.S. Geological Survey, Anchorage, AK.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634.

Kuipers, J. L. 2004. Grazing system and linear corridor influences on Greater Sage-Grouse (*Centrocercus urophasianus*) habitat selection and productivity. M.S. thesis, University of Wyoming, Laramie, WY.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

Lyon, A. G. 2000. The potential effects of natural gas development on Sage Grouse near Pinedale, Wyoming. M.S. thesis, University of Wyoming, Laramie, WY.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on Sage Grouse nest initiation and movement. Wildlife Society Bulletin 31:486-491.

Moynahan, B. J. 2004. Landscape-scale factors affecting population dynamics of Greater Sage-Grouse (*Centrocercus urophasianus*) in north-central Montana, 2001-2004. Ph.D. dissertation, University of Montana, Missoula, MT.

Niemuth, N. D., and M. S. Boyce. 1995. Spatial and temporal patterns of predation of simulated Sage Grouse nests at high and low nest densities: an experimental study. Canadian Journal of Zoology 73:819-825.

Nur, N., A. L. Holmes, and G. R. Geupel. 2004. Use of survival time analysis to analyze nesting success in birds: an example using Loggerhead Shrikes. Condor 106:457-471.

Patterson, R. L. 1952. The Sage Grouse in Wyoming. Sage Books, Inc., Denver, CO.

Pietrewicz, A. T., and A. C. Kamil. 1981. Search images and the detection of cryptic prey: an operant approach, p. 311-331. *In* A. C. Kamil and T. D. Sargent [eds.], Foraging behavior: ecological, ethological, and psychological approaches. Garland STPM Press, New York, NY.

Popham, G. P., and R. J. Gutierrez. 2003. Greater Sage-Grouse *Centrocercus urophasianus* nesting success and habitat use in northeastern California. Wildlife Biology 9:327-334.

Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs 62:277-314.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of Sage-Grouse in North America. Condor 106:363-376.

Schroeder, M. A., and L. A. Robb. 2003. Fidelity of Greater Sage-Grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildlife Biology 9:291-299.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage Grouse (*Centrocercus urophasianus*). *In* A. Poole and F. Gill [eds.], The Birds of North America, No. 425. The Birds of North America, Inc., Philadelphia, PA.

Slater, S. J. 2003. Sage-Grouse (*Centrocercus urophasianus*) use of different-aged burns and the effects of Coyote control in southwestern Wyoming. M.S. thesis, University of Wyoming, Laramie, WY.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practices of statistics in biological research. Third edition. W. H. Freeman and Company, New York, NY.

Taylor, J. 1976. The advantage of spacing-out. Journal of Theoretical Biology 59:485-490.

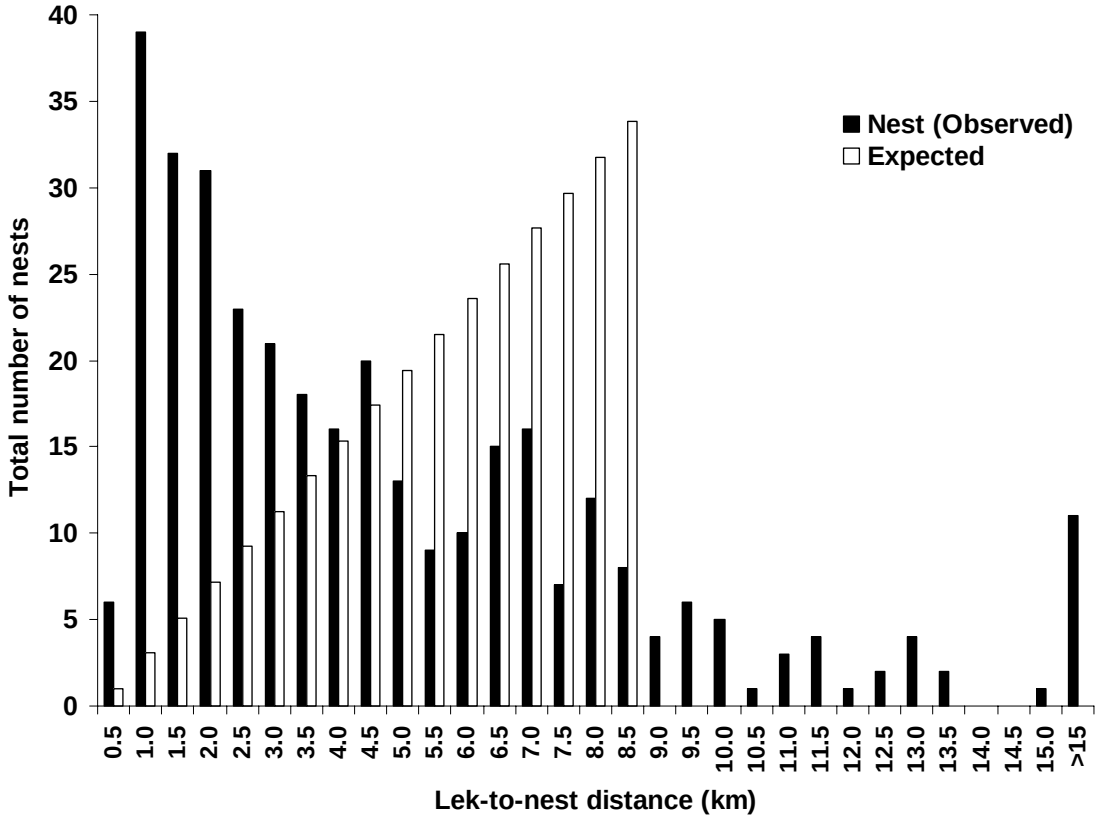
Trani, M. K. 2002. The influence of spatial scale on landscape pattern description and wildlife habitat assessment, p. 141-155. *In* J. M. Scott, P. J. Heglund, M. L. Morrison, et al., [eds.], Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, DC.

Wakkinen, W. L., K. P. Reese, and J. W. Connelly. 1992a. Sage Grouse nest locations in relation to leks. Journal of Wildlife Management 56:381-383.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992b. An improved spotlighting technique for capturing Sage Grouse. Wildlife Society Bulletin 20:425-426.

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of Sage Grouse hens in central Montana. Journal of Wildlife Management 38:630-633.

FIGURE 1. Distribution of Greater Sage-Grouse nests ($n$ = 340) based on lek-of-capture to nest distances in central and western Wyoming, 1994-2003 and expected numbers assuming uniformly distributed nests ($n$ = 296) within 8.5 km of a lek.


Nest (Observed)
Expected
Total number of nests
Lek-to-nest distance (km)
0
5
10
15
20
25
30
35
40
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
9.0
9.5
10.0
10.5
11.0
11.5
12.0
12.5
13.0
13.5
14.0
14.5
15.0
>15

APPENDIX B

Wyoming Cooperative Fish and Wildlife Research Unit
University of Wyoming, Department 3166
Laramie, WY 82071
Telephone: (307) 766-5415; FAX: (307) 766-5400
Email (corresponding author): kmthomps@uwyo.edu



# GREATER SAGE-GROUSE EARLY BROOD-REARING HABITAT USE AND PRODUCTIVITY IN WYOMING

Kristin M. Thompson, Corresponding Author, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071.

Matthew J. Holloran, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071.

Steven J. Slater, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071.

Jarren L. Kuipers, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071; Present address: Nebraska Game and Parks Commission, Beatrice, NE 68310.

Stanley H. Anderson, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071.

ABSTRACT.—Populations of greater sage-grouse (*Centrocercus urophasianus*) have been declining throughout their range since the 1960s. Productivity, which includes the production and survival of young, is often cited as a factor in these declines. Greater sage-grouse at three sites in western Wyoming were radio-equipped and monitored to assess early brood-rearing (i.e, through 14 days post-

hatch) habitat use and productivity. Logistic and linear regression with Akaike's Information Criterion were used to evaluate early brood-rearing habitat use and to examine relationships between productivity and vegetation, insect, and weather parameters. Females with broods were found in areas with greater sagebrush canopy and grass cover, but lower numbers of invertebrates compared to random areas. The number of juveniles per female (estimated from wing barrel collections during fall harvest) was positively associated with the abundance of medium-length Hymenoptera and grass cover, and the proportion of females with confirmed chicks 14 days post-hatch was positively related to the abundance of medium-length Coleoptera and total herbaceous cover. Although the specific parameters varied slightly, greater sage-grouse productivity in Wyoming appeared to be associated with a combination of insect and herbaceous cover elements. Managing for abundant and diverse insect communities within dense protective sagebrush stands should help ensure high quality early brood-rearing habitat and increased greater sage-grouse productivity.

*Key words: Greater sage-grouse, early brood-rearing,* Centrocercus urophasianus*, habitat, productivity, sagebrush, invertebrate, forb*

Over the past 50 years, populations of greater sage-grouse (*Centrocercus urophasianus*) have experienced widespread declines (Patterson 1952, Braun 1998, Connelly et al. 2004). Extirpated from three states and one Canadian province by 1998, the bird is now the focus of conservation and management concern in much of its remaining range (Connelly et al. 2004). Wyoming remains a stronghold for greater sage-grouse, where breeding bird numbers were estimated at >20,000 in 1998 (Braun 1998). However, populations throughout the state have also suffered declines; breeding male numbers decreased by an average of 5.2% annually between 1965 and 2003 (Connelly et al. 2004).

Population declines in tetraonids are often attributed to changes in productivity (Blank et al. 1967, Bergerud 1988). Productivity (i.e., the production and survival of young) may be affected by a variety of mainly extrinsic factors, including food availability and weather. Invertebrates are essential in the first several weeks post-hatch, when chicks require a high-protein diet (Johnson and Boyce 1990). Insects dominated the diet of one-week old greater sage-grouse chicks in Idaho (Klebenow and Gray 1968), Montana (Peterson 1970), and Colorado (Huwer 2004). Greater sage-grouse broods were documented using areas with high arthropod abundance in Idaho (Fischer et al. 1996). A study using captive greater sage-grouse chicks in Wyoming found that all chicks denied insects during the first 10 days post-hatch died, whereas all chicks given insects during this time survived (Johnson and Boyce 1990).

After the first 1 or 2 weeks, forbs begin to gain importance in the diet of chicks. Forbs comprised 75% of the diet of juvenile greater sage-grouse in Montana (Peterson 1970), and were found in 100% of the crops of two-week-old greater sage-grouse chicks sampled in Idaho (Klebenow and Gray 1968). Productivity of greater sage-grouse in Oregon was higher in areas where chicks consumed a greater proportion of forbs and insects (Drut et al. 1994*a*), and the mass gain of human-imprinted chicks in Colorado was positively correlated with forb abundance in the diet (Huwer 2004). Forbs may also provide a food source for chicks by attracting invertebrates (Blenden et al. 1986, Hull et al. 1996, Jamison et al. 2002). Forb cover, including food forb cover, was higher at sites used by greater sage-grouse broods compared to non-brood sites in Colorado (Schoenberg 1982), Idaho (Klebenow 1969), Oregon (Drut et al. 1994*b*), Washington (Sveum et al. 1998), and Wyoming (Holloran 1999).

Weather may additionally influence productivity during the nesting and brood-rearing periods (April through August). Cold temperatures may delay nest initiation (Neave and Wright 1969) or stress incubating females (Smyth and Boag 1984). Spruce grouse (*Dendragapus canadensis*) incubating in cold and wet environments produced fewer chicks per hen (Smyth and Boag 1984), whereas productivity of sharp-tailed grouse (*Tympanuchus phasianellus*) was positively correlated with May average temperature (Flanders-Wanner et al. 2004). Newly hatched chicks have poorly developed thermoregulatory systems (Myhre et al. 1975, Aulie 1976), so they are vulnerable to extreme weather conditions during the early post-hatch period. A combination of low temperatures, continuous winds, and precipitation negatively influenced greater sage-grouse brood size during the early hatching period in Idaho (Dalke et al. 1963). The number of juveniles per adult sharp-tailed grouse harvested was positively associated with June average temperatures, but negatively correlated with June precipitation (Flanders-Wanner et al. 2004), and fall harvest numbers of ruffed grouse (*Bonasa umbellus*) were positively linked to temperatures in June (Ritcey and Edwards 1963).

Several studies have shown a relationship between brood habitat use and the availability of invertebrates (Erikstad 1985, Storch 1994, Fischer et al. 1996, Haulton et al. 2003) and forbs (Klebenow 1969, Peterson 1970, Wallestad 1971, Drut et al. 1994*b*, Sveum et al. 1998, Holloran 1999). Other vegetation variables, including sagebrush or shrub canopy cover (Klebenow 1969, Wallestad 1971, Schoenberg 1982, Klott and Lindzey 1990, Holloran 1999), shrub height (Dunn and Braun 1986, Martin 1970, Sveum et al. 1998, Holloran 1999), and grass or residual grass cover (Sveum et al. 1998, Holloran 1999) may also act to influence brood habitat use. Literature exists on the importance of vegetation, invertebrates, and weather to various grouse species. However, research investigating the influence of these factors on greater sage-grouse early brood-rearing habitat use is lacking, and some of the factors potentially influencing productivity remain largely speculative. Additionally, most work has

focused on the independent importance of these variables; little has been done to examine their relative importance, or their interactions. Our objectives were to determine the specific habitat components associated with greater sage-grouse early brood habitat use and establish which factors were most strongly related to greater sage-grouse productivity.

## Study Area

The research was conducted at three sites in western Wyoming. The 30,400 ha Pinedale study area (42º45′N, 109º55′W) is located at elevations ranging between 2140 and 2300 m, has a mean temperature during the nesting/brood-rearing period (April-August) of 10.1º C, and April-August precipitation averages 14.7 cm. The 45,900 ha Lander site (42º33′N, 108º29′W) is located at elevations ranging between 1730 and 2470 m. Temperatures during the nesting and brood-rearing periods average 15.7º C, and mean precipitation between April and August is 17.8 cm. The 55,000 ha Kemmerer site (45º53′N, 110º54′W) is located at elevations ranging between 1900 and 2510 m. Mean temperature between April and August is 11.4º C, and the average precipitation during this same time is 14 cm (Western Regional Climate Center, Reno, NV). For detailed description of study areas see Lyon 2000, Slater 2003, and Kuipers 2004.

All three sites are dominated by sagebrush (*Artemisia* spp.), mainly Wyoming big sagebrush (*A. tridentata wyomingensis*). Other common shrub species include basin big sagebrush (*A. t. tridentata*), mountain big sagebrush (*A. t. vaseyana*), saltbrush (*Atriplex* spp.), rabbitbrush (*Chrysothamnus* spp.), and bitterbrush (*Purshia* spp.). Wheatgrass (*Elymus* and *Agropyron* spp.) and brome (*Bromus* spp.) dominate the grass family, while western yarrow (*Achillea millefolium*), dandelion (*Taraxacum officinale*), and lupine (*Lupinus* spp.) are among the most common forbs (taxonomy Stubbendieck et al. 2003).

## Methods

Data were collected at the Pinedale site between 1999 and 2003, at the Lander site between 2000 and 2003, and at the Kemmerer site between 2000 and 2002, for a total of 12 site-years (e.g., Pinedale 1999, Pinedale 2000, Pinedale 2001, etc.). Female greater sage-grouse were captured at leks in the early spring of each year using spotlighting and hoop-netting techniques (Giesen et al. 1982, Wakkinen et al. 1992). Females were fitted with 19.5 or 25.5-g wire-necklace radio-transmitters (Advanced Telemetry Systems, Inc., Isanti, MN) and tracked with hand-held radio-telemetry receivers and three-element Yagi antennas. Females were located within the first two weeks of incubation to determine nest locations, and nest fate (successful or unsuccessful) was determined when the female left the

nesting area. A nest was considered successful if ≥1 egg hatched, determined by presence of detached eggshell membranes (Girard 1939). Early brood use locations were obtained between 6 and 14 days post-hatch for females whose nests successfully hatched. For comparison with early brood locations (i.e., use habitat plots), random habitat locations were obtained by random generation of easting and northing locations within the study areas.

Vegetation and insect characteristics were measured at both use and random plots. Sagebrush canopy cover (%) was estimated at each plot using the line-intercept method (Canfield 1941), in which two perpendicular 30-m transects were centered on each plot. A 1 m-wide belt transect was created over the 30-m transects to estimate live sagebrush density as the number of plants per square meter (counted plants included all plants where ≥50% of the plant was within the belt transect). Live sagebrush height (cm) was estimated as the maximum height, excluding flowering stalks, of each sagebrush plant encountered during the line-intercept sampling. Ground cover (%) of herbaceous species (new [i.e., current year's growth] grasses, residual [i.e., standing dead] grasses, and forbs) was estimated using the Daubenmire (1959) method: a 20×50-cm open-ended frame was placed over sampling plots located at 0, 1, and 2.5 m from the center of each transect (12 total frames per plot). We converted categorical estimates of herbaceous cover to percentages (1 = 2.5%, 2 = 15%, 3 = 37.5%, 4 = 62.5%, 5 = 85%, 6 = 97.5%; Daubenmire 1959) for each of the 12 frames per plot; converted cover estimates from the 12 frames were averaged to derive a single estimate for each variable per plot. Herbaceous vegetation variables included total herbaceous cover (all new and residual grasses and forbs), forb cover (including winterfat [*Eurotia lanata*] and fringed sagewort [*A. frigida*]), new grass cover, and residual grass cover. Ground cover estimates were also calculated for litter and bare ground. The height of new and residual grasses (cm) was determined by measuring the tallest grasses that occurred relatively frequently within each Daubenmire frame (heights were meant to be representative of the herbaceous community; single very tall blades were not included). Height estimates from the 12 Daubenmire frames were averaged to derive single grass height estimates per plot.

Arthropods were sampled using pitfall traps (Greenslade 1964) established along the vegetation transects at distances of 0, 1, 2.5, 7, and 15 m from the center (17 total pitfall traps per plot). Traps remained open for 48 hours. Isopropanol was used to kill and preserve trapped insects. Trap contents were sorted to order, except for arachnids, which were sorted to class. Arthropods were further sorted into three length categories using guidelines developed from Patterson (1952) and Whitmore et al. (1986). Arthropods <3 cm were considered small, 3 to 11 cm were considered medium, and those >11 cm were classified as large. Soft-bodied larva, such as grubs and caterpillars, were an exception; the medium length category contained arthropods between 3 and 15 cm, and only those >15 cm were

considered large. The medium length class was considered the length class of invertebrate most likely to be selected for and eaten by foraging chicks. Per plot abundances were calculated for each order and length category of invertebrates.

## Statistical Analysis

All site-years with five or fewer use plots were removed because the small sample size did not allow for accurate representation of the site; this removal left 8 site-years for use in further analyses. The data for these remaining site-years were winsorized (i.e., outliers in an ordered array were replaced by their neighboring values; Sokal and Rohlf 1995). Data were winsorized because examination of the data revealed that single outlying data points (e.g., pitfall traps located on anthills) were unduly influencing site values in certain instances.

Habitat Use.—Data were standardized by site (by subtracting the mean and dividing by the standard deviation; Sokal and Rohlf 1995) to minimize any influence of site on the results. We used logistic regression to examine habitat use relationships (use vs. random; $n = 262$). From our original group of variables, we selected 11 variables to represent three vegetation and insect components. Variable selection was based on both correlation analyses and published literature (including Klebenow 1969, Dunn and Braun 1986, Klott and Lindzey 1990, Drut et al. 1994*b*, Fischer et al. 1996, Pyle and Crawford 1996, and Holloran 1999). Where correlation analyses revealed strong correlations between variables (e.g., between sagebrush canopy cover, total shrub canopy cover, and litter cover), one variable from the group was selected based on its importance in the literature. The abundances of several insect variables, including Orthoptera, were too small to be used in analyses. Sagebrush canopy cover, live sagebrush density, and sagebrush height represented the shrub component, total forb cover, total grass (new + residual grass) cover, mean grass (new + residual grass) height, and total herbaceous cover represented the herbaceous component, and total invertebrate abundance, total Hymenoptera abundance, medium-length Hymenoptera abundance, and medium-length Coleoptera abundance represented the insect component. Because this research was primarily exploratory in nature, all possible two and three variable combinations were used in logistic regression analyses. To reduce multicollinearity, we did not include variable combinations containing variables correlated by a Pearson's correlation coefficient ($r$) >0.70. Our suite of candidate models included 62 models. Models were ranked using a small-sample size bias adjusted Akaike's Information Criterion ($AIC_c$; Burnham and Anderson 2002). Akaike weights ($w_i$) were used to assess the relative importance of each vegetation and insect variable in distinguishing between use and random sites (Burnham and Anderson 2002). Cumulative Akaike weights were estimated from the entire set of models.

PRODUCTIVITY.—Productivity was measured by two variables: juveniles per female and the proportion of females with confirmed chicks 14 days post-hatch. Juveniles per female numbers were obtained from the Wyoming Game and Fish Department and were calculated using juvenile to adult ratios in wing barrel collections in the fall harvest (Autenrieth et al. 1982, Connelly et al. 2000; data from Wyoming Game and Fish Department harvest reports, Cheyenne, WY). To ensure that juveniles per female estimates were comparable to our habitat measurements, we only used harvest estimates from areas where radio-equipped females were located during the hunting season. The proportion of females with confirmed chicks was defined as the percentage of successfully nesting females with ≥1 chick alive 14 days post-hatch. The presence of chicks was based on visual confirmation and brooding females' reaction to researcher presence (Schroeder et al. 1999). We relocated successfully nesting females recorded as having no chicks alive 2 to 5 days following the initial location to confirm brood loss. Vegetation, insect, and weather variables were again selected based on correlation analyses and their importance in the literature (including Dalke et al. 1963, Klebenow and Gray 1968, Peterson 1970, and Drut et al. 1994*a*). Vegetation parameters included total forb cover, total grass cover, mean grass height, and total herbaceous cover; the insect component was comprised of total invertebrate abundance, total Hymenoptera abundance, medium-length Hymenoptera abundance, and medium-length Coleoptera abundance. We used one-way analysis of variance (ANOVA) to examine the effect of site and year on the variables; those variables that differed significantly by site or year ($P \leq 0.1$) were standardized by site (Sokal and Rohlf 1995).

Weather data were obtained from the Western Regional Climate Center (Western Regional Climate Center, Reno, NV). Where data were unavailable, we extrapolated (using kriging techniques in a GIS; Burrough and McDonnell 1998) using data from nearby weather stations. To minimize any effects of site, both temperature and precipitation variables were calculated as a percent of average (period of record 1948 – 2004). It seemed likely that the interaction of temperature and precipitation could have a greater effect on productivity than either variable alone, so we created a combination temperature/precipitation (TempPre) variable, calculated by dividing temperature by precipitation. Therefore, a hot and dry month would have a high TempPre value, whereas a wet and cold month would have a low TempPre value. The TempPre variable was developed for April – May (AprMay_TempPre), June (Jun_TempPre), and July – August (JulAug_TempPre). Because estimates of the proportion of females with confirmed chicks were generated by mid-June, JulAug_TempPre was included only in the juveniles per female analysis.

We generated a suite of models using our selected vegetation, insect, and weather variables. To avoid over-parameterizing the models (Hosmer and Lemeshow 1989), variable combinations were

limited to 2 variables. All possible 2-variable combinations (except those in which the variables were correlated to each other by $r > 0.70$) were included in the multiple regression analysis, with either juveniles per female or the proportion of females with confirmed chicks as the dependent variable. Our suite of candidate models included 39 models for use in the juveniles per female analysis and 32 models for the proportion of females with confirmed chicks analysis. Mean site-year data ($n$ = 8 site-years) were used for all productivity analyses. Akaike's Information Criterion with a small-sample bias adjustment ($AIC_c$) was used to select the most parsimonious model(s), and Akaike weights ($w_i$) were used to determine the relative importance of the habitat and insect components (Burnham and Anderson 2002). Cumulative variable weights were estimated from the entire set of models. Productivity analyses were conducted using mean site-year data obtained from random plots (vs. use plots). The weather variables and the juveniles per female numbers used in our analyses were site-level data, and we believed that data collected from random plots were more representative of annual site conditions.

All spatial analyses were conducted using ArcView GIS v3.2 (ESRI, Inc. 1998), and statistical analyses were conducted using Minitab Release 13 (Minitab, Inc. 1994) and SAS v8.2 (SAS Institute, Inc. 1990).

## RESULTS

Data used in habitat use analyses (i.e., site-years with more than 5 use plots) included Pinedale 1999 ($n$ = 9 use plots [i.e., locations for 9 different females with broods], 9 random plots), 2000 ($n$ = 8 use, 8 random), 2002 ($n$ = 16 use, 22 random), and 2003 ($n$ = 15 use, 24 random); Lander 2001 ($n$ = 7 use, 29 random), 2002 ($n$ = 9 use, 19 random), and 2003 ($n$ = 10 use, 39 random); and Kemmerer 2002 ($n$ = 8 use, 30 random). Productivity analyses were conducted using mean data from these years ($n$ = 8 site-years). Hymenoptera were the most common arthropods sampled, making up nearly 60% of the total arthropod abundance in both use and random habitats. Coleoptera were also fairly common, comprising just over 20% of the total arthropod abundance. Most Hymenoptera (73%) and Coleoptera (62%) collected were adults, and were within the medium-length category. The majority of the shrub cover was comprised of sagebrush; mean sagebrush canopy cover from use and random locations combined was 20.0% ($\pm s_{\bar{x}}$; ±0.7). Mean live sagebrush density was 1.7 (±0.1) plants/$m^2$; mean sagebrush height was 27.2 (±0.6) cm. Total herbaceous cover averaged 26.2% (±1.1); total forb cover and total grass cover averaged 4.9% (±0.4) and 9.0% (±0.3), respectively. Mean grass + residual grass height was 10.7 (±0.2) cm.

HABITAT USE.—Fourteen of our 62 models had $AIC_c$ values within 2 units of the minimum $AIC_c$ value (Table 1), suggesting substantial support (Burnham and Anderson 2002). Thirteen of the 14

models statistically fit the data (Hosmer-Lemeshow goodness-of-fit test statistics). In accordance with AIC principles (Burnham and Anderson 2002) all models were retained in the analysis (post hoc examination of the data after removing models that did not statistically fit the data [Hosmer and Lemeshow 1989] indicated that conclusions did not differ from the original analysis: cumulative Akaike weights indicating relative variable importance were virtually unaffected). Based on $AIC_c$ weights, the top model was only marginally better in predicting habitat use than were the other 13 candidate models (i.e., evidence ratios $\leq$2.7; Burnham and Anderson 2002). However, although none of the models was clearly the best, the cumulative Akaike weight was fairly substantial for the sagebrush cover variable (0.71), indicating that it may be a good predictor of habitat use. Examination of regression data directional trends suggested that broods were using areas with increased sagebrush canopy cover and density, total grass cover, and mean grass height, and decreased invertebrate abundance compared to random areas (Table 1). Forb abundance was slightly positive, but appeared in only one of the top 14 models.

PRODUCTIVITY.—Two models in the juveniles per female analysis fell within 2 units of the minimum $AIC_c$ value (Burnham and Anderson 2002). The top model contained the terms medium-length Hymenoptera abundance and total grass cover, and had an $AIC_c$ weight of 0.46. The second-ranked model included the variables medium-length Hymenoptera abundance and medium-length Coleoptera abundance ($AIC_c$ weight 0.17). The number of juveniles per female was positively associated with each of the independent variables in these top models. Based on cumulative $AIC_c$ weights, the most important parameters influencing juveniles per female appeared to be medium-length Hymenoptera abundance and total grass cover (Table 2).

The analysis of the proportion of females with confirmed chicks 14 days post-hatch yielded one highly plausible model, which contained the variables total herbaceous cover and medium-length Coleoptera abundance. The $AIC_c$ weight associated with this model was 0.98 and the evidence ratio was 57.3, suggesting that, given the data, this model was likely to be the best model (Burnham and Anderson 2002). The proportion of females with confirmed chicks was positively associated with both total herbaceous cover and medium-length Coleoptera abundance. Total herbaceous cover and medium-length Coleoptera abundance were also the most important individual parameters, based on cumulative $AIC_c$ weights (Table 2).

## DISCUSSION

Greater sage-grouse broods in Wyoming used habitats with greater sagebrush and grass cover, but fewer insects compared to random sites. The abundance of forbs did not appear to play a large role in

early brood habitat use. Though numerous researchers have examined habitat use by broods, results are somewhat inconsistent. Similar to the results of our study, greater sage-grouse in Colorado used areas with greater sagebrush canopy cover than random sites (Dunn and Braun 1986); however, that study included not only females with broods, but juveniles and unsuccessfully nesting females. Schoenberg (1982) found no significant difference in sagebrush cover between brood use sites and random sites, whereas Klebenow (1969), Klott and Lindzey (1990), and Holloran (1999) documented brood use of sites with lower sagebrush or shrub cover than random sites. Greater sage-grouse broods in Idaho used areas with greater abundance of Hymenoptera than non-brood locations (Fischer et al. 1996). Numerous studies of other galliform species have found similar results: capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), lesser prairie-chicken (*Tympanuchus pallidicinctus*), and ruffed grouse broods have been documented selecting areas with greater invertebrate abundances than available areas (Storch 1994, Baines et al. 1996, Jamison et al. 2002, Haulton et al. 2003). In contrast, our broods were found in areas with lower amounts invertebrates than were generally available.

One potential reason for discrepancies between our results and those from other studies is that investigator presence had an effect on habitat use. Although we made every attempt to avoid disturbance to birds while radio-tracking, it is possible that once broods heard or sighted investigators, the birds changed their focus from foraging to escape. This could have biased our results toward security cover (i.e., increased sagebrush cover) and away from foraging habitat (i.e., increased arthropods and forbs). Greater sage-grouse are often found near habitat edges (Dunn and Braun 1986), so even small-scale movements of 5 to 10 m may have been enough to shift birds between different habitat types. Although we do not believe that we influenced brood habitat use, if broods did move during the tracking process it would suggest that they were feeding in areas closely associated with suitable security cover.

We believe a more likely explanation is based on temporal differences between studies. Our study examined brood habitat use early in the brood-rearing period (before chicks were two weeks old). Holloran (1999) collected data on chicks between 2 and 4 weeks of age, Klebenow (1969) examined habitat use by broods up to 7 weeks of age, and Klott and Lindzey (1990) obtained brood locations throughout the summer. Grouse chicks experience heavy losses within the first few weeks of life. Survival of greater sage-grouse chicks to 21 days old in Idaho ranged from 21 to 50% (Burkepile et al. 2002), and between 14 and 33% of chicks survived to 50 days of age in Washington and Canada (Schroeder 1997, Aldridge and Brigham 2001). Crawford et al. (2004) averaged the results of 3 studies to come up with an estimated 10% survival rate from hatch to the first potential breeding season. These studies did not examine how much mortality occurred during the first 14 days; however, Holloran

(1999) documented the majority of chick loss during the first 2 to 3 weeks. Patterson (1952) suggested that although a myriad of factors may be involved, losses to predation potentially account for the greatest amount of juvenile mortality in greater sage-grouse. In addition, several authors suggest that predation may be one factor limiting annual tetraonid productivity (Batterson and Morse 1948, Marcström et al. 1988, Baines 1991).

Greater sage-grouse broods in Wyoming appeared to be selecting habitats with increased security cover during the first two weeks post-hatch. Chicks are generally not capable of flight before 10 days to two weeks of age (Girard 1937, Wallestad 1975), thus the presence of dense protective cover may be even more important for females with younger broods than for older broods that have alternate means of escape. The need for foraging areas in close proximity to protective cover has been well documented (Klebenow 1969, Wallestad 1971, Klott and Lindzey 1990, Sveum et al. 1998, Holloran 1999). Insect abundances were negatively correlated with sagebrush cover ($r$ = -0.15 total arthropods; -0.12 optimal-length Hymenoptera; -0.11 total Hymenoptera), thus lower levels of this component in brood use areas in Wyoming were likely an artifact of these correlations and not selection.

Forb cover did not appear to be a driving factor in early brood habitat use. Although many studies have documented brood use of sites with high forb abundance (Klebenow 1969, Klott and Lindzey 1990, Sveum et al. 1998, Holloran 1999), these studies examined habitat use later in the brood-rearing period. Because we estimated early brood habitat use to 14 days post-hatch, forbs may not yet have been the main component of the diet. Patterson (1952) suggests that vegetation begins to gain importance in chick diets after the first few weeks of life. Klebenow and Gray (1968), Peterson (1969) and Huwer (2004) found that invertebrates dominated the diet of greater sage-grouse chicks during the first week, before forbs began to gain importance as a food source.

The ratio of juveniles to adult females in the fall harvest appeared to be most strongly influenced by invertebrate abundance and grass cover. Our top two models both included medium-length Hymenoptera abundance. Hymenoptera, which in our study consisted mainly of ants (Formicidae), have been shown to be an important food item for young chicks; ants were found in 75% of the crops of birds 1 to 4 weeks old in Montana (Peterson 1970) and in up to 100% of the crops of juvenile greater sage-grouse collected in Idaho (Klebenow and Gray 1968). Johnson and Boyce (1990) found that insects were crucial for survival of young sage grouse chicks, and studies of several other galliform species have found that invertebrate abundance was positively associated with productivity (Green 1984, Hill 1985, Park et al. 2001). Total grass cover was the top vegetation variable; nearly 60% of the $AIC_c$ weight was attributed to models that included this variable. It likely served a protective function by screening foraging broods from potential predators.

The factors associated with the proportion of females with confirmed chicks appeared to be well defined. AIC analysis yielded only one highly plausible model containing the variables medium-length Coleoptera abundance and total herbaceous cover. Like Hymenoptera, Coleoptera are often a principal component in juvenile greater sage-grouse diets (Klebenow and Gray 1968, Peterson 1970). Total herbaceous cover was comprised of both grasses and forbs. Therefore, it may have served a dual function of providing both protection and food sources. Total forb cover was positively correlated with both medium-length Hymenoptera ($r = 0.68$) and medium-length Coleoptera ($r = 0.81$) abundances. Whereas forb cover did appear in a second-tier model (i.e., $\Delta AIC_c$ between 2 and 4) in the juveniles per female analysis, it was not strongly related to the proportion of females with confirmed chicks. Again, because we examined this measure of productivity by 14 days post-hatch, forbs may not yet have been the major component of the diet.

We found virtually no relationship between weather and productivity. It is possible that short-lived, extreme weather conditions (e.g., heavy rainfall, severe cold spell) influenced productivity, but these occurrences were not detectable using annual weather data. However, the trends we did see were consistent; all weather variables were positively associated with our two measures of productivity. Warm and dry conditions appeared to be more favorable for productivity than cold and wet conditions.

Our study suggests that abundant medium-length insects within heavy sagebrush cover will be most beneficial to juvenile greater sage-grouse. During the early brood-rearing period, broods used sites within or near dense (average 20% canopy cover) sagebrush cover, and increased productivity was positively associated with abundance of insects and herbaceous cover. Although managing directly for invertebrates is likely not feasible, it may be possible to indirectly manage for insect abundance through the manipulation of vegetation. Invertebrate biomass has been found to be positively correlated to forb abundance (Southwood and Cross 1969, Blenden et al. 1986, Hull et al. 1996, Jamison et al. 2002); thus, enhancement of the forb component could serve a dual function by directly providing a food resource while ensuring the availability of insects. Development and maintenance of a productive forb layer should not come at the expense of sagebrush cover, however. The overriding factor affecting habitat use by greater sage-grouse broods appeared to be the presence of protective sagebrush cover; therefore, this cover should be maintained while increasing the understory herbaceous layer. Managing for a productive, diverse understory within dense sagebrush stands should help ensure high quality early brood-rearing habitat, and enhance the potential for increased greater sage-grouse productivity.

## ACKNOWLEDGMENTS

Funding was provided by the Wyoming Game and Fish Department, Bureau of Land Management, Department of Energy, 3-Shot Sage-grouse Foundation, Yellowstone-to-Yukon Initiative, EnCana Oil and Gas, and the Animal Damage Management Board. We thank D.R. Edmunds, R.A. Holloran, B.K. Holtby, M.A. Kaemingk, A.G. Lyon, Mr. and Mrs. T.W. Malmberg, C.M. Sazama, C.G. Taber, Mr. and Mrs. N.A. Tratnik, and G.L. Wilson for assistance with field research. France Flying Service (Rawlins, WY) and Mountain Air Research (Driggs, ID) provided logistical support. We thank A.D. Apa, A.J. Carlson, J.W. Connelly, W.A. Hubert, D.D. Paulson, S.E. Richman, and an anonymous reviewer for valuable comments on earlier versions of this manuscript.

## LITERATURE CITED

ALDRIDGE, C.L. AND R.M. BRIGHAM. 2001. Nesting and reproductive activities of greater sage-grouse in a declining northern fringe population. Condor 103:537-543.

AULIE, A. 1976. The pectoral muscles and the development of thermoregulation in chicks of willow ptarmigan (*Lagopus lagopus*). Comparative Biochemistry and Physiology 53A:343-346.

AUTENRIETH, R., M. MOLINI, AND C. BRAUN. 1982. Sage grouse management practices. Western States Sage Grouse Committee, Technical Bulletin 1. Twin Falls, Idaho. 42 pp.

BAINES, D. 1991. Factors contributing to local and regional variation in black grouse breeding success in northern Britain. Ornis Scandinavica 22:264-269.

——, I.A. WILSON, AND G. BEELEY. 1996. Timing of breeding in Black Grouse *Tetrao tetrix* and Capercaillie *Tetrao urogallus* and distribution of insect food for the chicks. Ibis 138:181-187.

BATTERSON, W.M. AND W.B. MORSE. 1948. Oregon sage grouse. Oregon Fauna Serv. 1. Oregon Game Commission, Portland. 29 pp.

BERGERUD, A.T. 1988. Population ecology of North American grouse. Pages 578-685 *in* A.T. Bergerud and M.W. Gratson, editors, Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis.

BLANK, T.H., T.R.E. SOUTHWOOD, AND D.J. CROSS. 1967. The ecology of the partridge. I. Outline of population processes with particular reference to chick mortality and nest density. Journal of Animal Ecology 36:549-556.

BLENDEN, M.D., M.J. ARMBRUSTER, T.S. BASKETT, AND A.H. FARMER. 1986. Evaluation of model assumptions: the relationship between plant biomass and arthropod abundance. Pages 11-14 *in* J. Verner, M.L. Morrison, and C.J. Ralph, editors, Modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison.

BRAUN, C.E. 1998. Sage grouse declines in western North America: what are the problems? Pages 139-156 *in* Proceedings of the 1998 Western Association of State Fish and Wildlife Agencies, Jackson, WY.

BURKEPILE, N.A., J.W. CONNELLY, D.W. STANLEY, AND K.P. REESE. 2002. Attachment of radiotransmitters to one-day-old sage grouse chicks. Wildlife Society Bulletin 30:93-96.

BURNHAM, K.P. AND D.R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York, NY. 488 pp.

BURROUGH, P.A. AND R.A. MCDONNELL. 1998. Principles of geographical information systems. Oxford University Press, New York, NY. 333 pp.

CANFIELD, R. 1941. Application of the line intercept method in sampling of range vegetation. Journal of Forestry 39:386-394.

CONNELLY, J. W., M.A. SCHROEDER, A.R. SANDS, AND C.E. BRAUN. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

——, S.T. KNICK, M.A. SCHROEDER, AND S.J. STIVER. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, WY. 601 pp.

CRAWFORD, J.A., R.A. OLSON, N.E. WEST, J.C. MOSLEY, M.A. SCHROEDER, T.D. WHITSON, R.F. MILLER, M.A. GREGG, AND C.S. BOYD. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2-19.

DALKE, P.D., D.B. PYRAH, D.C. STANTON, J.E. CRAWFORD, AND E.F. SCHLATTERER. 1963. Ecology, productivity, and management of sage grouse in Idaho. Journal of Wildlife Management 27:811-841.

DAUBENMIRE, R.F. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43-64.

DRUT, M.S., W.H. PYLE, AND J.A. CRAWFORD. 1994*a*. Technical note: diets and food selection of sage grouse chicks in Oregon. Journal of Range Management 47:90-93.

——, J.A. CRAWFORD, AND M.A. GREGG. 1994*b*. Brood habitat use by sage grouse in Oregon. Great Basin Naturalist 54:170-176.

DUNN, P.O. AND C.E. BRAUN. 1986. Summer habitat use by adult female and juvenile sage grouse. Journal of Wildlife Management 50:228-235.

ERIKSTAD, K.E. 1985. Growth and survival of willow grouse chicks in relation to home range size, brood movements and habitat selection. Ornis Scandinavica 16:181-190.

ESRI, INC. 1998. Introduction to ArcView® GIS. Environmental Systems Research Institute, Inc., Redlands, CA. 604 pp.

FISCHER, R.A., K.P. REESE, AND J.W. CONNELLY. 1996. An investigation of fire effects within xeric sage grouse brood habitat. Journal of Range Management 49:194-198.

FLANDERS-WANNER, B.L., G.C. WHITE, AND L.L. MCDANIEL. 2004. Weather and prairie grouse: dealing with effects beyond our control. Wildlife Society Bulletin 32:22-34.

GIESEN, K.M., T.J. SCHOENBERG, AND C.E. BRAUN. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224-231.

GIRARD, G.L. 1937. Life history, habits and food of the sage grouse, Centrocercus urophasianus Bonaparte. University of Wyoming Publications, Publication 3. University of Wyoming, Laramie. 56 pp.

——. 1939. Notes on life history of the shoveler. Transactions of the North American Wildlife Conference 4:364-371.

GREEN, R.E. 1984. The feeding ecology and survival of partridge chicks (*Alectoris rufa* and *Perdix perdix*) on arable farmland in East Anglia. Journal of Applied Ecology 21:817-830.

GREENSLADE, P.J.M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). Journal of Animal Ecology 33:301-310.

HAULTON, G.S., D.F. STAUFFER, R.L. KIRKPATRICK, AND G.W. NORMAN. 2003. Ruffed grouse (*Bonasa umbellus*) brood microhabitat selection in the southern Appalachians. American Midland Naturalist 150:95-103.

HILL, D.A. 1985. The feeding ecology and survival of pheasant chicks on arable farmland. Journal of Applied Ecology 22:645-654.

HOLLORAN, M.J. 1999. Sage grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. Master's thesis, University of Wyoming, Laramie.

HOSMER, D.W. AND S. LEMESHOW. 1989. Applied logistic regression. John Wiley & Sons, New York, NY. 307 pp.

HULL, S.D., R.J. ROBEL, AND K.E. KEMP. 1996. Summer avian abundance, invertebrate biomass, and forbs in Kansas CRP. Prairie Naturalist 28:1-12.

HUWER, S.L. 2004. Evaluating greater sage-grouse brood habitat using human-imprinted chicks. Master's thesis, Colorado State University, Fort Collins.

JAMISON, B.E., R.J. ROBEL, J.S. PONTIUS, AND R.D. APPLEGATE. 2002. Invertebrate biomass: associations with lesser prairie-chicken habitat use and sand sagebrush density in southwestern Kansas. Wildlife Society Bulletin 30:517-526.

JOHNSON, G.D. AND M.S. BOYCE. 1990. Feeding trials with insects in the diet of sage grouse chicks. Journal of Wildlife Management 54:89-91.

KLEBENOW, D.A. 1969. Sage grouse nesting and brood habitat in Idaho. Journal of Wildlife Management 33:649-661.

—— AND G.M. GRAY. 1968. Food habits of juvenile sage grouse. Journal of Range Management 21:80-83.

KLOTT, J.H. AND F.G. LINDZEY. 1990. Brood habitats of sympatric sage grouse and Columbian sharp-tailed grouse in Wyoming. Journal of Wildlife Management 54:84-88.

KUIPERS, J.L. 2004. Grazing system and linear corridor influences on greater sage-grouse (*Centrocercus urophasianus*) habitat selection and productivity. Master's thesis, University of Wyoming, Laramie.

LYON, A.G. 2000. The potential effects of natural gas development on sage grouse near Pinedale, Wyoming. Master's thesis, University of Wyoming, Laramie.

MARCSTRÖM, V., R.E. KENWARD, AND E. ENGREN. 1988. The impact of predation on boreal tetraonids during vole cycles: an experimental study. Journal of Animal Ecology 57:859-872.

MARTIN, N.S. 1970. Sagebrush control related to habitat and sage grouse occurrence. Journal of Wildlife Management 34:313-320.

MINITAB, INC. 1994. Minitab® User's Guide, Release 10 for Windows. State College, PA. 268 pp.

MYHRE, K., M. CABANAC AND G. MYHRE. 1975. Thermoregulatory behavior and body temperature in chicks of willow grouse (*Lagopus lagopus lagopus*). Poultry Science 54:1174-1179.

NEAVE, D.J. AND B.S. WRIGHT. 1969. The effects of weather and DDT spraying on a ruffed grouse population. Journal of Wildlife Management 33:1015-1020.

PARK, K.J., P.A. ROBERTSON, S.T. CAMPBELL, R. FOSTER, Z.M. RUSSELL, D. NEWBORN, AND P.J. HUDSON. 2001. The role of invertebrates in the diet, growth and survival of red grouse (*Lagopus lagopus scoticus*) chicks. Journal of Zoology, London 254:137-145.

PATTERSON, R.L. 1952. The sage grouse in Wyoming. Wyoming Game and Fish Commission. Sage Books, Inc., Denver, CO. 341 pp.

PETERSON, J.G. 1970. The food habitats and summer distribution of juvenile sage grouse in central Montana. Journal of Wildlife Management 34:147-155.

PYLE, W.H. AND J.A. CRAWFORD. 1996. Availability of foods of sage grouse chicks following prescribed fire in sagebrush-bitterbrush. Journal of Range Management 49:320-324.

RITCEY, R.W. AND R.Y. EDWARDS. 1963. Grouse abundance and June temperatures in Wells Gray Park, British Columbia. Journal of Wildlife Management 27:604-606.

SAS INSTITUTE, INC. 1990. SAS/STAT® User's Guide, Version 6. 4th edition. Volume 2. SAS Institute, Cary, NC. 846 pp.

SCHOENBERG, T.J. 1982. Sage grouse movements and habitat selection in North Park, Colorado. Master's thesis, Colorado State University, Fort Collins.

SCHROEDER, M.A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99:933-941.

——, J.R. YOUNG, and C.E. BRAUN. 1999. Sage grouse (*Centrocercus urophasianus*). Pages 1-28 *in* A. Poole and F. Gill, editors, The Birds of North America, No. 425. The Birds of North America, Inc., Philadelphia, PA.

SLATER, S.J. 2003. Sage grouse (*Centrocercus urophasianus*) use of different-aged burns and the effects of coyote control in southwestern Wyoming. Master's thesis, University of Wyoming, Laramie.

SMYTH, K.E. AND D.A. BOAG. 1984. Production in spruce grouse and its relationship to environmental factors and population parameters. Canadian Journal of Zoology 62:2250-2257.

SOKAL, R.R. AND F.J. ROHLF. 1995. Biometry. 3rd edition. W. H. Freeman, New York, NY. 887 pp.

SOUTHWOOD, T.R.E. AND D.J. CROSS. 1969. The ecology of the partridge. III. Breeding success and the abundance of insects in natural habitats. Journal of Animal Ecology 38:497-509.

STORCH, I. 1994. Habitat and survival of capercaillie *Tetrao urogallus* nests and broods in the Bavarian Alps. Biological Conservation 70:237-243.

STUBBENDIECK, J., S.L. HATCH, AND L.M. LANDHOLT. 2003. North American wildland plants: a field guide. 6th edition. University of Nebraska Press, Lincoln. 501 pp.

SVEUM, C.M., J.A. CRAWFORD, AND W.D. EDGE. 1998. Use and selection of brood-rearing habitat by sage grouse in south central Washington. Great Basin Naturalist 58:344-351.

WAKKINEN, W.L., K.P. REESE, J.W. CONNELLY, AND R.A. FISCHER. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425-426.

WALLESTAD, R.O. 1971. Summer movements and habitat use by sage grouse broods in central Montana. Journal of Wildlife Management 35:129-136.

——. 1975. Life history and habitat requirements of the sage grouse in central Montana. Division of Wildlife, Montana Department of Game and Fish. 65 pp.

WHITMORE, R.W., K.P. PRUESS, AND R.E. GOLD. 1986. Insect food selection by 2-week-old ring-necked pheasant chicks. Journal of Wildlife Management 50:223-228.

TABLE 1. Candidate models used to explain early brood-rearing habitat use of greater sage-grouse in Pinedale (1999-00, 2002-03), Lander (2001-2003), and Kemmerer (2002), WY. Models ($n$ = 62) were based on logistic regression analyses in which habitat type (use [$n$ = 82] or random [$n$ = 180]) was the dependent variable. Models were ranked according to $AIC_c$ methods (Burnham and Anderson 2002); only models with $\Delta AIC_c \leq 2$ are presented.

| Model[a] | K[b] | $\Delta AIC_c$ [c] | $w_i$ [d] | $\log_e L$ [e] | Goodness-of-fit [f] | Dir.[g] |
|---|---|---|---|---|---|---|
| Sage, invert | 3 | 0.00 | 0.07 | -159.45 | 7.46, $_8$, 0.49 | +, – |
| Sage, Hymenopt | 3 | 0.49 | 0.06 | -159.69 | 13.01, $_8$, 0.11 | +, – |
| Grass hgt, sage | 3 | 0.55 | 0.05 | -159.72 | 7.02, $_8$, 0.53 | +, + |
| Grass hgt, sage, invert | 4 | 0.87 | 0.05 | -159.85 | 7.42, $_8$, 0.49 | +, +, – |
| Grass cover, sage | 3 | 1.12 | 0.04 | -160.01 | 8.54, $_8$, 0.38 | +, + |
| Grass hgt, sage, Hymenopt | 4 | 1.18 | 0.04 | -159.01 | 8.75, $_8$, 0.36 | +, +, – |
| Grass cover, sage, invert | 4 | 1.34 | 0.04 | -159.09 | 5.84, $_8$, 0.67 | +, +, – |
| Sage, medium Hymenopt | 3 | 1.53 | 0.03 | -160.21 | 9.36, $_8$, 0.31 | +, – |
| Sage, herb | 3 | 1.56 | 0.03 | -160.23 | 11.22, $_8$, 0.19 | +, + |
| Herb, sage, invert | 3 | 1.57 | 0.03 | -160.69 | 4.89, $_8$, 0.77 | +, +, – |
| Sage, grass cover, Hymenopt | 3 | 1.67 | 0.03 | -159.20 | 7.67, $_8$, 0.47 | +, +, – |
| Liv_den, grass hgt | 3 | 1.72 | 0.03 | -159.25 | 16.94, $_8$, 0.03 | +, + |
| Sage, medium Coleopt | 3 | 1.78 | 0.03 | -160.30 | 12.48, $_8$, 0.13 | +, – |
| Forb, sage | 4 | 1.93 | 0.03 | -160.34 | 13.28, $_8$, 0.10 | +, + |

[a] Variables included in the presented models are live sagebrush canopy cover (sage), live sagebrush density (liv_den), mean grass height (grass hgt), total grass cover (grass cover), total forb cover (forb), total herbaceous cover (herb), total invertebrate abundance (invert), total Hymenoptera abundance (Hymenopt), medium-length Hymenoptera abundance (medium Hymenopt), and medium-length Coleoptera abundance (medium Coleopt). Medium-length insects were those ≥3 cm and ≤11 cm.

[b] Number of variables in model + intercept.

[c] Difference in Akaike's Information Criterion (with small-sample bias adjustment) values.

[d] Percent of total weight (from all 62 models) that can be attributed to specified model.

[e] Log-likelihood.

[f] Hosmer-Lemeshow (1989) goodness-of-fit test statistic, df, $P$-value.

[g] Direction of trend. Plus symbol indicates females with broods were using habitat with greater amounts of the variable; minus symbol indicates broods used habitats with lesser amounts.

TABLE 2. Total and standardized cumulative $AIC_c$ weights of variables used to predict juveniles per female (in fall wing barrel collections) and the proportion of females with confirmed chicks (14 days post-hatch) of greater sage-grouse in Pinedale (1999-00, 2002-03), Lander (2001-2003), and Kemmerer (2002), WY. Weights were standardized by the number of times a model (in the entire set of models) included the variable.

| | Juveniles per female | | Prop. of females w/confirmed chicks | |
|---|---|---|---|---|
| Variable[a] | Cum. $w_i$[b] | Std. cum. $w_i$[c] | Cum. $w_i$[b] | Std. cum. $w_i$[c] |
| Medium Hymenopt | 0.66 | 0.11 | 0.00 | 0.00 |
| Medium Coleopt | 0.28 | 0.04 | 0.98 | 0.16 |
| Hymenopt | 0.10 | 0.02 | 0.00 | 0.00 |
| Invert | 0.14 | 0.03 | 0.00 | 0.00 |
| Herb | 0.02 | 0.00 | 0.99 | 0.12 |
| Forb | 0.08 | 0.02 | 0.00 | 0.00 |
| Grass cover | 0.58 | 0.06 | 0.00 | 0.00 |
| Grass hgt | 0.02 | 0.00 | 0.00 | 0.00 |
| AprMay_TempPre | 0.02 | 0.00 | 0.02 | 0.00 |
| Jun_TempPre | 0.07 | 0.01 | 0.00 | 0.00 |
| JulAug_TempPre | 0.03 | 0.00 | NA | NA |

[a] Variables included in the table are medium-length Hymenoptera abundance (medium Hymenopt), medium-length Coleoptera abundance (medium Coleopt), total Hymenoptera abundance (Hymenopt), total invertebrate abundance (invert), total herbaceous cover (herb), total forb cover (forb), total grass cover (grass cover), mean new and residual grass height (grass hgt), percent of average April + May temperature/percent of average April + May precipitation (AprMay_TempPre), percent of average June temperature/percent of average June precipitation (Jun_TempPre), and percent of average July + August temperature/percent of average July + August precipitation (JulAug_TempPre). Medium-length insects were those ≥3 cm and ≤11 cm.

[b] Cumulative Akaike weight (Burnham and Anderson 2002).

[c] Standardized cumulative Akaike weight.

APPENDIX C

# GREATER SAGE-GROUSE RESEARCH IN WYOMING: AN OVERVIEW OF STUDIES CONDUCTED BY THE WYOMING COOPERATIVE FISH AND WILDLIFE RESEARCH UNIT BETWEEN 1994 AND 2005

Matthew J. Holloran, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Box 3166 University Station, Laramie, WY, 82071, USA.
holloran@uwyo.edu; 307 766 5415 (voice); 307 766 5400 (fax).

Stanley H. Anderson, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Box 3166 University Station, Laramie, WY, 82071, USA.





ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*) populations have been declining throughout Wyoming since the 1960s. Game and land managers, sportsmen organizations, and Wyoming citizens have been concerned over the plight of the sage-grouse for over a half-century, but this concern has escalated within the last decade. In 1994, the first of a series of 10 research projects on greater sage-grouse in Wyoming was initiated; the Wyoming Cooperative Research Unit was responsible for conducting these studies. The projects have focused on a wide array of objectives, including greater sage-grouse microsite and landscape scale seasonal habitat use and the identification of limiting seasonal habitats, the effects of mineral extraction activity on greater sage-grouse populations, greater sage-grouse seasonal use of habitats manipulated by fire, livestock grazing management system influences on greater sage-grouse productivity, and the response of greater sage-grouse populations to predator control programs. This report is a synopsis of the results from the research conducted by the Wyoming Cooperative Research Unit on greater sage-grouse since 1994. Detailed information pertaining to methods and site-specific results are found in the original job completion reports (Wyoming Game and Fish Department, Cheyenne, WY, USA) and theses (University of Wyoming, Laramie, WY, USA).

ACKNOWLEDGMENTS

Financial support was provided by the Wyoming Game and Fish Department, Bureau of Land Management, U.S. Department of Energy, Ultra Petroleum, Yellowstone-to-Yukon Initiative, EnCana Oil and Gas Inc., Shell Rocky Mountain Production LLC, Animal Damage Management Board, National Park Service, and Cowboy 3-Shot Sage-Grouse Foundation. We thank the following landowners for access: Bates Creek Cattle Company, Bousman Ranch, Carney Ranch, Ferris Mountain Ranch, Garrott Ranch, Julian Sheep Company, Little Sandy Grazing Association, Luther Ranch, Miles Cattle Company, Miller Estate, Red Bluff Ranch, Reed Ranch, Ruby Ranch, Sealy/Sawyer Ranch, Sommers Ranch, Stone Ranch, Mayo Ranch, Luman Ranch, Carney Ranch, Pope Cattle Company, and the Three-quarter Circle Ranch. Field assistance and technical support were provided by K. D. Downs, M. B. Hicks, R. A. Holloran, B. K. Holtby, M. A. Kaemingk, Mr. and Mrs. T. W. Malmberg, T. E. McCollum, R. C. Powell, C. M. Sazama, M. S. Stotts, C. G. Taber, K. M. Thompson, Mr. and Mrs. N. A. Tratnik, C. T. Weibel, G. L. Wilson, and J. A. Wyllie. We thank T. D. Moore (Wyoming Game and Fish Department) for laboratory analysis of hair and scat samples. Telemetry flights and lek surveys were conducted with the assistance of Cheney Flying Service (Casper, WY), France Flying Service (Rawlins, WY), and Mountain Air Research (Driggs, ID). Although I have specifically recognized those who were hired to assist with these projects, the people and organizations that voluntarily assisted with these projects would take volumes to list in their entirety; to all those with the Wyoming Game and Fish Department, Bureau of Land Management, National Park Service, Wyoming Cooperative Research Unit, and interested citizens, I personally want you to know that your assistance was sincerely appreciated.

TABLE OF CONTENTS

Abstract 1
Acknowledgements 2
Table of Contents 3
Introduction 4
Historical Sage-grouse Information 6
Factors Potentially Contributing to Historic Population Changes 8
Study Areas and Objectives by Study
Farson 10
Rawlins 10
Casper 11
Pinedale 12
Kemmerer 12
Jackson 13
Lander 14
Pinedale 15
Seasonal Habitat Selection
Nesting Habitat Selection 15
Nesting Success 18
Early Brood-rearing Habitat Selection and Success 20
Late Brood-rearing Habitat Selection and Success 22
Winter Habitat Selection 23
Seasonal Adult Survival 25
Livestock Grazing 26
Sagebrush Manipulation 29
Mineral Extractive Activities 32
Predator Control 36
Future Sage-grouse Research in Wyoming 39
Literature Cited 41
Table 1: Productivity estimates for greater sage-grouse populations studied by the Wyoming Cooperative Research Unit in central and western Wyoming, 1994-2004. 57
Figure 1: Study area locations for greater sage-grouse research projects conducted by the Wyoming Cooperative Research Unit, 1994-2005. 58

INTRODUCTION

The sage-grouse (*Centrocercus* spp.) is North America's largest grouse, and is a species uniquely adapted to and dependent on sagebrush (*Artemisia* spp.) for survival. Sage-grouse are renowned for their spectacular breeding displays, and have inspired Native Americans, naturalists, behavioral ecologists, photographers, and hunters throughout history (Schroeder et al. 1999). Recently, greater sage-grouse (*Centrocercus urophasianus*) entered the American spotlight because of the potential for listing under the Endangered Species Act (ESA). If the species were listed as nationally threatened, the management of millions of acres of sagebrush dominated land would be affected, with dramatic implications for the grazing, mining, farming, recreation, and other activities occurring on those lands (Johnsgard 2002). In January 2005, the U.S. Fish and Wildlife Service (USFWS) announced a not warranted 12-month finding for 3 petitions to list the greater sage-grouse as threatened or endangered throughout its current range. Although the best available scientific information suggested to the USFWS that greater sage-grouse were not currently warranted for protection under the ESA, concern for the species has remained high. Sage-grouse population maintenance requires a recognition of the intrinsic value of sagebrush dominated landscapes and the development of a comprehensive approach to sagebrush habitat conservation that involves commitments and partnerships between state, federal and tribal governments, academia, industry, private organizations, and landowners; "only through this concerted effort and commitment can we afford to be optimistic about the future of sagebrush ecosystems and their avifauna" (Knick et al. 2003:627).

Substantial areas in Wyoming, especially the southwestern portions of the state, are currently considered greater sage-grouse breeding population strongholds (Figure 1); compared to other states harboring sage-grouse populations, Wyoming currently has the highest percentage (67%) of potential sagebrush vegetation still in sagebrush habitats (Connelly et al. 2004). Braun (1998) estimated that in the spring of 1998, only Wyoming, Montana and Oregon contained greater sage-grouse (hereafter, "sage-grouse" refers to greater sage-grouse unless specifically indicated) populations of more than 20,000 birds. Additionally, Connelly et al. (2004) suggested that Wyoming currently represents a "key sage-grouse state." However, evidence suggests that sage-grouse populations in Wyoming have been declining over the last half of the 20$^{th}$ century.

Since 1965, sage-grouse breeding populations, as estimated through changes in the number of males occupying leks statewide, have declined by 5.2% annually and the average number of males per lek has declined 49% (Connelly et al. 2004). Between 1975-79 and 1990-94, Wyoming's statewide sage-grouse harvest declined 55%. Additionally, the number of harvested birds per hunter day (an index that accounts for hunter effort and participation) declined 52% between 1975-79 and 1995-99

(harvest and birds/day value comparisons made between the indicated 5-year period means; Wyoming Game and Fish Department harvest reports 1979-99, Cheyenne, WY, USA). Examples of relatively localized sage-grouse population changes in Wyoming during the latter half of the 20th century are common. From 1994-96, the Wyoming Cooperative Research Unit (University of Wyoming; WyCOOP) conducted a sage-grouse study in western Wyoming on the same study location as a portion of Robert Patterson's landmark study that culminated in his book *The Sage Grouse in Wyoming* (1952). When Patterson began his work on the Dry Sandy-Pacific Creek study area (northeast of Farson, WY) in 1949, he knew of 22 leks used during the breeding season by 1167 strutting males. In 1994, 5 leks comprising 210 males (Heath et al. 1997) were known to exist on the same study area, a decline of 77% in the number of active leks and 82% in the number of strutting males over 45 years. In the southeastern part of the state, the average total number of males strutting on 3 lek complexes (i.e., a group of closely spaced leks where inter-lek movements during a breeding season potentially occur) declined 46% between 1968-69 and 2000-01; additionally, average lek size, defined as the number of males per known lek within the complexes, declined 91% over the same time period (Bob Lanka, Wyoming Game and Fish Department Laramie Region, personal communication). Prior to the 1950s, Patterson (1952) estimated that 500 individual sage-grouse were resident in the Jackson Hole area (a relatively isolated population residing within and around Grand Teton National Park and the National Elk Refuge). In 2002-03, populations were conservatively estimated at less than 182 individuals, 64% below pre-1950 estimates. Additionally, the number of male sage-grouse counted on leks in the Jackson Hole area declined 76% over a 12-year period between 1990-91 and 2002-03 (Holloran and Anderson 2004). Although Wyoming wildlife and land managers have suspected that statewide sage-grouse populations have been declining for many decades, the identification of specific cause(s) for the declines have remained elusive.

Given the importance of Wyoming's sage-grouse populations and habitats, statewide declining populations, and the inability to identify specific reasons for the declines, game and land management agencies in the state initiated several studies beginning in 1994; the WyCOOP was responsible for conducting these studies. The general focus of these studies was to identify limiting seasonal habitats and investigate the potential effects of specific management actions on sage-grouse populations. Results from research projects conducted by the WyCOOP have played a pivotal role in the state's sage-grouse management goals, and were used extensively during the writing of the statewide Wyoming Greater Sage-grouse Conservation Plan (http://gf.state.wy.us/wildlife/wildlife_management/sagegrouse). These projects have resulted in 3 job completion reports, 4 masters' theses, and a dissertation; additionally, 2 students are currently working on their masters' projects at the University

of Wyoming. The following report consists of a synopsis of the sage-grouse studies conducted by the WyCOOP since 1994. I have organized the report around objectives investigated by the studies instead of around each study, thus the sections are focused on specific topics and not on specific study areas within the state. Each section consists of a brief literature review pertaining to the topic, followed by a discussion of the general findings from the Wyoming studies. For more detailed information pertaining to specific results and methods, consult the original job completion reports (Wyoming Game and Fish Department, Cheyenne, WY, USA) or theses (University of Wyoming, Laramie, WY, USA).

## HISTORICAL SAGE-GROUSE INFORMATION

Sage-grouse were historically distributed throughout the intermountain and northwestern states and southern regions of 3 Canadian provinces (Schroeder et al. 2004). Pre-settlement distributions included western Nebraska and the Dakotas, all of Montana, Idaho, Wyoming, Nevada and Utah, northwestern New Mexico, northern Arizona, western Colorado, portions of eastern California, Oregon and Washington, and southern British Columbia, Alberta, and Saskatchewan. In Wyoming, greater sage-grouse were historically found in all 23 counties (Patterson 1952). The original range of sage-grouse closely followed that of the historical distribution of big sagebrush (*Artemesia tridentata* sub-spp.), and was not continuous throughout the previously outlined area due to the presence of other habitat types (i.e, forested mountains; Patterson 1952).

The only information relating to the historical abundance of sage-grouse throughout the intermountain west and Wyoming comes from early anecdotal reports, which suggest that the bird was abundant throughout its range. Lewis and Clark were the first Europeans to encounter the species: "I [Lewis] saw a flock of the mountain cock, or a large species of heath hen [*Tympanuchus cupido cupido*] with a long pointed tail which the Indians informed us were common in the Rocky Mountains…" (Moulton 1987). John C. Fremont mentioned that the Crow Indians had named the upper Green River after the sage-grouse, and reported that the birds were "very abundant" in 1843; and in 1874, Elliott Coues suggested that sage-grouse were generally well known to early western explorers (Patterson 1952). Patterson and Cram (1949) indicated that old-time residents in Wyoming typically recalled historic sage-grouse numbers using expressions such as "flocks that blackened the sky" and "rode for miles horseback without being out of sight of birds." McDowell (1956) reported that in Goshen County, Wyoming, he interviewed an old-time resident who said that before eastern parts of the state (the area around Torrington, WY) were settled to farms and ranches, sage-grouse were so numerous that people gathered the eggs during the laying season for table use. One of the more interesting accounts is given by Dr. George B. Grinnell, relating his experience in central Wyoming (near Bates

Hole south of Casper, WY) during the fall of 1886: "The number of grouse which flew over the camp reminded me of the old time flights of Passenger Pigeons [*Ectopisties migratorius*] that I used to see when I was a boy. I have no means whatever of estimating the number of birds which I saw, but there must have been thousands of them" (Patterson 1952: after Bent 1932).

It is commonly believed that the sage-grouse began to decline over much of its range during the late 1890s and early 1900s, and continued to decline until the late 1930s (Griner 1939, Patterson 1952, Autenrieth 1981). In the mid-1910s, Hornaday (1916) wrote: "the fact is beyond controversy that unless something on a very broad scale is immediately done, they [sage-grouse] are doomed to early extinction" and demanded that western lawmakers take action to save the species. Similarly, William L. Simpson believed that under protections present in the early 1900s, the "sage hen will be practically extinct" in a decade (Hornaday 1916). Simpson further indicated that he "was over a large portion of the Shoshone Reservation [in central Wyoming] this last year [mid-1910s], and saw only a few [sage-grouse] where there used to be thousands" (Hornaday 1916). Fuller and Bole (1930) suggested that the "stately sage grouse must either radically change its attitude towards man, or face ultimate extermination…local hunters admit that the birds are ever on the decline, and are certainly far less plentiful now [late 1920s] than in 1914." Perhaps Girard (1937) best captured the current mood of the day when he commented that the "impending fate [of the sage-grouse] is extinction and has become so apparent within recent years that the time for words has passed and need for immediate action is imperative."

By the late 1930s, continued concern for the species by conservationists and increasing concern by sportsmen and managers led to widespread hunting season restrictions and closures; by 1937, only Montana had a regular open hunting season (Griner 1939). In 1937, the Wyoming Game and Fish Department issued the following statement concerning sage-grouse hunting in Wyoming (Anonymous 1937): "The commission regrets the necessity of having to take this action [hunting season closure]. However, in view of the rapid depletion of this magnificent game bird, its extinction in many parts of its former range, and the conditions found in all parts of the State, some drastic action becomes necessary if we are to save this fine game bird." Wyoming's sage-grouse hunting season was closed between 1937 and 1948 (Patterson 1952), similar to most states where the restrictions imposed on hunting initiated in the 1930s continued into the 1950s (Braun 1998).

Open hunting seasons in 7 states in the early 1950s coincided with an apparent widespread upward turn in sage-grouse population trends beginning in the late 1940s (Patterson 1952). In 1949, Patterson (1952) counted over 3241 males on 49 study leks in central Wyoming, and had one study lek where he estimated over 400 strutting cocks. Additionally, during the 1947-48 aerial census of

wintering pronghorn (*Antilocapra americana*), crews reported concentrations of sage-grouse flocks containing from "several hundred to several thousand birds" in Johnson, Natrona, Sweetwater, Carbon and Fremont counties, WY (Patterson 1952). However, it is generally believed that sage-grouse populations entered a second period of decline within a few years of this temporary reprieve.

Current sage-grouse breeding populations throughout western North America are approximately two to three times lower than those during the late 1960s, and populations declined on average 2% annually from 1965 to 2003 (Connelly et al. 2004). In 2000, greater sage-grouse occupied 56% of their pre-European settlement distribution (Schroeder et al. 2004). Connelly and Braun (1997) reported that long-term population declines prior to 1994 in states historically supporting the largest sage-grouse populations (Colorado, Idaho, Montana, Oregon, Wyoming) averaged 30%; in states and Canadian provinces historically supporting smaller populations, breeding populations declined by an average of 37%. Although harvest and lek count estimations should not be interpreted as absolute, they suggest that sage-grouse populations throughout North American have been trending downward at least since the late 1960s.

## FACTORS POTENTIALLY CONTRIBUTING TO HISTORIC POPULATION CHANGES

The list of potential factors contributing to sage-grouse range-wide declines essentially includes every imaginable human caused impact on the species and its habitats. Braun (1998) grouped the factors into 3 main categories: habitat loss, habitat degradation, and habitat fragmentation. Habitat loss includes agricultural conversion, energy and mineral development, and the building of towns, ranches, roads and reservoirs. Habitat degradation can result from sagebrush treatments (mechanical, chemical and fire), grazing, and the introduction of exotic plant species. And habitat fragmentation, defined as a process during which large expanses of habitat are transformed into a number of smaller patches (Fahrig 2003), is commonly caused by fences, power lines, roads, sagebrush treatments, as well as the presence of habitat loss factors previously outlined. Other factors such as hunting, predation, and drought have also been implicated (Braun 1998). The relative importance of these individual factors most likely has varied over the range of the sage-grouse as well as through time.

The factors most commonly implicated in the early declines between the 1900s and 1930s are excessive harvest, overgrazing, and agricultural development (Girard 1937, Rasmussen and Griner 1938, Patterson 1952). The first regulations providing protection for sage-grouse from hunting were established around the turn of the century; early protective measures were largely concerned with the establishment of closed seasons and not bag limits (Patterson 1952). An early account of a lone hunter in Wyoming harvesting 100 birds a day (Patterson 1952: after Burnett 1905) serves to illustrate the

level of pressure populations may have experienced during the early 1900s. Even when states began to expand hunting regulations, early opening dates, extended season length, high bag limits, and lack of enforcement acted to afford little real protection to the species (Hornaday 1916, Patterson 1952). The early decline of the sage-grouse also coincided with a period of intensive livestock grazing and agricultural development and settlement that likely fragmented and degraded the quality of sagebrush habitats (Griner 1939, Patterson 1952). Rangelands supporting the greatest numbers of sage-grouse were often those with the most productive soils; because of the soil conditions, these areas were commonly the first to be developed. Additionally, the drought of the 1930's likely further degraded sagebrush dominated areas and compounded the negative effects of poor quality habitats on sage-grouse populations (Patterson 1952).

Population recoveries in the late 1940s and 1950s were likely a result of improved range conditions; however, potential improvements in all 3 factors suggested as responsible for the early declines occurred during this period. Widespread hunting season closures, range improvement as the result of the Taylor Grazing Act of 1934 (Patterson 1952), and range reversion resulting from land abandonment after the drought and depression of the 1930s (Wallestad 1975) were probably responsible for the temporary range-wide increase in sage-grouse populations.

The beginning of the second period of decline could have been in response to increased sagebrush treatment. Aerial application of herbicides (primarily 2,4-D) and mechanical treatments gained popularity during the 1950s and resulted in the widespread eradication of sagebrush that continued into the 1960s (Wallestad 1975). Although the intensity of sagebrush treatment programs declined in the late 1960s, these programs in combination with renewed agricultural development during this period resulted in the degradation, alteration, and loss of substantial portions of the sagebrush dominated rangelands (Braun et al. 1976, Klebenow 1969).

It is more difficult to determine a single factor or group of factors responsible for sage-grouse population declines in recent decades and into the present. Braun (1998) suggests that a complexity of factors related to human caused habitat changes is responsible. Each population is likely subjected to habitat degradation arising from the long-term consequences of historic use of sagebrush habitats that may be influencing current conditions plus unique circumstances compounding the negative influence of suboptimal habitats. Although range-management techniques have improved over the last half of the 20$^{th}$ century, providing or managing sagebrush habitats for pre-settlement conditions is likely impossible as many key elements may no longer exist (Connelly et al. 2004). Connelly et al. (2004) estimated that approximately 47% (>234,700 km$^2$) of the area within the western United States that

potentially could be dominated by sagebrush was either in agricultural, urban, or industrial areas or in unsuitable habitats in 2003 (i.e., exotic grassland, burn, juniper woodland, etc.).

STUDY AREAS and OBJECTIVES by STUDY (FIGURE 1)

1. FARSON

*Heath, B. J., R. Straw, S. H. Anderson, and J. Lawson. 1997. Sage grouse productivity, survival, and seasonal habitat use near Farson, Wyoming. Job Completion Report, Wyoming Game and Fish Department, Cheyenne, WY, USA.*

The Farson study area was selected primarily because of the existence of historical population and vegetation data collected by Patterson (1952) during the late 1940s and early 1950s. The area supported some of the highest sage-grouse densities in the state, and had contiguous sagebrush cover that had not been drastically altered within the last 30 to 40 years. The primary objectives established for the study were to identify seasonal habitat components that limit sage-grouse productivity and decrease survival.

The study area was located approximately 30 km northeast of Farson, Wyoming in portions of Sweetwater, Sublette, and Fremont Counties. Annual precipitation averaged between 20 cm in the southwestern portions of the study area to 35 cm in the northeast, and was approximately 119% of normal during the study years (1994-96). Topography of the area was characterized by flat plains interrupted by rolling hills, ridges, and drainages. Overstory vegetation was dominated by Wyoming big sagebrush (*A. t. wyomingensis*), with mountain big sagebrush (*A. t. vaseyana*), basin big sagebrush (*A. t. tridentata*), black sagebrush (*A. nova*), low sagebrush (*A. arbuscula*), greasewood (*Sarcobatus vermiculatus*), and rabbitbrush (*Chrysothamnus* spp.) interspersed throughout.

2. RAWLINS

*Heath, B. J., R. Straw, S. H. Anderson, J. Lawson, and M. J. Holloran. 1998. Sage-grouse productivity, survival, and seasonal habitat use among three ranches with different livestock grazing, predator control, and harvest management practices. Job Completion Report, Wyoming Game and Fish Department, Cheyenne, WY, USA.*

The sagebrush steppe communities adjacent to Rawlins, Wyoming historically supported abundant sage-grouse populations. However, population declines within the area prompted local residents, especially members of a local sportsmen's organization (Cowboy 3-shot Sage Grouse

Foundation), to voice concern. In response to these concerns, the Wyoming Game and Fish Department initiated the Rawlins sage-grouse study. The overriding objectives of the study were to evaluate differences in sage-grouse productivity, habitat selection, and survival on 3 ranches with distinct grazing management, predator control, and harvest levels and provide insight into how these management strategies effected sage-grouse populations.

The study area was located approximately 25 km northeast of Rawlins, Wyoming in portions of Carbon County. Annual precipitation averaged 25 cm, and was approximately 104% of normal during the study years (1997-98). Topography of the area was generally flat to gently rolling hills with a predominantly Wyoming big sagebrush overstory. The foothills of the Ferris Mountains in the northern end of the study area were dominated by sand dunes with predominantly a silver sagebrush (*A. cana* spp.) and rabbitbrush overstory.

Grazing management between the 3 ranches differed in terms of livestock and level of use. One ranch grazed both cattle and sheep, and rotated pastures after a specific number of use-days; the other 2 ranches grazed cattle, and rotated pastures after 30% or 40% of the herbaceous vegetation was removed. Predator control differences were primarily between the cattle-sheep and cattle-only ranches. The ranch raising sheep employed a federal predator control program aimed primarily at coyote (*Canis latrans*) control; the other 2 ranches had no organized predator control programs, but allowed recreational predator hunting. Sage-grouse hunting opportunities between the 3 ranches ranged from unrestricted access to no hunting allowed.

3. CASPER

*Holloran, M. J. 1999. Sage grouse (Centrocercus urophasianus) seasonal habitat use near Casper, Wyoming. MS Thesis, University of Wyoming, Laramie, WY, USA.*

The final project concentrating primarily on sage-grouse seasonal habitat selection was conducted in an area with personal significance for people in the Wyoming Game and Fish Department. The primary objectives established for this study were to determine habitat conditions that were selected by sage-grouse and that influenced sage-grouse productivity and survival. Another objective of this study was to evaluate late-incubation chronology and identify nest predators using remote sensing cameras.

The study area was located approximately 35 km south of Casper, Wyoming in portions of Natrona County. Annual precipitation averaged 28 cm, and was approximately 125% of normal during the study years (1997-98). Topography was generally flat to gently rolling hills with predominantly

north and south aspects. The vegetation overstory was dominated by Wyoming big sagebrush, with silver sagebrush, Wyoming threetip sagebrush (*A. tripartita*), black sagebrush, and rabbitbrush dispersed throughout the study area.

4. PINEDALE

*Lyon, A. G. 2000. The potential effects of natural gas development on sage grouse near Pinedale, Wyoming. MS Thesis, University of Wyoming, Laramie, WY, USA.*

The emphasis of the studies changed from habitat selection to the investigation of specific land-use effects on sage-grouse beginning with this first of several Pinedale studies. The primary objective of the study was to quantify the potential effects of natural gas development activity on male and female sage-grouse seasonal habitat selection.

The study area was situated approximately 5 km south of Pinedale, Wyoming on an area locally known as the Mesa in Sublette County; the Mesa was situated within the Pinedale Anticline Project Area (PAPA) natural gas field. Annual precipitation averaged 30 cm, and was approximately 112% of normal during the study years (1998-99). Topographically, the Mesa was relatively flat with a series of north/south-running draws circumventing the southern and northern portions of the study area. Overstory vegetation was dominated by Wyoming big sagebrush.

The first natural gas well was drilled in the PAPA in 1939; however, only 23 additional wells were drilled in the project area prior to 1997. In May, 1998, the BLM approved limited exploratory drilling of 45 wells prior to completion of the Environmental Impact Statement (EIS); the EIS was being drafted during this study and was not completed until after the conclusion of the study. Therefore, the primary gas related disturbance during the years of the study was traffic related, and the results pertained primarily to the influence traffic had on breeding male and female sage-grouse.

5. KEMMERER

*Slater, S. J. 2003. Sage-grouse (Centrocercus urophasianus) use of different-aged burns and the effects of coyote control in southwestern Wyoming. MS Thesis, University of Wyoming, Laramie, WY, USA.*

The lack of agreement among land management personnel as to the appropriate role of prescribed fire in Wyoming's sage-grouse habitats necessitated the Kemmerer study. The primary objectives of the study were to document seasonal sage-grouse use, and describe the vegetation and

insect characteristics of burned areas compared to the overall landscape. An additional objective for this study was to determine the effect a coyote control program had on sage-grouse productivity and survival and on predator species composition.

The study area was situated approximately 30 km west of Kemmerer, Wyoming in Lincoln County. Annual precipitation averaged 26 cm, and was approximately 50% of normal during the study years (2000-02). Topography varied throughout the area with ridges, basins and draws as common features. Overstory vegetation was dominated by Wyoming and mountain big sagebrush, with low, basin big, and black sagebrush, serviceberry (*Amelanchier alnifolia*), rabbitbrush, and snowberry (*Symphoricarpos* spp.) interspersed throughout the study area.

Four different burns ranging in age from 2 to 26 years were present within the study area; between approximately 20 and 80% of the shrub overstory was removed by fire from these burns. Intensive coyote control by aerial gunning and other means was performed within the study area during the study to protect domestic sheep. A control area (located approximately 25 km south of the main study area) with no organized predator control was established for comparison purposes.

6. JACKSON

*Holloran, M. J., and S. H. Anderson. 2004. Greater sage-grouse seasonal habitat selection and survival in Jackson Hole, Wyoming. Job Completion Report, Wyoming Game and Fish Department, Cheyenne, WY, USA.*

A relatively unique, isolated population of sage-grouse in the Jackson Hole valley has experienced substantial declines since the early 1990s; the population is currently approximately 65% below sustainable (Connelly et al. 2000b) levels. Because of the recreational importance of this population (situated within and around Grand Teton National Park), the Jackson study was initiated to investigate possible reasons for the declines. The primary objectives of this study were to document sage-grouse seasonal habitat selection and survival, identify the limiting seasonal range(s), and quantify the habitat conditions associated with sustainable and increasing productivity.

The study area was situated primarily within Grand Teton National Park and the National Elk Refuge approximately 10 km north of Jackson, Wyoming in Teton County. Annual precipitation averaged 51 cm, and was between 77 and 111% of normal during the study years (1999-2002). Topography varied substantially throughout the study area, with relatively flat valley floors traversing quickly into generally east and west facing foothills. Overstory vegetation was dominated by mountain and Wyoming big sagebrush, with basin big, low and tall threetip (*A. tripartita tripartita*) sagebrush

interspersed throughout. A substantial antelope bitterbrush (*Purshia tridentata*) community covered portions of the study area. Additionally, the sagebrush dominated areas were interspersed with pockets of aspen (*Populus tremuloides*), conifer (*Pinus, Pseudotsuga, Picea* spp.), and cottonwood (*Populus angustifolia*), predominantly on northern and northwestern aspects and along watercourses.

7. LANDER

*Kuipers, J. L. 2004. Grazing system and linear corridor influences on greater sage-grouse (Centrocercus urophasianus) habitat selection and productivity. MS Thesis, University of Wyoming, Laramie, WY, USA.*

One of the primary questions facing western land management agencies is the potential influence of livestock grazing on sagebrush dominated habitats and sage-grouse populations; the Lander study tackled this subject. The primary objectives of the study were to describe the response of sagebrush dominated ecosystems to livestock grazing under 4 different grazing schemes, and to describe sage-grouse habitat use, productivity and survival relative to these grazing systems. An additional objective was to determine the influence linear corridors (i.e., livestock trails, roads, fence lines) had on sage-grouse nest success probabilities.

The study area was situated approximately 25 km southeast of Lander, Wyoming in Fremont County. Annual precipitation averaged 34 cm, and was approximately 68% of normal during the study years (2000-03). Topography consisted of several relatively flat benches stepping upwards in elevation into the foothills of the Wind River Mountains. A series of north-south running draws were prominent features throughout the study area. Overstory vegetation was dominated by Wyoming big sagebrush, with patches of snowberry, aspen, and conifer (*Juniperus osteosperma, J. scopulorum*) interspersed throughout the study area.

Three different livestock (cattle) gazing systems were present on the study area; a 4$^{th}$ area was included as a non-livestock grazed control. The 3 grazing systems were rotational with 4.5 month grazing periods from mid-May through September. Rotation systems included: (1) differed rotational (spring deferment alternated annually in a 2 paddock system with >45% forage utilization); (2) summer grazed rest rotational [livestock rotation between a 10 paddock system, paddocks grazed primarily during the summer, complete rest from livestock in 2 to 10 paddocks annually during the study, 1 paddock twice-over grazed (same paddock grazed twice in a grazing season) during the study, and 35 to 45% forage utilization]; and (3) spring and fall grazed rest rotational (rotation between a 10 paddock system, paddocks grazing primarily during spring and fall, complete rest from livestock in 1 to 3

paddocks annually during the study, 27% of the paddocks twice-over grazed during the study, and 35 to 45% forage utilization).

8. PINEDALE

*Holloran, M. J. In Preparation. Greater sage-grouse (Centrocercus urophasianus) population response to natural gas field development in western Wyoming. PhD Dissertation, University of Wyoming, Laramie, WY, USA.*

The amount of sagebrush dominated lands potentially influenced by natural gas and oil development has increased dramatically in recent years; however, limited information exists as to the response of sage-grouse to this development. The second Pinedale study was initiated as a continuation of Lyon's (2000) research outlined above. The primary objective of the study was to quantify the potential effects of natural gas development activity on sage-grouse populations and seasonal habitat selection.

The study area was expanded approximately 35 km south and east from the original concentration of areas on the Mesa. Annual precipitation was approximately 87% of normal during the study years (2000-04). Overstory vegetation within the expanded portions of the study area was also dominated by Wyoming big sagebrush, with rabbitbrush, greasewood and saltbush (*Atriplex* spp.) interspersed throughout.

The final EIS for the PAPA was approved in July 2000. Full development of the PAPA is expected to continue for the next 10 to 15 years. The BLM's record of decision approved construction of 700 producing wells with minimum densities of 1 well per 16 ha (equivalent to 16 wells per section), 645 km of pipeline, and 445 km of road. According to information supplied by the Wyoming Oil and Gas Conservation Commission (Casper, WY, USA), between 1998 and 2004 approximately 340 natural gas wells were drilling on the PAPA; if surrounding areas are included, approximately 780 wells became active during the study (i.e., including the substantial development occurring within the Jonah natural gas fields situated south of the PAPA).

SEASONAL HABITAT SELECTION

*NESTING HABITAT SELECTION*

Sage-grouse females retire into the vicinity of their nest location within a few days of being bred, and remain relatively sedentary until they nest (Patterson 1952). No concealment strategies are attempted at the nest except that afforded by natural cover and the hen's cryptic plumage coloration

pattern (Rassmussen and Griner 1938). Egg laying takes 7 to 10 days, incubation lasts 25 to 29 days, and average clutch sizes are between 6.5 and 9.1 eggs (Patterson 1952, Schroeder et al. 1999). Reproductive effort (nesting propensity) estimates in sage-grouse range from 68 to 93% (Connelly et al. 1993, Schroeder 1997). However, research on follicular development indicates that between 91 and 98% of females breed annually (Braun 1979). The differences may hinge on the nutritional status of pre-laying hens, as a higher nutrient composite diet (sagebrush and forbs) results in increased nesting effort and clutch sizes (Barnett and Crawford 1994). See Table 1 for nesting propensity estimates from throughout Wyoming. Re-nesting rates <25% are typically reported (Patterson 1952, Eng 1963, Hulet 1983, Connelly et al. 1993, Sveum et al. 1998b); however, Schroeder (1997) reported re-nesting rates >80% in Washington. Reduced male lek attendance and infertility (caused by reductions in testis development) are associated with the timing of rebreeding attempts, suggesting that limitations to re-nesting are imposed by the male (Eng 1963). Sage-grouse are relatively long lived tetraonids, thus re-nesting is not necessarily beneficial after weighing the benefits and costs of the increased parental investment in a second clutch (Bergerud 1988).

Sage-grouse nesting habitat is often a broad area between winter and summer range (Klebenow 1969). Average distances between nests and nearest known leks vary from 1.1 to 6.2 km (Autenrieth 1981, Wakkinen et al. 1992, Fischer 1994), but distance from lek of female capture to nest may be >80 km (Lyon 2000). Protection of sage-grouse nesting habitat within 3.2 km of occupied leks has been a standard management recommendation since the 1970s (Braun et al. 1977, Connelly et al. 2000b); however, research in fragmented (Aldridge and Brigham 2001, Schroeder and Robb 2003) and contiguous (Bradbury et al. 1989, Wakkinen et al. 1992) habitats suggest these recommendations may offer limited or unsubstantiated protection to nesting areas. Using data collected throughout Wyoming, Holloran and Anderson (2005) investigated the spatial relationship between lek location and nest distributions. The authors concluded that nest distributions were related to lek location within 5 km of the lek, but cautioned that, because of increased nest success probabilities for dispersing individuals (i.e., females nesting >5 km from a lek), nesting habitats situated beyond the 5 km lek buffer could be important for population viability.

Most sage-grouse nests are located under sagebrush plants (Girard 1937, Patterson 1952, Rothenmaier 1979). In southeastern Idaho, however, Connelly et al. (1991) reported that 21% of sage-grouse hens nested under shrub species (rabbitbrush, snowberry, and bitterbrush) other than sagebrush, but hatching success for non-sagebrush nests was 22% compared to 53% for sagebrush nests. In California, Wyoming big sagebrush and mixed shrub communities were used for nesting in proportion to their availability (Popham and Gutierrez 2003). A congregation of several individual shrubs of

different heights and decadence stages are normally selected as nest sites (Pyrah 1970). To reduce conspicuousness, it is advantageous for sage-grouse hens to choose patches with uniform sagebrush heights and sizes if these plants meet nesting requirements (Wakkinen 1990).

Distances between consecutive-year nests (individual females followed through consecutive nesting seasons) suggest female fidelity to specific nesting areas. Fischer et al. (1993), in Idaho, reported that distances between sage-grouse nests in consecutive years represented 3.5% of median annual movements, suggesting fidelity for specific nesting areas. In Wyoming, the probability that observed consecutive-year nest spacing occurred randomly was between 1.2 and 2.6%, suggesting nesting site-area fidelity for consecutive year nesting females (Holloran and Anderson 2005). Additionally, although sample sizes were low (n = 3), yearling females nested in the same general area as their mother (Lyon 2000), suggesting fidelity for a specific area could carry over to subsequent generations.

Selection of specific habitat features within a landscape by nesting sage-grouse has been extensively documented. Connelly et al. (2000b) suggested that sagebrush nesting habitat should range between 15 and 25% canopy cover. Females preferentially selected areas with sagebrush 36 to >63.5 cm tall and with canopies 15 to >50% for nesting in Utah (Rasmussen and Griner 1938). Rothenmaier (1979) reported that mean sagebrush canopy cover was 21.6% and average sagebrush height was 30.6 cm at nests in southeastern Wyoming. In western Wyoming, 83% of nests were under bushes between 25 and 51 cm tall (average nest bush height 35.6 cm; Patterson 1952). In central Montana, all nests were located in areas with >15% sagebrush canopy cover (Wallestad and Pyrah 1974). And, in northeastern California, sage-grouse avoided low sagebrush for nesting and used big sagebrush and mixed shrub cover in proportion to their availability (Popham 2000).

In southeastern Idaho, nests within a threetip sagebrush vegetation type were found in areas with increased big sagebrush density, basal area of grasses, and threetip sagebrush canopy cover relative to random plots within the same habitat type; overall, total shrub canopy cover was greater at nests relative to random locations (Klebenow 1969). In southeastern Idaho, Wakkinen (1990) reported that nests had taller grasses compared to random locations. Adding a year of data to Wakkinen's (1990) study, Fischer (1994) indicated that nests had increased nest bush total area, increased ground obstructing cover (from 5 m), increased lateral obstructing cover (from 2.5 m), and increased total shrub canopy cover relative to random sites. In southcentral Washington, nests were consistently located in areas with increased shrub cover and taller shrubs compared to randomly-selected sites (Sveum et al. 1998b). The cover of short (<18 cm) grasses and bare ground were consistently lower, and vertical cover height (obstructing cover from 4 m) and litter cover were consistently greater at nests

relative to available sites (Sveum et al. 1998b). Nests were located in areas with taller average sagebrush relative to random plots in central Montana (Wallestad and Pyrah 1974). And, in southern Canada, nests were located in areas with increased sagebrush canopy cover and sagebrush density compared to random locations (Aldridge and Brigham 2002).

Combining vegetation data collected at sage-grouse nest sites from 7 different areas in central and southwestern Wyoming between 1994 and 2002 (studies mentioned below), Holloran et al. (2005) reported that a combination of increased total shrub canopy cover, sagebrush height, and residual grass cover and height were important determinants of sage-grouse selected nesting habitat relative to available nesting habitat. Nests near Casper, Rawlins, Farson, and Jackson, Wyoming had increased total shrub canopy cover relative to available nesting habitats. Live sagebrush heights were taller at nests compared to random locations in Casper, Pinedale, Jackson, and Kemmerer. Additional shrub variable differences reported in Wyoming included increased live sagebrush and dead sagebrush density at nests compared to available habitat. Herbaceous differences at nests relative to random plots included: taller live and residual grasses, increased live and residual grass cover, increased total herbaceous cover, increased non-food forb and total forb cover, and decreased bare ground.

Consistently throughout the range of studied sage-grouse populations, nests were located under larger sagebrush bushes with more obstructing cover relative to within patch characteristics. Selected nesting habitat had more sagebrush canopy cover and taller sagebrush compared to available habitats. Other relatively consistent differences included: increased sagebrush density, taller live and residual grasses, increased live and residual grass cover, and decreased bare ground at selected nesting sites compared to randomly-selected sites (Klebenow 1969, Wallestad and Pyrah 1974, Wakkinen 1990, Fischer 1994, Sveum et al. 1998b, Aldridge and Brigham 2002, Holloran et al. 2005).

*NESTING SUCCESS*

Nesting success in sage-grouse ranges from 15 to 86% (Schroeder et al. 1999); apparent nest success within Wyoming varied from 6 to 79% (Table 1). In Utah, nesting success was highest in areas with sagebrush >46 cm tall, with canopies >50%, and "where a good understory of grasses and weeds were present;" the presence of a good herbaceous understory interspersed throughout sagebrush stands increased the probability of a successful hatch relative to sagebrush stands of equal density without the understory (Rasmussen and Griner 1938). Sagebrush canopy cover was greater at successful vs. unsuccessful sage-grouse nests in Montana (Wallestad and Pyrah 1974). Sveum et al. (1998b) reported that successful nests in Washington had increased residual herbaceous cover compared to unsuccessful nests. In Oregon, tall (>18 cm) residual grass cover and medium height (40 to 80 cm) shrub cover were

greater at successful vs. unsuccessful nests (Crawford et al. 1992, Gregg et al. 1994), and a combination of shrub and herbaceous screening cover were important for nest success in Idaho (Connelly et al. 1991). Successful nests in southern Canada had taller grasses, taller palatable forbs, and decreased grass cover relative to unsuccessful nests (Aldridge and Brigham 2002). In California, percent rock cover, total shrub height, and visual obstruction were greater at successful than unsuccessful nest sites (Popham 2000). Hausleitner (2003) reported that successful nests in northwestern Colorado had increased average forb and grass cover and taller grasses compared to unsuccessful nests.

Successful artificial sage-grouse nests consistently (variable included in ≥2 logistic regression models) had more forb and total sagebrush canopy cover, taller grasses, and decreased numbers of sagebrush plants within 0.5 m compared to unsuccessful artificial nests (Watters et al. 2002). DeLong et al. (1995) reported that a combination of greater amounts of tall (>18 cm) grass and medium height (40 to 80 cm) shrub cover at artificial sage-grouse nests in southeastern Oregon increased the probability of success.

Heath et al. (1996) maintained that the chance of a sagebrush nest successfully hatching will increase 30% if it is within herbaceous vegetation exhibiting 20% canopy cover and heights of 15 to 30 cm. The residual herbaceous component is important during the initial stages of incubation because nests are initiated prior to the growing season for most grasses and forbs (Crawford et al. 1992, Heath et al. 1996).

Barnett and Crawford (1994) suggest that consumption of forbs during the pre-laying period may affect reproductive success by improving nutritional status of hens. Braun (1981) reported that less than 50% of yearling hens were successful, whereas at least 50% of the adult hens were successful in Colorado, and adult hens in Montana experienced higher nest success than yearlings (Wallestad and Pyrah 1974). However, no significant differences in nest success between different age groups were reported in Idaho and Washington (Connelly et al. 1993, Schroeder 1997).

Batterson and Morse (1948), after extensive nest studies concluded that "the greatest single limiting factor of sage-grouse is nest predation by ravens (*Corvus corax*);" 51% nest success was realized on raven control areas compared to 6% on uncontrolled areas. Conversely, Patterson (1952) reported that 42% of sage-grouse nest predation in Wyoming was due to Richardson's and thirteen-lined ground squirrels (*Spermophilus* spp.). Interestingly, the percentage of bird and eggshell fragments in most coyote (*Canis latrans*) prey base studies ranges from 2 to 5%, suggesting minimal impact (Johnson and Hansen 1979, Reichel 1991, Heath et al. 1996). Common ravens, black-billed magpies (*Pica pica*), ground squirrels, red foxes (*Vulpes vulpes*) and badgers (*Taxidea taxus*) are reported as

predominant sage-grouse nest predators (Patterson 1952, Autenrieth 1981, Connelly et al. 1991, Heath et al. 1996).

Data from 7 different areas in central, western, and southwestern Wyoming combined suggested that a combination of increased residual grass cover and height were the best determinants of successful compared to unsuccessful sage-grouse nests (Holloran et al. 2005). Successful nests had taller residual grasses, and increased residual grass and forb cover relative to unsuccessful nests near Farson, Wyoming. In Casper, food-forb cover tended to be higher at successful nests relative to unsuccessful nests. Nests destroyed by avian predators near Kemmerer, Wyoming consistently had decreased overhead cover (live sagebrush and total shrub canopy cover) and increased lateral cover (herbaceous cover and height) relative to nests in general and mammalian destroyed nests. Successful nests in Jackson had increased live and residual grass height and residual grass cover compared to unsuccessful nests.

Vegetation consistently higher at successful compared to unsuccessful sage-grouse nests throughout the range of studied populations included: live and residual grass height, residual vegetative cover, forb cover and visual obstruction (Wakkinen 1990, Gregg et al. 1994, Sveum et al. 1998b, Popham 2000, Aldridge and Brigham 2002, Hausleitner 2003, Holloran et al. 2005). These observations suggest that sage-grouse nesting success is influenced predominantly by the herbaceous understory; this conclusion, given that sage-grouse nesting success varies annually (Connelly et al. 2000b) while the sagebrush overstory does not change dramatically between years, seems sensible.

*EARLY BROOD-REARING HABITAT SELECTION and SUCCESS*

I consider early brood-rearing the time broods remain within the sagebrush dominated uplands associated with nesting locations; the amount of time broods spend in these habitats varies annually and throughout the range of the species. A key factor associated with sage-grouse productivity is brood-rearing habitat availability (Crawford et al. 1992). Low chick recruitment has been proposed as a factor limiting sage-grouse population stability (Connelly and Braun 1997), and most chick mortality occurs prior to the flight stage (2 to 3 weeks) when decreased mobility increases vulnerability to predation and starvation (Patterson 1952, Autenrieth 1981). Sage-grouse chicks require protein-rich foods, including insects and forbs, for survival (1 to 10 days post-hatch) and optimal development (10 to 45 days post-hatch; Johnson and Boyce 1990). Sage-grouse productivity in Oregon was higher in areas where chick diets consisted of 80% forbs and insects compared to where chicks ate primarily (65%) sagebrush (Drut et al. 1994a).

Sage-grouse chicks are precocial and move immediately following hatch to search for food (Patterson 1952); early brood-rearing areas occur in upland sagebrush habitats relatively close to nest sites (Connelly 1982, Berry and Eng 1985). Early brood-rearing areas (between 2 weeks post-hatch and prior to July 8) were located between 1.6 and 3.2 km of the nest near Rawlins (Heath et al. 1998), and between 0.2 and 5.0 km of the nest during the first 4 weeks post-hatch near Pinedale, Wyoming (Lyon 2000). In Kemmerer, 80% of early brood locations were within 1.5 km of the nest (Slater 2003). During June and July in central Montana, brood use areas averaged 86 ha and there were no apparent movements that indicated a daily use of free water (Wallestad 1971).

Brood-use sites within big sagebrush dominated habitat type in southeastern Idaho had decreased big sagebrush density and canopy cover, and increased percent frequency of yarrow (*Achillea lanulosa*), lupine (*Lupinus caudatus*), dandelion (*Taraxacum officinale*) and salsify (*Tragopogon dubius*) compared to random locations within the same habitat type (mean brood ages between 1 to 8 weeks; Klebenow 1969). Conversely, early brood-rearing (hatch through 7 weeks) locations had increased sagebrush cover compared to random locations in southern Canada (Aldridge and Brigham 2002). Total forb and food forb cover were higher, and residual herbaceous cover and height were lower at early brooding areas relative to random locations in south-central Washington (Sveum et al. 1998a).

Dead sagebrush density was higher at early brood-rearing (habitat use prior to July 8) compared to random locations near Farson, Wyoming. Near Rawlins, early brood use areas had increased sagebrush height, increased live grass and total herbaceous cover, and decreased effective vegetation height (Robel pole read from 10m) compared to random locations. A combination of increased residual grass and total forb cover, and decreased effective vegetation height were the best predictors of selected early brood-rearing (between 2 and 4 weeks post-hatch) compared to available habitats near Casper. Early brood-rearing locations had decreased live sagebrush and total shrub canopy cover, increased residual grass and total herbaceous cover, and food-forb cover tended to be higher, relative to available habitats. Near Pinedale, early brood-rearing (through 4 weeks post-hatch) locations had decreased live sagebrush density, live sagebrush and total shrub canopy cover, and bare ground and increased total herbaceous cover compared to available habitat. And, in Jackson, brooding females (hatch through 2 weeks post-hatch) selected areas with increased total shrub canopy cover and sagebrush height, food forb cover and forb diversity, and decreased live and residual grass cover. Chick survival during brooding stages in Wyoming is presented in Table 1.

Thompson et al. (*in review*) combined early brood-rearing (hatch through 2 weeks post-hatch) data collected from 3 sites in central and southwestern Wyoming between 1999 and 2003, and found

that during the early brood-rearing period, broods used sites within or near dense (average 20% canopy cover) sagebrush cover, and increased productivity was positively associated with abundance of insects and herbaceous cover. Females with broods were found in areas with greater sagebrush canopy and grass cover, but lower numbers of invertebrates compared to random areas. However, the number of juveniles per female (estimated from wing barrel collections during fall harvest) was positively associated with the abundance of Hymenoptera and grass cover, and the proportion of females with confirmed chicks 14 days post-hatch was positively related to Coleoptera abundance and total herbaceous cover.

*LATE BROOD-REARING HABITAT SELECTION and SUCCESS*

Sage-grouse broods remain in sagebrush habitats until range desiccation induces them to move to riparian habitats still supporting succulent vegetation (Peterson 1970, Wallestad 1971, Neel 1980, Fisher et al. 1997). However, brooding females may remain in upland habitats if suitable microsite conditions (i.e., swales, ditches, springs) are found (Wallestad 1971). Stand structure and food availability are characteristics most frequently associated with habitat selection by brooding hens during the summer (Klebenow 1969, Autenrieth 1981, Aldridge and Brigham 2002). Chick diets during the summer consist of primarily forbs and insects (Klebenow and Grey 1968, Drut et al. 1994b), while sagebrush stands provide escape and thermal cover (Peterson 1970, Wallestad 1971, Crawford et al. 1992).

Open water has been suggested as a limiting factor for summering sage-grouse. Autenrieth et al. (1982) inferred that water was important to sage-grouse, and Patterson (1952) suggested that water markedly affected the species' summer distribution. However, movements to agricultural lands or high elevation summer range are probably in response to lack of succulent forbs in an area rather then a lack of free water (Connelly and Doughty 1989). It has been suggested that grouse do not commonly use water developments even during relatively dry years, but instead obtain moisture from consuming succulent vegetation (Connelly 1982, Connelly and Doughty 1989). Moreover, water developments tend to attract other animals and thus may serve as a predator "sink" for grouse (Connelly and Doughty 1989). Free water reservoirs can, however, provide islands of succulent vegetation (Wallestad 1971) and this use of water developments may be enhanced by placing them along migration routes or close to summer range (Connelly and Doughty 1989).

In Farson, Wyoming, visual obstruction (from 10 m), food forb, total forb, and litter cover were higher, and grass cover was lower at selected late brood-rearing locations compared to available summering habitats (i.e., areas potentially suitable for summering grouse, or areas with succulent

herbaceous vegetation throughout the summer). Near Casper, brooding females selected areas with increased food forb cover and decreased residual grass cover relative to available summering areas. Late-brooding females in the Pinedale area selected locations with increased total shrub canopy cover, and in Jackson, used summer habitats were in areas with proportionally increased food forb cover (relative to total cover) compared to available summering habitats. No differences were detected between used and available late brooding locations near Rawlins.

In areas where riparian habitats were limiting, drought conditions concentrated birds, resulting in increased predation rates and increased adult hen fall mortality. Fall mortality was caused by hunting and predation, the majority of which occurred during September. In 1994, 62% of the annual mortality occurred during September, presumably because drought conditions concentrated birds on riparian areas. Results from Casper in 1998 and Pinedale in 2004 indicated that sage-grouse preferred to remain within sagebrush dominated habitats throughout the summer, and resorted to concentrating on riparian corridors only after upland forb desiccation. This information suggests that riparian area (and associated succulent vegetation) distribution and extent could be important to sage-grouse survival.

*WINTER HABITAT SELECTION*

Sage-grouse may travel many kilometers or only short distances between seasonal ranges (Eng and Schladweiler 1972); migratory populations often travel 80 to 160 km (50 to 100 miles) to winter ranges (Patterson 1952), while sedentary populations merely increase flock size and move from meadows into sagebrush during the winter (Autenrieth 1981). A precipitation event (usually snow) or a drop in the temperature initiates migration, which begins in late August (in advance of snow accumulation) and continues until December (Dalke et al. 1960, Berry and Eng 1985, Connelly et al. 1988). Winter habitat is probably the most limiting seasonal habitat (Patterson 1952, Beck 1977), with sage-grouse over a broad summering area congregating on smaller, traditional wintering grounds (Beck 1977, Berry and Eng 1985).

Selection of wintering habitats by sage-grouse is influenced by snow depth and hardness, topography (i.e., elevation, slope, and aspect), and vegetation height and density (Batterson and Morse 1948, Gill 1965, Greer 1990, Schroeder et al. 1999). The primary requirement of wintering sage-grouse is sagebrush exposure above the snow (Patterson 1952, Hupp and Braun 1989, Schroeder et al. 1999, Connelly et al. 2000b, Crawford et al. 2004). During the winter, sage-grouse could be restricted to <10% of the sagebrush dominated lands in any given area (Beck 1977). Sage-grouse populations will utilize critical winter habitat once every 8 to 10 years, these locations providing food and thermal protection when increased snow pack has covered most surrounding areas (Heath et al. 1996). Winter

ranges are characterized by large expanses of dense sagebrush (>20% sagebrush canopy cover) on land with south to west-facing slopes of <5% gradient (Eng and Schladweiler 1972, Beck 1977). Robertson (1991) reported that sage-grouse in Idaho selected areas with increased Wyoming big sagebrush canopy cover and average height compared to available habitats during the winter.

During severe winters, flat area usage diminishes after snow pack exceeds 30 cm, and drainages and steeper southwest facing slopes are used (Autenrieth 1981, Hupp and Braun 1989). Drainages are sheltered from the wind and contain taller sagebrush stands, snow drifts (used for roosting to escape extreme cold), and closed shrub canopies, which combined provide food and reduce thermoregulatory costs (Hupp and Braun 1989, Homer et al. 1993, Heath et al. 1996). Because sagebrush exposure is critical for feeding, wind scoured ridge-tops provide suitable foraging areas until wind velocities exceeding 15 to 25 kph force grouse off these areas (Eng and Schladweiler 1972, Beck 1977). Sage-grouse distribution during the winter is primarily a reflection of sagebrush exposure and topographic categories (slope and aspect).

Sage-grouse feed during almost all weather conditions and subsist on a diet consisting solely of sagebrush during the winter (Patterson 1952, Beck 1977). Remington and Braun (1985) contend that sage-grouse selectively feed on Wyoming big sagebrush due to its relatively high crude protein (nitrogen) content and reduced monoterpene levels compared to other big sagebrush sub-species. But, Welch et al. (1991), comparing food selection by captured wild birds, found that sage-grouse prefer mountain big sagebrush. However, because of the high elevation requirements for mountain big sagebrush growth, this shrub is typically covered by snow during the winter, and not available. Sage-grouse express preference while selecting both foraging plants and sites, but are capable of shifting their eating habits when either sagebrush quantity or quality becomes limiting (Remington and Braun 1985, Welch et al. 1991). Again, sage-grouse distribution is affected by sagebrush exposure rather than differences in nutritional quality of forage (Hupp and Braun 1989).

In Wyoming, the Jackson area has the best possibility of sage-grouse limiting winter habitats; based on the correlation between winter precipitation and changes in the number of males occupying leks, winter habitat could be limiting this population. In Jackson, sage-grouse selected areas with increased sagebrush canopy cover and height, and decreased sagebrush density relative to available sagebrush dominated areas. Additionally, 89% of wintering locations were on southern or western aspects, and 98% of the selected winter sites were on slopes <10%.

SEASONAL ADULT SURVIVAL

Zablan et al. (2003), using band-recovery data from over 6,000 banding individuals in Colorado, estimated 59% annual survival for adult females, 78% for yearling females, 37% for adult males, and 63% for yearling males. In Wyoming, 67% annual survival for females and 59% for males was estimated from over 3,000 banded individuals (Schroeder et al. 1999 after June 1963). Moynahan (2004) investigated factors influencing monthly survival of female sage-grouse in Montana, and reported that breeding status (nesting or non-nesting), environmental condition, and exposure to hunting resulted in variable seasonal survival probabilities. Environmentally, severe winter weather (heavy snow and extreme cold) and the emergence of West Nile virus (Naugle et al. 2004) reduced sage-grouse survival during an annual winter and fall period, respectively, whereas drought conditions (throughout the year) resulted in increased annual survival (Moynahan 2004).

In Farson, survival from April through October (period length due to battery life of radio-transmitters) varied seasonally and annually; survival ranged from 50% to 80%. During the Farson study, 49% of the females that nested successfully survived from May through October, with 60% of the mortalities occurring in September; only 22% of brooding females survived September 1994. Heath et al. (1997) suggested that drought conditions during 1994 resulted in birds concentrating on limited available summering habitat, facilitating prey search for both hunters and natural predators. Regardless, because of the apparent susceptibility of brooding females during an early September hunting season (although harvest was not identified specifically as the primary source of mortality), the Wyoming Game and Fish Department shifted the sage-grouse season opener from September 1 to the 2$^{nd}$ weekend in the month throughout Wyoming in 1995.

Female sage-grouse survival from April to October in Rawlins averaged 73%, with no apparent seasonal variability. In Jackson, female summer (April through August) and winter (September through March) survival averaged 88% and 83% respectively; however, the Jackson study was conducted during 4 years of below normal winter precipitation. Changes in long-term lek counts correlated well with winter precipitation levels, suggesting that reported winter survival probabilities were higher than typically experienced in the Jackson Hole area. Seasonal survival in Lander ranged from 69 to 94%, with the lowest survival occurring during April through June (average 79%). However, there was no apparent variability in spring survival during breeding (April 81%), nesting (May 86%), or brooding (June 83%) periods. Female annual survival (April through March) in Kemmerer ranged from 54 to 80%; the greatest proportion of mortalities occurred during April and September.

LIVESTOCK GRAZING

Livestock grazing and its potential effect on sagebrush-dominated ecosystems is one of the most contentious and argued issues underlying the management and use of these habitats (Connelly et al. 2004). Domestic livestock have grazed over most sage-grouse occupied habitats, and this use is typically repetitive with annual or biennial grazing periods of varying timing and length (Braun 1998). Scientific evidence suggests that livestock grazing did not increase sagebrush distributions (Peterson 1995), but reduced the herbaceous understory and increased sagebrush densities (Vale 1975, Tisdale and Hironaka 1981). Some argue that sagebrush steppe ecosystems within the intermountain west (and their associated plant communities) did not evolve with heavy wild ungulate grazing as did the grasslands of central North America, and conclude historic and present livestock utilization has probably resulted in vegetative changes (Mack and Thompson 1982, Miller et al. 1994) and declines in species richness (Reynolds and Trost 1980). Part of this reasoning is that grazing by large ungulates results in the permanent loss of cryptogamic crusts (non-vascular plants of algae, lichens, mosses and diatoms; Pieper 1994) through trampling (Mack and Thompson 1982). Mack and Thompson (1982) maintain that if the crusts represent a component in the evolutionary process of plant establishment throughout the intermountain west, than large ungulates could not have been present, even at low densities.

However, paleoecological records support that the intermountain west evolved with large ungulate grazing (Burkhardt 1995). At the time of the Pleistocene Ice Age (2.5 million years ago), the flora was essentially the same as modern flora, including sagebrush, grass and forb species (as indicated by pollen core samples; Tidewell et al. 1972, Barnosky et al. 1987). There is evidence to support abundant, widespread bison herds within the intermountain west prior to the 1800s (Schroedl 1973, Agenbroad 1978, Butler 1978), and that there was an ecological void (relatively small numbers of large ungulates) when the first Europeans arrived in the area (Burkhardt 1995). Savory (1988) argues that historic movement and grazing patterns were different from recent patterns due to predator influences resulting in tightly packed ungulate herds (a theory supported in part by changes in elk movement patterns when wolves were reintroduced into Yellowstone National Park).

Johnson (1987), comparing 56 photographs taken in Wyoming in 1870 with present day photographs, reported that the ecological change has been relatively small, and the overall impression was one of stability (as cited in Bennett 1992). Additionally, a study examining the vegetative differences between grazed and exclosed plots (excluded from grazing for 31 years, on average) throughout the intermountain west found no landscape scale differences in: (1) native or exotic species richness, (2) species diversity, (3) species evenness, and (4) cover of grasses, forbs, and shrubs

(Stohlgren et al. 1999). However, Pieper (1994) maintains that removing livestock from rangelands grazed from the early 1900's is unlikely to return ecosystems to their pristine conditions; and Connelly et al. (2004) contend that our previous history of livestock grazing has influenced soils and plant composition which continue to influence current patterns and processes.

There is little scientific data linking grazing practices to sage-grouse population levels (Connelly and Braun 1997). However, comparing sage-grouse seasonal habitat requirements (outlined above) to studies investigating the response of the habitat to livestock grazing can provide suggestions. Short-term rotational grazing patterns (vs. continuous grazing patterns) benefit native grass and forb production (Derner et al. 1994), which are key habitat features associated with hatching success and hen pre-laying nutrition. However, heavy spring and spring-fall grazing are detrimental to upland herbaceous understories essential for sage-grouse nesting success, whereas fall utilization is neither detrimental nor advantageous (Mueggler 1950, Laycock 1979, Owens and Norton 1990). Insect diversity and density are positively correlated with herbaceous density and diversity (Hull et al. 1996, Jamison et al. 2002), thus spring or spring-fall grazing could also negatively impact young chick survival. Stocking rate appears to be the variable impacting residual grass stubble height (important during the initial stages of nest incubation), with high stocking rates reducing heights (Owens and Norton 1990, Derner et al. 1994). Conversely, spring grazing at high stocking rates is potentially beneficial on sage-grouse winter range, while heavy fall utilization is detrimental (because of differing impacts to sagebrush densities; Wright 1970, Owens and Norton 1990, Angell 1997). Holloran et al. (2005) reported that reducing the amount of residual grass in sagebrush habitats could negatively impact the quantity and quality of sage-grouse nesting habitat, and suggested annual grazing in nesting habitat, regardless of the timing, could negatively impact the following year's nesting success. The importance of annual and seasonal range monitoring and subsequent removal of livestock as utilization reaches capacity cannot be over-emphasized (Holechek 1996, Thurow and Taylor 1999).

Livestock distribution patterns (which are directly linked with water availability) and impacts to riparian habitats primarily influence sage-grouse late brood-rearing and summering habitats. The transition zones or ecotones between types (upland sagebrush and wet meadow) provide food forbs with associated protective cover and are important areas for sage-grouse broods (Klebenow 1982). However, meadows that are heavily invaded by sagebrush and heavy vegetation on ungrazed meadows are not utilized by sage-grouse (Oakleaf 1971, Klebenow 1982). High stocking rates in areas with limited water resource availability are detrimental to forage productivity surrounding water sources (Hall and Bryant 1995, Dobkin et al. 1998). Summer grazing on riparian habitats also appears to concentrate livestock on riparian corridors, resulting in decreased low vegetative growth (typically the

forb communities essential in sage-grouse summer diets) and the extent of the hyporheic zone (reducing the lateral extent of succulent vegetation associated with the riparian corridor). However, sage-grouse use grazed instead of ungrazed meadows where protective cover conditions are otherwise equal (Neel 1980). Grazing increases the quality of the forb resource (by interrupting and delaying maturation) and increases accessibility to low-growing food forbs (by producing patchy small openings) sought by sage-grouse (Neel 1980, Evans 1996). Bryant (1982) suggests that stocking pastures containing riparian zones with cow/calf pairs (vs. yearlings) during the cooler part of the grazing season will decrease adverse livestock impacts to the riparian habitats. Additionally, Neel (1980) maintains that rest-rotation grazing can beneficially impact sage-grouse summering habitat if moderate stocking levels are maintained, and rest is afforded a given meadow every 3 years.

The Lander, Wyoming study was primarily focused on the potential effects of livestock grazing management practices on sage-grouse productivity (Kuipers 2004). The study suggested that reduced forage utilization, extended periods of rest, and reduced spring grazing could provide conditions suitable for sage-grouse nesting and early brooding during periods of extensive drought (precipitation 68% of normal during study). Grazing system (based on rotation period) appeared to be less important than stocking rates and season of use. Herbaceous cover and height estimates were consistently lower in livestock grazed relative to non-grazed pastures; residual and live grass height and cover and forb cover were lower in deferred (essentially season long grazing) compared to rotation systems, and grass and forb cover were lower in spring – fall grazed compared to summer grazed rotation systems. Interestingly, bare ground doubled during the time of the study in pastures grazed season long. Shrub components did not appear to be influenced by grazing system. Kuipers (2004) concluded that pastures grazed during the summer and the non-grazed control pastures best mimicked suitable sage-grouse nesting and early brood-rearing habitat during an extensive drought.

The Rawlins study compared 3 ranches with differing grazing management schemes; a non-grazed control was not available for this study (Heath et al. 1998). Live grass height appeared to be least impacted by rotating cattle after 30 instead of 40% forage utilization. Average live and residual grass heights were shorter on the sheep and cattle ranch with >50% utilization compared to the cattle only ranches with <40% utilization. Shrub and herbaceous cover variables did not differ between ranches. Heath et al. (1998) concluded that ranches where the only grazing management difference was 30 compared to 40% forage utilization did not differ in terms of nesting and early brood-rearing habitat condition, but that >50% utilization reduced nesting and brooding habitat quality.

SAGEBRUSH MANIPULATION

The current consensus (although highly speculative) is that historic sagebrush-steppe ecosystems were a mosaic of successional shrub age classes created and maintained by fire regimes ranging in frequency from 10-110 years (Klebenow 1972, Wright et al. 1979, Winward 1991). Selective (patchy) fires appear to have been normal in most sagebrush shrublands, while larger fires at lower frequencies occurred in other areas, depending on the climate, topography, plant composition, and aridity of the site (Paige and Ritter 1999). However, after a review of the ecological literature pertaining to sagebrush ecosystems, Tisdale and Hironaka (1981) concluded that because most sagebrush species are sensitive to fire and that early explorers found sagebrush abundant throughout the region, fire must have been historically infrequent.

During most of the 20$^{th}$ century, the sagebrush habitat management consent was that fire should be used to control shrubs (sagebrush) to increase productivity, nutritional quality, and forage availability for livestock (Harniss and Murray 1973, Bunting 1989). Presently, the landscape goal for sagebrush systems in Wyoming is to promote a mosaic of shrub age classes and canopy covers across large, contiguous stands; prescribed fire has been identified as a management option to accomplish this goal (Kilpatrick 2000, Wyoming Interagency Vegetation Committee 2002). However, Lommasson (1948), after studying sagebrush stands for 31 years (1915-45) in Montana, concluded that sagebrush will continue to reproduce and maintain itself indefinitely under natural conditions; over time, sites favorable for sagebrush growth will eventually become (and be maintained in) a multi-aged stand.

Burning results in the greatest reduction of sagebrush cover and has the most protracted effect on sagebrush when compared to other treatments (Watts and Wambolt 1996). Since most species of big sagebrush can only recover by seed, burning significantly lengthens the time required for re-establishment (Vale 1974, Braun 1987). Recovery from a burn to a 20% sagebrush canopy exceeds 35-40 years in Wyoming big sagebrush habitat types, 25 years in basin big sagebrush types, and 15-25 years in mountain big sagebrush sites (Harniss and Murray 1973, Wright and Bailey 1982, Bunting et al. 1987, Winward 1991, Watts and Wambolt 1996). Additionally, Watts and Wambolt (1996) reported that Wyoming big sagebrush canopy cover had reestablished at levels below original levels 30 years post-burn, which indicates that historic wildfires had to have been infrequent for current sagebrush canopies (in untreated sagebrush) to be maintained. Although sagebrush in a burn in Idaho was approaching pre-burn density 30 years post-burn, the majority of the plants in the burned plots were less than 6 inches tall (Harniss and Murray 1973), indicating that the plant community was far from a climax community. However, these fire recovery intervals were estimated from plant recovery evidence. Combining fire-scar data with these recovery estimates, Baker (*in press*) reported that the

best available estimates of fire rotation (i.e., the average interval in which fire would impact each point in a landscape) are 100 to 240 years in Wyoming big sagebrush and 70 to 200 years in mountain big sagebrush. The author went on to conclude that fire suppression likely has had little effect in most sagebrush communities, and that the reintroduction of fire into these systems is currently not a restoration need (Baker *in press*).

The overall effect of sagebrush treatments on sage-grouse populations is largely dependent on the vegetative response, the status of the population, and the type of habitat treated. Increasing sage-grouse populations and populations below their potential carrying capacity do not appear to be adversely affected by the treatment of sagebrush (Wallestad 1975, Martin 1990). However, neither do they show a positive response through an increase in relative abundance (Wallestad 1975, Martin 1990, Fischer et al. 1996). In contrast, Connelly et al. (1994) found that a declining population declined to a much greater extent in treated areas relative to untreated areas. Destruction of wintering and nesting habitat is believed to have the greatest potential to reduce the total capacity of an area to support a sage-grouse population (Wallestad 1975, Connelly and Braun 1997).

Relatively large treatment areas typically result in sage-grouse declines (Klebenow 1970). A >20% sagebrush crown reduction on >350 ha treatment blocks caused a reduction in the number of cocks on adjacent strutting grounds in Montana (Martin 1970, Wallestad 1975). Connelly et al. (2000a) reported that the negative effects of a 57% sagebrush crown removal project on a sage-grouse breeding population (estimated by lek counts) included: (1) increased loss of leks; (2) increased decline in average cock lek attendance; and (3) increased decline in the mean number of cocks per lek when comparing treatment to control areas in Idaho (findings applicable to low precipitation zones dominated by Wyoming big sagebrush). In Montana, sage-grouse use of a treatment area (2,4-D spray strips) was restricted almost exclusively to remnant sagebrush patches (Martin 1970). And, the loss of a relatively large portion of wintering sagebrush dominated habitat to plowing resulted in a substantial decline (73%) in the number of strutting male sage-grouse on adjacent leks in Montana (Swenson et al. 1987).

There is almost no justification for removing sagebrush in areas where winter cover for sage-grouse is limited (Klebenow 1972). Sagebrush removal on winter range can significantly reduce the availability of tall sagebrush that provides critical cover and food, especially during severe winters (Schneegas 1967, Robertson 1991). In Idaho, the removal of 60% of the sagebrush cover (in a mosaic pattern) resulted in a significant decline in the use of these sites for winter range (34 and 42% of locations pre- versus 6% post-burn; Connelly et al. 1994).

There is disagreement regarding the result of sagebrush removal on the breeding activities of sage-grouse. Some researchers have reported a significant decrease in lek attendance by cocks

(Wallestad 1975, Connelly et al. 1994), whereas others have found no clear effect (Gates 1983, Martin 1990, Benson et al. 1991, Fischer 1994). Shrub removal reduced the availability of cover surrounding leks (breeding adults avoided manipulated areas for feeding, loafing, and roosting; Martin 1990), and birds migrated from altered breeding grounds earlier than normal in Idaho (Fischer et al. 1997). However, in areas with limited suitable lekking grounds, sagebrush removal could be an effective tool to create open areas for breeding, provided there is sagebrush nearby for escape and feeding (Dalke et al. 1960, Connelly et al. 1981, Phillips et al. 1986).

Nesting habitat is especially susceptible to burning because of relatively high fuel loads characteristic of this habitat (Connelly et al. 1994). Sage-grouse restrict their nesting use of manipulated areas to remaining patches of live sagebrush (Connelly et al. 1994, Fischer 1994). Although some research has found similar nesting densities and success between burned and unburned areas (Klebenow 1970, Fischer 1994), large reductions in the amount of available nesting habitat will reduce the capacity of an area, and result in the clustering of nests within the remaining sagebrush patches and increasing predatory pressure (Niemuth and Boyce 1995). In addition, coyotes (*Canis latrans*) are reportedly able to increase following sagebrush treatment (Wright 1974), and habitat fragmentation and the creation of edges may reduce the difficulty of foraging by predators (Burger et al. 1994, Braun 1998). However, lower nest predation rates may occur in recovering treated sagebrush as the sagebrush treatment reduces the long-term density of larger mammalian prey (rabbits; *Lepus* and *Sylvilagus* spp. and ground squirrels; *Spermophilus* spp.) and subsequently reduces predator densities (Ritchie et al. 1994).

The inability of sagebrush removal treatments to consistently increase forbs or insects limits their utility as a tool for sage-grouse brood-rearing habitat management (Gates 1983, Martin 1990, Connelly et al. 1994, Nelle 1998). Klebenow (1970) reported that broods did not use treated areas for 2 years post-treatment. Additionally, Connelly et al. (1994) reported that the abundance and biomass of ants was reduced the 2$^{nd}$ and 3$^{rd}$ years post-treatment in southeastern Idaho (Fischer et al. 1996); grasshopper densities were reduced by 60% the first year after a prescribed burn in Arizona (Bock and Bock 1991); and 6 years after a big sagebrush wildfire in southeastern Washington, half of the ground dwelling beetle species were less abundant on burned sites, and overall beetle abundance was reduced by 20% (Rickard 1970). In contrast, the abundance of ants and beetles on the Upper Snake River Plain in Idaho was significantly greater in a 1-year old burn, but had returned to unburned levels 3 to 5 years post-burn (Nelle et al. 2000).

Relative to unburned control sites, burning in sagebrush habitats near Kemmerer, Wyoming, resulted in reduced sagebrush and total shrub cover, increased common burn shrub (i.e., rabbitbrush in

particular) cover, and did not stimulate herbaceous production during drought conditions (precipitation 50% of normal during study; Slater 2003). However, sage-grouse did not avoid burned habitats for nesting providing that adequate structural cover (shrub overstory cover) within the burns existed, and nesting within burned areas (relative to outside burns) did not negatively influence the probability of a successful hatch. Although burning did not improve relative (to non-burned habitats) forb or herbaceous cover or insect numbers, females nesting within a burn moved shorter distances from nests to early brooding sites, suggesting that burning created areas attractive for brood-rearing. General grouse burn-use observations (throughout spring and summer periods) suggested birds feed and loaf in both burned and unburned portions of the burns, with locations concentrated relatively close (within 60 m) to the interface between these two habitats. Slater (2003) concluded by cautioning that drought likely played a significant role in shaping the findings reported in the study, and that low nest success (average 24% during study) and productivity (average 0.3 chicks fledged in August per female), although probably impacted by the drought, suggested that burning could influence sage-grouse beyond the spatial scale of the burn itself.

MINERAL EXTRACTION ACTIVITIES

The magnitude of energy development impacts on wildlife resources throughout North America is relatively unknown. Generally, gregarious species (i.e., sage-grouse during the breeding season) are more severely affected by a disturbance than are solitary species, and hunted species will exhibit a greater avoidance of road-related disturbances than will their unhunted conspecifics (PRISM Environmental Management Consultants 1982). Potential impacts of mineral extraction development to sage-grouse include: (1) direct habitat loss from well, road, pipeline, and transmission line construction, (2) the replacement of mature plant and animal communities with lower successional stages of plants and associated fauna, (3) increased human activity causing avoidance and displacement, (4) pumping noise causing displacement and reducing breeding efficiency, (5) increased legal and illegal harvest (it has been estimated that game violations increase by 3 times in remote areas undergoing intensive development; Bay 1989), (6) direct mortality associated with evaporation ponds and associated diseases (Naugle et al. 2004), and (7) reduced water tables resulting in herbaceous vegetation loss (USDI BLM 1979, Schoenburg and Braun 1982, Braun 1986, Braun 1987, TRC Mariah Associates Inc. 1997, Connelly et al. 2004). Sage-grouse leks within 0.4 km of coalbed methane (CBM) wells in northern Wyoming had significantly fewer males per lek and lower annual rates of population growth compared to leks situated >0.4 km from a CBM well (Braun et al. 2002). The extirpation of 3 lek complexes within 0.2 km of oil field infrastructure in Alberta, Canada, was

associated with the arrival of oil field-related disturbance sources (Braun et al. 2002, Aldridge and Brigham 2003). Additionally, the number of displaying males on 2 leks within 2 km of active coal mines in northern Colorado declined by approximately 94% over a 5-year period following an increase in mining activity (Braun 1986, Remington and Braun 1991).

Roads constructed for mineral exploration and production may result in the development of permanent travel routes, improved public access, increased long-term traffic related disturbance to previously inaccessible regions, indirect noise impacts (to leks ≤1 km from the road; Braun 1998), and direct mortality (USDI BLM 1979, PRISM Environmental Management Consultants 1982, Braun 1998). Generally, road effect-distances (the distance from a road at which a population density decrease is detected) are positively correlated with increased traffic density and speed, and are more severe in years when wildlife population sizes are low (Forman and Alexander 1998). However, Ingelfinger (2001), studying the potential effects of road disturbance on sagebrush steppe passerines along the Pinedale Anticline, reported that sagebrush obligate bird densities were reduced within 100 m of a road, regardless of traffic volumes. The author suggested that habitat edge avoidance or changes in passerine species composition along the roads (i.e., increased horned lark abundance) explained sagebrush obligate declines (Ingelfinger 2001). The upgrade of haul roads associated with surface coal mining activity in North Park, Colorado resulted in one sage-grouse lek (50 m from a road) becoming inactive, and an 83% reduction in the number of displaying cocks on another lek (500 m from a road) within 3 years post-upgrade (Braun 1986, Remington and Braun 1991). Additionally, patch occupancy probabilities of Gunnison sage-grouse (*Centrocercus minimus*) in Colorado were positively correlated with distance to roads, suggesting avoidance (Oyler-McCance 1999).

Although transmission line construction does not cause direct habitat loss, sage-grouse avoidance of vertical structure, due to altered raptor distributions and raptor species composition within relatively flat landscapes, results in habitat exclusion (≤1 km wide band centered on power lines; USDI BLM 1979, Braun 1998). The construction of transmission line structures located within 200 m of an active sage-grouse lek and between the lek and cock day use areas in northeastern Utah resulted in a 72% decline in the mean number of strutting cocks and an alteration in daily dispersal patterns during the breeding season within 2 years (Ellis 1985). The frequency of raptor-sage-grouse interactions during the breeding season increased 65%, and golden eagle (*Aquila chrysaetos*) interactions increased 47% between pre- and post-transmission line construction (Ellis 1985). Transmission lines constructed in southeastern Colorado significantly increased: (1) raptor density within 400 m of the towers, and (2) overall raptor populations in the total census area; although the towers represented <2% of the available perches, 81% of all perched raptors recorded were on them (Stahlecker 1978).

The effects of noise on wildlife include: (1) masking signals that influence courtship, grouping, escape, etc., and (2) direct effects on behavioral and physiological processes (Bromley 1985 after Memphis State University 1971). Masking vocal communication of birds, especially sounds that may mask acoustic cues necessary for reproduction, may be the most negative influence of noise (Reijnen et al. 1995). Gibson and Bradbury (1985) reported that male sage-grouse mating success was more closely related to individual differences in strut display effort and sound characteristics (i.e., lek attendance, strut display rate, and the temporal and frequency characteristics of the whistle emitted towards the end of the strut display) than to territorial or morphological characteristics. Gibson (1989) further indicated that the acoustic component of the strut display alone (produced by hidden audio speakers situated on a lek) was attractive to females. Although it is unknown if unnatural noises associated with anthropogenic activity (i.e., gas and oil development operations, traffic) disrupt females' ability to evaluate males' displays, it seems reasonable that noises within the range of those emitted by sage-grouse males (within the frequency bands 300-1200 Hz; Dantzker et al. 1999) could mask courtship acoustics and influence breeding behavior and lek attendance.

Sage-grouse populations apparently decline in response to mineral development activity; however, establishing causality has remained elusive. Remington and Braun (1991) theorized that regional distributions rather than numbers of breeding sage-grouse were altered by coal mining activity in Colorado. This displacement theory is additionally supported by several studies: greater sage-grouse in Alberta, Canada avoided nesting in areas with increased levels of human development (i.e., roads, well sites, urban habitats, cropland), and females with chicks avoided areas with high densities of visible oil wells (Aldridge 2005); lesser prairie-chickens (*Tympanuchus pallidicinctus*) in Kansas selected habitats removed from anthropogenic features (Hagen 2003); and Gunnison sage-grouse in Colorado avoided roads (Oyler-McCance 1999). Potential negative effects to population levels also have been suggested: Aldridge (2005) reported that greater sage-grouse chick survival decreased as well densities within 1 km of brooding locations increased in Canada, and Hagen (2003) suggested that a lesser prairie-chicken population impacted by anthropogenic activity in Kansas had lower nest success and female survival probabilities compared to a non-impacted population.

Sage-grouse response to natural gas field development has been studied in the Pinedale area since 1998. The first 2 years (1998-99) of the study were concentrated on the northern end of the Pinedale Anticline Project Area (the Mesa), and were primarily investigating the reaction of female sage-grouse breeding on road-disturbed compared to undisturbed leks (Lyon 2000, Lyon and Anderson 2003). Females breeding on disturbed leks initiated nests less frequently (65%) than undisturbed individuals (89%); additionally, for females that were followed for consecutive nesting seasons, 56%

breeding on disturbed leks initiated nests both years compared to 82% of the females breeding on undisturbed leks. Females disturbed during the breeding season moved on average twice as far from the lek to nest compared to undisturbed females (4.1 vs. 2.1 km, respectively); 26% of the disturbed females nested within 3 km of the lek compared to 91% of the undisturbed females. For those females that nested, hatching success and early brood-rearing brood survival probabilities did not differ between disturbed and undisturbed females. Lyon (2000) also reported that sage-grouse breeding and summering throughout the entire upper Green River region (including areas extending north of Pinedale approximately 70 km to Green River Lakes) were concentrating on the Mesa and areas approximately 15 km south of the New Fork River during the winter.

The second phase of the Pinedale study incorporated data from Lyon's (2000) study, expanded the study area to include the entire Pinedale Anticline Project Area, and continued to investigate the response of sage-grouse populations to the development of a natural gas field (Holloran *in preparation*). Because the EIS was completed in 2000, we were able to investigate all aspects of gas development versus concentrating on road related disturbance impacts. Over the long-term, sage-grouse in the Pinedale area apparently were excluded from breeding within or near the development boundaries of a natural gas field. Declines in the number of displaying males were positively correlated with decreased lek-to-gas field-related disturbance source (i.e., active drilling rig, producing well pad, main haul road) distances, increased traffic volumes within 3 km of leks, and increased potential for greater noise intensity at leks. The results suggested that well densities exceeding 1 well per 283 ha within 3 km of a lek negatively influence male lek attendance, and rates of lek attendance decline increased on leks located relatively centrally within the developing gas field (i.e., producing wells occupying $\geq$3 directional quadrates around the lek). Adult male displacement and minimal juvenile male recruitment could be contributing to declines in the number of breeding males on impacted leks. Additionally, predatory species' responses to gas field development could be responsible for decreased male survival probabilities on leks situated on the edges of the developing field and could be extending the gas field's range-of-influence.

Female nest site selection results suggested that site-tenacious adult females did not disperse in response to increased levels of gas development within selected nesting locations; however, subsequent generations apparently avoided gas field infrastructure during the nesting period. Additionally, portions of the yearling female breeding cohort apparently avoided breeding on leks situated relatively near the developing field. Population growth differences between impacted and non-impacted populations of individuals suggest that natural gas related impacts negatively influenced female greater sage-grouse population growth. In general, most of the variability in population growth differences between

treatment and control populations was explained by lower annual survival (especially of adult females) buffered to some extent by higher productivity in treatment populations. Interestingly, disturbed female annual survival was primarily influenced during the early brooding and summering stages, after and not during actual gas development impact (individuals were primarily subjected to natural gas activity during the breeding and nesting seasons). Because treatment and control individuals summered in generally the same areas (and these areas were not situated close to the developing gas field), this suggests that individuals subjected to gas development activity during the spring were reacting hormonally and that the hormonal reaction was predisposing them to predation during the summer (most birds that died were killed by predators vs. dying from other causes). Holloran (*in preparation*) concluded that regional sage-grouse population levels as well as population distribution were negatively influenced by the development of a natural gas field.

PREDATOR CONTROL

Predation is commonly believed to have played an important role in shaping nearly every aspect of avian life history. Mortality due to predation can be high, particularly during early life stages (Cote and Sutherland 1997). The loss of nests to predators is the most damaging to sage-grouse populations, as production of young and recruitment may be affected (Braun 1998). However, although predation could play a role in reducing sage-grouse production, the quality of breeding habitat is believed to be an overriding factor controlling the importance of predation (Connelly et al. 1994, Braun 1998).

Despite the number of factors influencing predation rates, there is little doubt that the majority of unsuccessful nests are lost to predation (Patterson 1952, Gregg et al. 1994, Heath et al. 1997, Holloran 1999). Throughout Wyoming, >95% of 246 failed nests were attributed to predators (Holloran et al. 2005). Additionally, studies in Oregon report a high incidence of chick predation during the early brood-rearing period (Willis et al. 1993). Ravens and various hawks are known to take young grouse during this stage (Girard 1937, Patterson 1952). Also, preliminary findings in Idaho suggest that a significant portion of young chick loss results from red fox predation (J. W. Connelly, Idaho Department of Fish and Game, personal communication).

Vegetation consistently higher at successful compared to unsuccessful sage-grouse nests throughout the range of studied populations included live and residual grass height, residual vegetative cover, forb cover and visual obstruction (Wakkinen 1990, Gregg et al. 1994, Sveum et al. 1998b, Popham 2000, Aldridge and Brigham 2002, Hausleitner 2003, Holloran et al. 2005). Other studies on ground nest predation suggest that the penetrability of vegetation surrounding nests, as influenced by spatial heterogeneity, may be more important than concealment at the nest (Bowman and Harris 1980,

Schranck 1972, Crabtree et al. 1989). Additionally, high nest densities due to habitat fragmentation or the lack of quality nesting habitat, habitat size, and the presence of edges, fencerows, or trails may increase predation rates by reducing foraging difficulty for predators (Mankin and Warner 1992, Burger et al. 1994, Niemuth and Boyce 1995, Braun 1998, Holloran and Anderson 2005).

The density and distribution of predators is also likely to affect nest predation rates. Nest and brood predation, as influenced by changes in coyote and raven abundance in particular, have been identified by some researchers as an important factor limiting annual productivity (Batterson and Morse 1948, Willis et al. 1993). High predator densities may also cause some predators to increase their use of foods that are normally of less importance. The alternative prey hypothesis predicts that predators shift their diet from usual prey sources to alternative prey sources during times of primary prey scarcity (Angelstam et al. 1984, Lindstrom et al. 1986). High predator densities, overall or relative to preferred prey sources, may result in increased consumption of normally unimportant food sources. Nest losses of black grouse were low (11%) in a small rodent peak years and high (78%) in a small rodent crash years (Angelstam et al. 1984).

Due to its effect on bird populations and the difficulty of controlling other factors, predation is often seen as an important source of mortality that can be reduced if necessary (Cote and Sutherland 1997). Predator control is currently conducted in many areas used by sage-grouse to reduce predation on livestock that share these ranges. Predation is generally of greatest concern to sheep and various studies have documented the significant impact of predators on these range animals (Tigner and Larson 1977, McAdoo and Klebenow 1978, Scrivner et al. 1985). In a review of 20 studies on the effectiveness of predator removal in protecting bird populations, it was found that removal can reduce early mortality, but that it may not increase the breeding bird population to any great extent (Cote and Sutherland 1997). The effectiveness of predator control appears to be influenced by the status of the target population. Stable and increasing populations appear to respond positively to predator removal, while declining populations are likely to continue declining (Cote and Sutherland 1997).

Commonly cited mammalian sage-grouse and nest predators, namely red foxes, coyotes, bobcats (*Felis rufus*), and badgers, have a great overlap of diets (Patterson 1952, Voigt and Earle 1983, Major and Sherburne 1987, Dibello et al. 1990). As a result, resource competition likely exists and the failure to remove all predator species may simply allow the remaining species to increase in their absence. Using trapping as an index to population, Robinson (1961) found that a decrease in coyote numbers over a 20-year period corresponded to an increase of bobcat, badger, skunk (*Mephitis mephitis*), and other carnivores. Other species interactions must be considered as well. Studies of red fox/coyote interactions have shown that red foxes strongly avoid the territories of coyotes. Because

coyotes generally have much larger home ranges, their presence may seriously limit the fox population of an area (Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987, Harrison et al. 1989). As coyote control became more effective during the 1930s and 1940s, the number of coyotes in farmland areas was reduced and red fox populations began to expand, with red fox becoming more numerous relative to recorded history beginning in the late 1940's (Sargeant et al. 1987). Predator removal is generally focused on the coyote because it is responsible for the vast majority of sheep predator kills (Tigner and Larson 1977, Taylor et al. 1979). However, it may not be an important sage-grouse nest predator (Patterson 1952). Diet studies of the coyote indicate that birds as a whole contribute <7% of the yearly dry weight consumed (Johnson and Hansen 1979, Reichel 1991). In contrast, the red fox is known to be a significant predator of ground nesting ducks and eggs (Sargeant 1972).

In Casper, remote-sensing cameras were placed at 33 sage-grouse nests to identify nest predators (Holloran 1999, Holloran and Anderson 2003). Four of the monitored nests were unsuccessful; an elk (*Cervus elaphus*), badger, and black-billed magpie were directly responsible for 3 of the 4 losses, and repeated disturbance by cattle caused the 4$^{th}$ female to abandon. Interestingly, Patterson (1952) reported that most sage-grouse nest loss in Wyoming was attributable to ground squirrels; however, both thirteen-lined and Richardson's ground squirrels were documented at sage-grouse nests in Casper, yet none of these nests were destroyed. The probability of a successful hatch was negatively related to the amount of time females spent away from the nest during incubation-feeding times, and food forb cover tended to be higher at successful compared to unsuccessful nests. This suggests that forb cover within dense sagebrush patches could reduce the amount of time a female remains off the nest during incubation and result in increased nest success probabilities.

Comparing ranches with different predator control management (intensive vs. recreational predator control) near Rawlins, Heath et al. (1998) reported that control measures could potentially have counteracted some of the effect of substandard nesting habitat (primarily in terms of short residual grass heights on the sheep and cattle ranch). However, predator control did not influence brooding period chick or adult annual survival. Heath et al. (1998) concluded that predator control had limited value to sage-grouse populations.

In Kemmerer, Slater (2003) compared predator density and species composition and sage-grouse productivity in 2 areas, 1 with extensive coyote control and 1 with limited recreational predator control. The results suggested that the coyote control program decreased coyote abundance, but that badger abundance was increased in the coyote control area (although a direct link between decreased coyote and increased badger abundance was not established). However, nest success and brood

survival did not differ between the 2 areas, suggesting reduced coyote abundance and coyote control did not benefit sage-grouse populations.

An interesting theory pertaining to nest depredation probabilities and the presence of potential predator travel corridors (i.e., trails) was investigated in Lander (Kuipers 2004). In terms of trail configuration within 100 m of sage-grouse nests, important predictors of nest success were trail absence within 25 m, and trail presence at 100 m. Kuipers (2004) theorized that if trails represented attractive travel paths for predators, trail presence close to a nest would increase nest detection probabilities, whereas trails farther away would act to draw predators away from a nest and increase hatching probabilities.

## FUTURE SAGE-GROUSE RESEARCH in WYOMING

Although the WyCOOP has recently been involved in numerous research projects investigating questions from general sage-grouse seasonal habitat use and survival to specific aspects of sagebrush habitat management and how they influence sage-grouse biology, several questions that surfaced as a result of those projects remain uninvestigated. The WyCoop currently is addressing 3 of these questions.

Results from the first 2 Pinedale studies suggest that sage-grouse leks situated relatively near extractive mineral developments ultimately become unoccupied. However, indications from these studies are that adult birds are reluctant to disperse from a disturbance, both during the breeding and nesting/early brood-rearing seasons. During the initial phases of the study, birds were captured from leks along the Pinedale Anticline that were either being impacted by gas development, or had the potential to be impacted in the future. This resulted in one of two possible scenarios for the sample population. (1) If a lek was being impacted during the year in question, all the birds using that lek during that year were willing to disregard the potential impact, and our entire sample consisted of these individuals. Thus, we do not know if the sample population was representative of the population as a whole, or consisted solely of individuals able to ignore the presence of gas field activity (presumably adults, which is supported by data collected by Braun 1986). Or, (2) if a lek was impacted one year following initial capture of individuals from that lek (i.e., a pre- vs. post-treatment type of comparison), all the collared individuals returning would be adult birds, and less willing to disperse. Therefore, the first 2 phases of the Pinedale study may not have accurately documented the response of the yearling population to natural gas field development. A scenario where limited yearling recruitment was occurring on leks within gas fields could result in the gradual declines to extinction witnessed at highly impacted leks on the Pinedale Anticline. Thus, a major question remains: "Are juvenile (i.e., yearling)

sage-grouse that would normally be using a lek disturbed by gas development using the impacted lek, moving to another lek, or not breeding?" By radio-equipping juvenile sage-grouse in the fall, and tracking those individuals through the following breeding season, the potential influence of natural gas development on the yearling cohort is currently being investigated by the WyCOOP.

The scale of the landscape used by sage-grouse changes throughout seasons and differs between populations. Site area fidelity [established for nesting habitat (Berry and Eng 1985, Fischer et al. 1993, Holloran and Anderson 2005) and surmised for other seasonal habitats (Berry and Eng 1985)] suggests that the "landscape" for an individual hen during different life-history stages is relatively small. The overall landscape requirements for an individual are the conglomeration of these seasonal habitats combined with the necessary migration corridors (the length of these corridors will be different between and within populations). Thus, the landscape question becomes one of seasonal habitat requirements on a relatively small scale, the juxtapositional requirements of those seasonal habitats, and the habitats required to move between those seasonal ranges. The majority of the published research has been concerned with describing microsite selection within seasonal habitats and microsite adequacy of those selected habitats (i.e., use vs. available and successful vs. unsuccessful studies). Little information is available on gross selection parameters within seasonal ranges (i.e., distance to edge, sagebrush patch size requirements, spatial extent of nesting habitat required), juxtapostional requirements between seasonal ranges (i.e., distances between nesting and brooding habitats and the relationship between distances moved and productivity, summer habitat dispersion and adult/chick survival), or the habitat requirements of transitional ranges (i.e., habitat use and requirements during migration). The other 2 questions currently being investigated by the WyCOOP are concerned with gross seasonal habitat selection and habitat use during the spring and fall transition periods. Seasonal locations from the studies conducted by the WyCOOP since 1994 are being used to quantify habitat selection at the scale of the landscape, essentially investigating the question: "Are sage-grouse females selecting seasonal habitats based on landscape features beyond the spatial scale of microsite habitat conditions?" Additionally, radio-equipped birds from migratory and sedentary populations in the Lander area are being used to investigate transitional-range habitat use, and to investigate survival and productivity differences between migratory and non-migratory individuals.

Additional sage-grouse research is being conducted in Wyoming by personnel from other universities. In the northern part of the state (from the Sheridan region south to Gillette), research investigating the potential effects of coal bed methane (CBM) development on sage-grouse distributions and population growth is being conducted by the University of Montana. Sage-grouse population level impacts of West Nile virus (WNv) outbreaks and the potential influence CBM

evaporation ponds have on WNv prevalence are also being investigated (Dr. David E. Naugle, University of Montana, Missoula, MT, USA). In the Pinedale and Lander areas, a project aimed at experimentally determining the behavioral response of breeding sage-grouse to noise associated with natural gas development activity is being conducted by the University of California, Davis (Dr. Gail L. Patricelli, University of California Davis, Davis, CA, USA). Wyoming is currently at the forefront of research investigating the impacts certain land-use management practices have on sage-grouse populations, especially the potential effects of resource extraction activity. The concern over sage-grouse is not likely to dissipate in the near future; the need for continued research and modifications to land-use practices remains high.

LITERATURE CITED

Agenbroad, L. D. 1978. Buffalo jump complexes in Owyhee County, Idaho. Plains Anthropologist 23:313-321.

Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. PhD Dissertation, University of Alberta, Edmonton, Alberta, Canada.

Aldridge, C. L., and R. M. Brigham. 2001. Nesting and reproductive activities of Greater Sage-Grouse in a declining northern fringe population. Condor 103:537-543.

Aldridge, C. L., and R. M. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Canada. Journal Wildlife Management 66:433-444.

Aldridge, C. L., and R. M. Brigham. 2003. Distribution, abundance, and status of the greater sage-grouse, *Centrocercus urophasianus*, in Canada. Canadian Field-Naturalist 117:25-34.

Angell, R. F. 1997. Crested wheatgrass and shrub response to continuous or rotational grazing. Journal Range Management 50:160-164.

Angelstam, P., E. Lindstrom, and P. Widen. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. Oecologia 62:199-208.

Anonymous. 1937. Sage hen season closed. Wyoming Wildlife 2.

Autenrieth, R. E. 1981. Sage grouse management in Idaho. Wildlife Bulletin 9, Idaho Department of Fish and Game, Boise, ID, USA.

Autenrieth, R., W. Molini, and C. Braun (eds.). 1982. Sage grouse management practices. Western States Sage Grouse Committee Technical Bulletin Number 1. Twin Falls, ID, USA.

Baker, W. L. *In Press*. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin 00:000-000.

Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of sage grouse hens in Oregon. Journal Range Management 47:114-118.

Barnosky, C. W., P. M. Anderson, and P. J. Bartleim. 1987. The northwestern U. S. during deglaciation: vegetational history and paleoclimate implications. Geology of North America Volume K3, North America and adjacent oceans during the last deglaciation. The Geological Society of America, Boulder, CO, USA.

Batterson, W. M., and W. B. Morse. 1948. Oregon sage grouse. Oregon Fauna Series 1, Oregon Game Commission, Portland, OR, USA.

Bay, K. G. 1989. Writing the rules of progress: a look at oil and gas development in the midwest. Proceedings of the 43rd Midwest Fish and Wildlife Conference, Wichita, KS, USA.

Beck, T. D. I. 1977. Sage grouse flock characteristics and habitat selection in winter. Journal Wildlife Management 41:18-26.

Bennett, L. E. 1992. Soil conservation service (SCS) brush project: final report. Wyoming Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY, USA.

Benson, L. A., C. E. Braun, and W. C. Leininger. 1991. Sage grouse response to burning in the big sagebrush type. Proceedings: Issues and Technology in the Management of Impacted Western Wildlife, Thorne Ecological Institute 5:97-104.

Bergerud, A. T. 1988. Survival and breeding strategies of grouse. Pages 473-577 *in* A. T. Bergerud and M. W. Gratson, (eds.). Adaptive Strategies and population ecology on northern grouse. University of Minnesota Press, Minneapolis, MN, USA.

Berry, J. D., and R. L. Eng. 1985. Interseasonal movements and fidelity to seasonal use areas by female sage grouse. Journal Wildlife Management 49:237-240.

Bock, C. E. and J. H. Bock. 1991. Response of grasshoppers (Orthoptera: Acrididae) to wildfire in a southeastern Arizona grassland. American Midland Naturalist 125:162-167.

Bowman, G. B., and L. D. Harris. 1980. Effect of spatial heterogeneity on ground-nest predation. Journal Wildlife Management 44:806-813.

Bradbury, J. W., R. M. Gibson, C. E. McCarthy, and S. L. Vehrencamp. 1989. Dispersion of displaying male sage grouse II: the role of female dispersion. Behavioral Ecology and Sociobiology 24:15-24.

Braun, C. E. 1979. Evolution of the effects of changes in hunting regulations on sage grouse populations. Game Research Report, Project W-37-R-32. Job 9a., Colorado Division of Wildlife, Denver, CO, USA.

Braun, C. E. 1981. Vulnerability and population characteristics of sage grouse in Moffat County. Final Report, Federal Aid Project W-37-R-34, Work Plan 3, Job 11. Colorado Division of Wildlife, Denver, CO, USA.

Braun, C. E. 1986. Changes in sage grouse lek counts with advent of surface coal mining. Proceedings: Issues and Technology in the Management of Impacted Western Wildlife, Thorne Ecological Institute 2:227-231.

Braun, C. E. 1987. Current issues in sage grouse management. Proceedings of the Western Association of State Fish and Wildlife Agencies 67:134-144.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139-156.

Braun, C. E., M. F. Baker, R. L. Eng, J. S. Gashwiler, and M. H. Schroeder. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin 88:165-171.

Braun, C. E., T. E. Britt, and R. O. Wallestad. 1977. Guidelines for maintenance of sage grouse habitats. Wildlife Society Bulletin 5:99-106.

Braun, C. E., O. O. Oedekoven, and C. L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage grouse. Transactions North American Wildlife and Natural Resources Conference 67:337-349.

Bromley, M. 1985. Wildlife management implications of petroleum exploration and development in wildland environments. U.S. Department of Agriculture, Forest Service, Intermountain Research Station General Technical Report INT-191. Ogden, UT, USA.

Bryant, L. D. 1982. Response of livestock to riparian zone exclusion. Journal Range Management 35:780-785.

Bunting, S. C. 1989. Forest site preparation and range improvement. Pages 103-106 *in* D. M. Baumgartner, D. W. Breuer, B. A. Zamora, L. F. Neuenschwander, and R. H. Wakimoto (eds.). Proceedings: Prescribed fire in the intermountain region symposium.

Bunting, S. C., B. M. Kilgore, and C. L. Bushey. 1987. Guidelines for prescribed burning in sagebrush-grass rangelands in the northern Great Basin. U.S. Department of Agriculture, General Technical Report. INT-231, Forest Service Intermountain Research Station. Ogden, UT, USA.

Burger, L. D., L. W. Burger, Jr., and J. Faaborg. 1994. Effects of prairie fragmentation on predation of artificial nests. Journal Wildlife Management 58:249-254.

Burkhardt, J. W. 1995. Herbivory in the intermountain west: an overview of evolutionary history, historic cultural impacts and lessons from the past. Pacific Northwest Range Short Course, Boise, ID, USA.

Butler, R. B. 1978. Bison hunting in the desert west before 1800: the paleoecological potential and the archaeological reality. Plains Anthropologist 23:106-112.

Connelly, J. W. 1982. An ecological study of sage grouse in southeastern Idaho. PhD Dissertation, Washington State University, Pullman, WA, USA.

Connelly, J. W., W. J. Arthur, and O. D. Markham. 1981. Sage grouse leks on recently disturbed sites. Journal Range Management 52:153-154.

Connelly, J. W., H. W. Browers, and R. J. Gates. 1988. Seasonal movements of sage grouse in southeastern Idaho. Journal Wildlife Management 52:116-122.

Connelly, J. W., and L. A. Doughty. 1989. Sage grouse use of wildlife water developments in southeastern Idaho. Pages 167-172 *in* G. K. Tsukamoto and S. J. Striver (eds.). Wildlife water development: a proceedings of the wildlife water development symposium.

Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage grouse use of nest sites in southeastern Idaho. Journal Wildlife Management 55:521-524.

Connelly, J. W., W. L. Wakkinen, A. D. Apa, K. P. Reese, and J. W. Fischer. 1993. Re-nesting by sage grouse in southeastern Idaho. Condor 94:1041-1043.

Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and J. W. Fischer. 1994. Sage grouse ecology report. Job Completion Report W-160-R-19 Subproject 9, Idaho Department of Fish and Game, Boise, ID, USA.

Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse (*Centrocercus urophasianus*) populations in western North America. Wildlife Biology 3:229-234.

Connelly, J. W., K. P. Reese, R. A. Fischer, and W. L. Wakkinen. 2000a. Response of sage grouse breeding population to fire in southeastern Idaho. Wildlife Society Bulletin 28:90-95.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000b. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:1-19.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, WY, USA.

Cote, I. M., and W. J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. Conservation Biology 11:395-405.

Crabtree, R. L., L. S. Broome, and M. L. Wolfe. 1989. Effects of habitat characteristics on gadwall nest predation and nest-site selection. Journal Wildlife Management 53:129-137.

Crawford, J. A., M. A. Gregg, M. S. Drut, and A. K. DeLong. 1992. Habitat use by female sage grouse during the breeding season in Oregon. Final Report. Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Witson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal Range Management 57:2-19.

Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1960. Seasonal movements and breeding behavior of sage grouse in Idaho. Transactions of North American Wildlife and Natural Resource Conference 25:396-407.

Dantzker, M. S., G. B. Deane, and J. W. Bradbury. 1999. Directional acoustic radiation in the strut display of male sage grouse *Centrocercus urophasianus*. Journal Environmental Biology 202:2893-2909.

DeLong, A. K., J. A. Crawford, and D. C. DeLong. 1995. Relationship between vegetational structure and predation of artificial sage grouse nests. Journal Wildlife Management 59:88-92.

Derner, J. D., R. L. Gillen, F. T. McCollum, and K. W. Tate. 1994. Little bluestem tiller defoliation patterns under continuous and rotational grazing. Journal Range Management 47:220-225.

Dibello, F. J., S. M. Arthur, and W. B. Krohn. 1990. Food habits of sympatric coyotes, *Canis latrans*, red foxes, *Vulpes vulpes*, and bobcats, *Lynx rufus*, in Maine. Canadian Field Naturalist 104:403-408.

Dobkin, D. S., A. C. Rich, and W. H. Pyle. 1998. Habitat and avifaunal recovery from livestock grazing in a riparian meadow system of the northwest Great Basin. Conservation Biology 12:209-221.

Drut, M. S., J. A. Crawford, and M. A. Gregg. 1994a. Brood habitat use by sage grouse in Oregon. Great Basin Naturalist 54:170-176.

Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994b. Diets and food selection of sage grouse chicks in Oregon. Journal Range Management 47:90-93.

Ellis, K. L. 1985. Distribution and habitat selection of breeding male sage grouse in northeastern Utah. MS Thesis, Brigham Young University, Provo, UT, USA.

Eng, R. L. 1963. Observations on the breeding biology of male sage grouse. Journal Wildlife Management 27:841-846.

Eng, R. L., and P. Schladweiler. 1972. Sage grouse winter movements and habitat use in central

Montana. Journal Wildlife Management 36:141-146.

Evans, C. C. 1986. The relationship of cattle grazing to sage-grouse use of meadow habitat on the Sheldon National Wildlife Refuge. MS Thesis, University of Nevada, Reno, NV, USA.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review Ecology, Evolution, and Systematics 34:487-515.

Fischer, R. A. 1994. The effects of prescribed fire on the ecology of migratory sage grouse in southeastern Idaho. PhD Dissertation, University of Idaho, Moscow, ID, USA.

Fischer, R. A., A. D. Apa, W. L. Wakkinen, and K. P. Reese. 1993. Nesting-area fidelity of sage grouse in southeastern Idaho. Condor 95:1038-1041.

Fischer, R. A., K. P. Reese, and J. W. Connelly. 1996. An investigation of fire effects within xeric sage grouse brood habitat. Journal Range Management 49:194-198.

Fischer, R. A., W. L. Wakkinen, K. P. Reese, and J. W. Connelly. 1997. Effects of prescribed fire on movements of female sage grouse from breeding to summer ranges. Wilson Bulletin 109:82-91.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecological Systems 29:207-231.

Fuller, A. B., and B. P. Bole, Jr. 1930. Centrocercus urophasianus (Bonaparte). Sage grouse. Observations on some Wyoming Birds, Cleveland Museum Natural History Science Publication 1:37-80.

Gates, R. J. 1983. Sage grouse, lagomorph, and pronghorn use of a sagebrush grassland burn site on the Idaho National Engineering Laboratory. MS Thesis, Montana State University, Bozeman, MT, USA.

Gibson, R. M. 1989. Field playback of male display attracts females in lek breeding sage grouse. Behavioral Ecology and Sociobiology 24:439-443.

Gibson, R. M. and J. W. Bradbury. 1985. Sexual selection in lekking sage grouse: phenotypic correlates of male mating success. Behavioral Ecology and Sociobiology 18:177-123.

Gill, R. B. 1965. Distribution and abundance of a population of sage grouse in North Park, Colorado. MS Thesis, Colorado State University, Fort Collins, CO, USA.

Girard, G. L. 1937. Life history, habits, and food of the sage grouse *Centrocercus urophasianus* Bonaparte. University of Wyoming Publication 3. University of Wyoming, Laramie, WY, USA.

Greer, R. 1990. Sage grouse habitat requirements and development. Habitat Extension Bulletin Number 31. Habitat Extension Services, Wyoming Game and Fish Department, Laramie, WY, USA.

Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetational cover and predation of sage grouse nests in Oregon. Journal Wildlife Management 58:162-166.

Griner, L. A. 1939. A study of the sage grouse (*Centrocercus urophasianus*), with special reference to the life history, habitat requirements, and numbers and distribution. MS Thesis, Utah State Agricultural College, Logan, UT, USA.

Hagen, C. A. 2003. A demographic analysis of Lesser Prairie-Chicken populations in southwestern Kansas: survival, population viability, and habitat use. PhD Dissertation, Kansas State University, Manhattan, KS, USA.

Hall, F. C., and L. Bryant. 1995. Herbacious stubble height as a warning of impending cattle grazing damage to riparian areas. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-362. Portland, OR, USA.

Harniss, R. O. and R. B. Murray. 1973. 30 years of vegetal change following burning of sagebrush-grass range. Journal Range Management 26:322-325.

Harrison, D. J., J. A. Bissonette, and J. A. Sherburne. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. Journal Wildlife Management 53:181-185.

Hausleitner, D. 2003. Population dynamics, habitat use and movements of greater sage-grouse in Moffat County, Colorado. MS Thesis, University of Idaho, Moscow, ID, USA.

Heath, B., R. Straw, S. Anderson, and J. Lawson. 1996. Proceedings of sage grouse workshop. Pinedale, WY, USA.

Heath, B. J., R. Straw, S. H. Anderson, and J. Lawson. 1997. Sage grouse productivity, survival, and seasonal habitat use near Farson, Wyoming. Job Completion Report. Wyoming Game and Fish Department, Cheyenne, WY, USA.

Heath, B. J., R. Straw, S. H. Anderson, J. Lawson, and M. J. Holloran. 1998. Sage-grouse productivity, survival, and seasonal habitat use among three ranches with different livestock grazing, predator control, and harvest management practices. Job Completion Report. Wyoming Game and Fish Department, Cheyenne, WY, USA.

Holechek, J. L. 1996. Drought in New Mexico: prospects and management. Rangelands 18:225-227.

Holloran, M. J. 1999. Sage grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. MS Thesis, University of Wyoming, Laramie, WY, USA.

Holloran, M. J., and S. H. Anderson. 2003. Direct identification of Northern sage-grouse, *Centrocercus urophasianus,* nest predators using remote sensing cameras. Canadian Field-Naturalist 117:308-310.

Holloran, M. J., and S. H. Anderson. 2004. Greater sage-grouse seasonal habitat selection and survival in Jackson Hole, Wyoming. Job Completion Report, Wyoming Game and Fish Department, Cheyenne, WY, USA.

Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742-752.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal Wildlife Management 69:638-649.

Holloran, M. J. In Preparation. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. PhD Dissertation, University of Wyoming, Laramie, WY, USA.

Homer, C. G., T. C. Edwards, Jr., R. D. Ramsey, and K. P. Reese. 1993. Use of remote sensing methods in modeling sage grouse winter habitat. Journal Wildlife Management 57:78-84.

Hornaday, W. T. 1916. Save the sage grouse from extinction, a demand from civilization to the western states. New York Zoological Park Bulletin 5:179-219.

Hulet, B. V. 1983. Selected responses of sage-grouse to prescribed fire, predation and grazing by domestic sheep in southeastern Idaho. MS Thesis, Brigham Young University, Provo, UT, USA.

Hull, S. D., R. J. Robel, and K. E. Kemp. 1996. Summer avian abundance, invertebrate biomass, and forbs in Kansas CRP. Prairie Naturalist 28:1-12.

Hupp, J. W., and C. E. Braun. 1989. Topographic distribution of sage grouse foraging in winter. Journal Wildlife Management 53:823-829.

Ingelfinger, F. M. 2001. The effects of natural gas development on sagebrush steppe passerines in Sublette County, Wyoming. MS Thesis, University of Wyoming, Laramie, WY, USA.

Jamison, B.E., R.J. Robel, J.S. Pontius, and R.D. Applegate. 2002. Invertebrate biomass: associations with lesser prairie-chicken habitat use and sand sagebrush density in southwestern Kansas. Wildlife Society Bulletin 30:517-526.

Johnsgard, P. A. 2002. Grassland grouse and their conservation. Smithsonian Institution Press, Washington D.C., USA.

Johnson, K. L. 1987. Sagebrush over time: a photographic study of vegetation change in Wyoming 1870-1986. Agricultural Experimental Station Publication 50, University of Wyoming, Laramie, WY, USA.

Johnson, G.D. and M. S. Boyce. 1990. Feeding trials with insects in the diet of sage grouse chicks.

Journal Wildlife Management 54:89-91.

Johnson, M. K. and R. M. Hansen. 1979. Coyote food habits on the Idaho National Engineering Laboratory. Journal Wildlife Management 43:951-956.

Kilpatrick, S. 2000. Using prescribed fire to manage sagebrush communities in occupied sage grouse habitats of Wyoming. 22nd Western States Sage and Columbian Sharp-tailed Grouse Symposium, Redmond, OR, USA.

Klebenow, D. A. 1969. Sage grouse nesting and brood habitat in Idaho. Journal Wildlife Management 33:649-662.

Klebenow, D. A. 1970. Sage grouse vs. sagebrush control in Idaho. Journal Range Management 23:396-400.

Klebenow, D. A. 1972. The habitat requirements of sage grouse and the role of fire in management. Tall Timbers Fire Ecology Conference 12:305-315.

Klebenow, D. A. 1982. Livestock grazing interactions with sage grouse. Pages 113-123 *in* J. M. Peck and P. D. Dalke (eds.). Wildlife-Livestock Relationships Symposium: Proceedings 10, Coeur d'Alene, ID, USA.

Klebenow, D. A., and G. M. Gray. 1968. Food habits of juvenile sage grouse. Journal Range Management 21:80-83.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634.

Kuipers, J. L. 2004. Grazing system and linear corridor influences on greater sage-grouse (*Centrocercus urophasianus*) habitat selection and productivity. MS Thesis, University of Wyoming, Laramie, WY, USA.

Laycock, W. A. 1979. Management of sagebrush. Rangelands 1:207-210.

Lindstrom, E., P. Angelstam, P. Widen, and H. Andren. 1986. Do predators synchronize vole and grouse fluctuations? An experiment. Oikos 48:121-124.

Lommasson, T. 1948. Succession in sagebrush. Journal Range Management 1:19-21.

Lyon, A. G. 2000. The potential effects of natural gas development on sage grouse near Pinedale, Wyoming. MS Thesis, University of Wyoming, Laramie, WY, USA.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486-491.

Mack, R. N., and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. American Naturalist 119:757-773.

Major, J. T. and J. A. Sherburne. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. Journal Wildlife Management 51:606-616.

Mankin, P. L., and R. E. Warner. 1992. Vulnerability of ground nests to predation on an agricultural habitat island in east-central Illinois. American Midland Naturalist 128:281-291.

Martin, N. S. 1970. Sagebrush control related to habitat and sage grouse occurrence. Journal Wildlife Management 34:313-320.

Martin, R. C. 1990. Sage grouse responses to wildfires in spring and summer habitats. MS Thesis, University of Idaho, Moscow, ID, USA.

McAdoo, J. K., and D. A. Klebenow. 1978. Predation on range sheep with no predator control. Journal Range Management 31:111-114.

McDowell, K. 1956. The proud strutter. Wyoming Wildlife 20:4-7.

Miller, R. F., T. J. Svejcar, and N. E. West. 1994. Implications of livestock grazing in the intermountain sagebrush region: plant composition. Pages 101-146 *in* M. Vavra, W. A. Laycock, and R. D. Pieper (eds.). Ecological Implications of livestock herbivory in the west. Society for Range Management, Denver, CO, USA.

Moulton, G. E. (ed.). 1987. Journals of the Lewis and Clark Expedition. Volume 4. University of Nebraska Press, Lincoln, NE, USA.

Moynahan, B. J. 2004. Landscape-scale factors affecting population dynamics of greater sage-grouse (*Centrocercus urophasianus*) in north-central Montana, 2001-2004. PhD Dissertation, University of Montana, Missoula, MT, USA.

Mueggler, W. F. 1950. Effects of spring and fall grazing by sheep on vegetation of the upper snake river plains. Journal Range Management 3:308-315.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Dato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: pending crisis for greater sage-grouse. Ecology Letters 7:704-713.

Neel, L. A. 1980. Sage grouse response to grazing management in Nevada. MS Thesis, University of Nevada, Reno, NV, USA.

Nelle, P. J. 1998. The long-term effects of fire on sage grouse nesting and brood –rearing habitats on the Upper Snake River Plain. MS Thesis, University of Idaho, Moscow, ID, USA.

Nelle, P. J., K. P. Reese, and J. W. Connelly. 2000. Long-term effect of fire on sage grouse nesting and brood-rearing habitats in the Upper Snake River Plain. Journal Range Management 53-586-591.

Niemuth, N. D., and M. S. Boyce. 1995. Spatial and temporal patterns of predation of simulated sage grouse nests at high and low nest densities: an experimental study. Canadian Journal Zoology 73:819-825.

Oakleaf, R. J. 1971. The relationship of sage grouse to upland meadows in Nevada. Job Final Report, Federal Aid Project W-48-2, Nevada Department of Fish and Game, Reno, NV, USA.

Owens, M. K., and B. E. Norton. 1990. Survival of juvenile basin big sagebrush under different grazing regimes. Journal Range Management 43:132-135.

Oyler-McCance, S. J. 1999. Genetic and habitat factors underlying conservation strategies for Gunnison sage-grouse. PhD Dissertation, Colorado State University, Fort Collins, CO, USA.

Paige, C., and S. A. Ritter. 1999. Birds in a sagebrush sea: managing sagebrush habitats for bird communities. Partners in Flight Western Working Group, Boise, ID, USA.

Patterson, R. L. 1952. The sage grouse in Wyoming. Wyoming Game and Fish Commission and Sage Books. Denver, CO, USA.

Patterson, R. L., and D. Cram. 1949. Sage grouse in the west. Wyoming Wildlife 8:10-13.

Peterson, J. G. 1970. The food habits and summer distribution of juvenile sage grouse in central Montana. Journal Wildlife Management 34:147-155.

Peterson, J. G. 1995. Ecological implications of sagebrush manipulation. Wildlife Management Division Montana Fish, Wildlife, and Parks, Federal Aid in Wildlife Restoration Project W-101-R-2, Helena, MT, USA.

Phillips, R. L., D. E. Biggins and A. B. Hoag. 1986. Coal surface mining and selected wildlife-a ten year study near Decker, Montana. Proceedings, Issues and Technology in the Management of Impacted Western Wildlife. Thorne Ecological Institute 2:235-244.

Pieper, R. 1994. Ecological implications of livestock grazing. Pages 177-211 *in* M. Vavra, W. A. Laycock, and R. D. Pieper (eds.). Ecological Implications of livestock herbivory in the west. Society for Range Management, Denver, CO, USA.

Popham, G. P. 2000. Sage grouse nesting habitat in northeastern California. MS Thesis, Humboldt State University, Arcata, CA, USA.

Popham, G. P. and R. J. Gutierrez. 2003. Greater sage-grouse *Centrocercus urophasianus* nesting success and habitat use in northeastern California. Wildlife Biology 9:327-334.

PRISM Environmental Management Consultants. 1982. A review of petroleum industry operations and other land use activities affecting wildlife. The Canadian Petroleum Association, Calgary, Alberta, Canada.

Pyrah, D. B. 1970. Sage grouse habitat research in central Montana. *In* E. F. Schlatterer and D.B. Pyrah (eds.). Ecological effects of chemical and mechanical sagebrush control. Montana Fish and Game Department Completion Report, Project W-105-R-4:293-300, Helena, MT, USA.

Rassmussen, D. I., and L. A. Griner. 1938. Life history and management studies of the sage grouse in Utah, with special reference to nesting and feeding habits. Transactions of the North American Wildlife and Natural Resources Conference 3:852-864.

Reichel, J. D. 1991. Relationships among coyote food habits, prey populations, and habitat use. Northwest Science 65(3):133-137.

Reijnen, R., R. Foppen, C. ter Braak, and J. Thissen. 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. Journal Applied Ecology 32:187-202.

Remington, T. E., and C. E. Braun. 1985. Sage grouse food selection in winter, North Park, Colorado. Journal Wildlife Management 49:1055-1061.

Remington, T. E. and C. E. Braun. 1991. How surface coal mining affects sage grouse, North Park, Colorado. Proceedings, Issues and Technology in the Management of Impacted Western Wildlife. Thorne Ecological Institute 5:128-132.

Reynolds, R. T., and C. H. Trost. 1980. The response of native vertebrate populations to crested wheatgrass planting and grazing by sheep. Journal Range Management 33:122-125.

Rickard, W. H. 1970. Ground dwelling beetles in burned and unburned vegetation. Journal Range Management 23:293-294.

Ritchie, M. E., M. L. Wolfe, and R. Danvir. 1994. Predation of artificial sage grouse nests in treated and untreated sagebrush. Great Basin Naturalist 54:122-129.

Robertson, M. D. 1991. Winter ecology of migratory sage grouse and associated effects of prescribed fire in southern Idaho. MS Thesis, University of Idaho, Moscow, ID, USA.

Robinson, W. B. 1961. Population changes of carnivores in some coyote-control areas. Journal Mammalogy 42:510-515.

Rothenmaier, D. 1979. Sage grouse reproductive ecology: breeding season movements, strutting ground attendance and site characteristics, and nesting. MS Thesis, University of Wyoming, Laramie, WY, USA.

Sargeant, A. B. 1972. Red fox spatial characteristics in relation to waterfowl predation. Journal Wildlife Management 36:225-236.

Sargeant, A. B., M. A. Sovada, and R. J. Greenwood. 1987. Responses to three prairie ground squirrel species, *Spermophilus franklinii, S. richardsonii, and S. tridecemlineatus*, to duck eggs. Canadian Field-Naturalist 101:95-97.

Savory, A. 1988. Holistic resource management. Island Press. Washington D. C., USA.

Schneegas, E. R. 1967. Sage grouse and sagebrush control. Transactions North American Wildlife and Natural Resource Conference 32:270-274.

Schoenburg, T. J., and C. E. Braun. 1982. Potential impacts of strip mining on sage grouse movements and habitat use. Job Completion Report. Federal Aid Project W-37-R-35, Work Plan 3, Job 12, Colorado Division of Wildlife, Denver, CO, USA.

Schranck, B. W. 1972. Waterfowl nest cover and some predation relationships. Journal Wildlife Management 36:182-186.

Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 9:378-385.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Pages 1-28 *in* A. Poole and F. Gill, editors. The birds of North America, No. 425. The Birds of North America, Philadelphia, PA, USA.

Schroeder, M. A., and L. A. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildlife Biology 9:291-299.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of Sage-grouse in North America. Condor 106:363-376.

Schroedl, G. F. 1973. The archeological occurrence of bison in the Southern Plateau. Washington State University Lab of Anthropology, Report of Investigation 51, Pullman, WA, USA.

Scrivner, J. H., W. E. Howard, A. H. Murphy, and J. R. Hays. 1985. Sheep losses to predators on a California range, 1973-1983. Journal Range Management 38:418-421.

Slater, S. J. 2003. Sage-grouse (*Centrocercus urophasianus*) use of different-aged burns and the effects of coyote control in southwestern Wyoming. MS Thesis, University of Wyoming, Laramie, WY, USA.

Stahlecker, D. W. 1978. Effect of a new transmission line on wintering prairie raptors. Condor 80:444-446.

Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications 9:45-64.

Sveum, C. M., J. A. Crawford, and D. Edge. 1998a. Use and selection of brood-rearing habitat by sage grouse in south-central Washington. Great Basin Naturalist 58: 344-351.

Sveum, C. M., W. D. Edge, and J. A. Crawford. 1998b. Nesting habitat selection by sage grouse in south-central Washington. Journal Range Management 51:265-269.

Swenson, J. E., C. A. Simmons, and C. D. Eustace. 1987. Decrease of sage grouse *Centrocercus urophasianus* after ploughing of sagebrush steppe. Biological Conservation 41:125-132.

Taylor, R. G., J. R. Workman, and J. E. Bowns. 1979. The economics of sheep predation in southwestern Utah. Journal Range Management 32:317-321.

Thompson, K. M., M. J. Holloran, S. J. Slater, J. L. Kuipers, and S. H. Anderson. *In Review*. Greater sage-grouse early brood-rearing habitat use and productivity in Wyoming. Western North American Naturalist 00:000-000.

Thurow, T. L. and C. A. Taylor. 1999. Viewpoint: the role of drought in range management. Journal Range Management 52:413-419.

Tidewell, W. D., S. R. Rashforth, and D. Simper. 1972. Evolution of floras in the intermountain region. Volume 1 *in* A. Cronquist, A. H. Cronquist, H. H. Holmgren, and J. L. Reveal (eds.). Intermountain flora, Hafner Publishing Company, New York, NY, USA.

Tigner, J. R. and G. E. Larson. 1977. Sheep losses on selected ranches in southern Wyoming. Journal Range Management 30:244-252.

Tisdale, E. W., and M. Hironaka. 1981. The sagebrush-grass region: a review of the ecological literature. Idaho Forest, Wildlife and Range Experiment Station Bulletin 33, Moscow, ID, USA.

TRC Mariah Associates Inc. 1997. Environmental impact statement for the Jonah Field II natural gas development project, Sublette County, Wyoming. Draft Wildlife Technical Report, Laramie, WY, USA.

United States Department of Interior Bureau of Land Management. 1979. Kemmerer resource area oil and gas leasing environmental assessment record. Bureau of Land Management, Rock Springs District, WY, USA.

Vale, T. R. 1974. Sagebrush conversion projects: an element of contemporary environmental change in the western United States. Biological Conservation 6:274-284.

Vale, T. R. 1975. Presettlement vegetation in the sagebrush-grass area of the intermountain west. Journal Range Management 28:32-36.

Voigt, D.R. and B.D. Earle. 1983. Avoidance of coyotes by red fox families. Journal Wildlife Management 47:852-857.

Wakkinen, W. L. 1990. Nest site characteristics and spring-summer movements of migratory sage grouse in southeastern Idaho. MS Thesis, University of Idaho, Moscow, ID, USA.

Wakkinen, W. L., K. P. Reese, and J. W. Connelly. 1992. Sage grouse nest locations in relation to leks. Journal Wildlife Management 56:381-383.

Wallestad, R. O. 1971. Summer movements and habitat use by sage grouse broods in central Montana. Journal Wildlife Management 35:129-136.

Wallestad, R. O. 1975. Life history and habitat requirements of sage grouse in central Montana. Montana Fish and Game Department Technical Bulletin, Helena, MT, USA.

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. Journal Wildlife Management 38:630-633.

Watters, M. E., T. L. McLash, C. L. Aldridge, and R. M. Brigham. 2002. The effect of vegetation structure on predation of artificial greater sage-grouse nests. Ecoscience 9:314-319.

Watts, M. J., and C. L. Wambolt. 1996. Long-term recovery of Wyoming big sagebrush after four treatments. Journal Environmental Management 46:95-102.

Welch, B. L., F. J. Wagstaff, and J. A. Robertson. 1991. Preference of wintering sage grouse for big sagebrush. Journal Range Management 44:462-465.

Willis, M. J., G. P. Keister, Jr., D. A. Immell, D. M. Jones, R. M. Powell, and K. R. Durbin. 1993. Sage grouse in Oregon. Wildlife Research Report 15, Oregon Department of Fish and Wildlife, Portland, OR, USA.

Winward, A. H. 1991. A renewed commitment to management of sagebrush grasslands. Agricultural Experiment Station Special Report 880. Oregon State University, Corvallis, OR, USA.

Wright, H. A. 1970. Responses of big sagebrush and three-tip sagebrush to season of clipping. Journal Range Management 23:20-22.

Wright, H. A. 1974. Range burning. Journal Range Management 27:5-11.

Wright, H. A., and A. W. Bailey. 1982. Fire ecology: United States and southern Canada. Wiley and Sons, New York, NY, USA.

Wright, H. A., L. F. Nuenschwander, and C. M. Britton. 1979. The role and use of fire in sagebrush grass and pinyon juniper plant communities. A state-of-the-art review, U.S. Department of Agriculture, Forest Service, General Technical Report INT-58.

Wyoming Interagency Vegetation Committee. 2002. Wyoming guidelines for managing sagebrush communities with emphasis on fire management. Wyoming Game and Fish Department and Wyoming Bureau of Land Management, Cheyenne, WY, USA.

Zablan, M. A., C. E. Braun, and G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal Wildlife Management 67:144-154.

Table 1: Productivity estimates for greater sage-grouse populations studied by the Wyoming Cooperative Research Unit in central and western Wyoming, 1994-2004. Nesting propensity is the apparent number of potential females documented incubating, nesting success is the apparent probability of hatching ≥1 egg, and brood success is the apparent number of successfully nesting females fledging ≥1 chick the last 2 weeks in August.

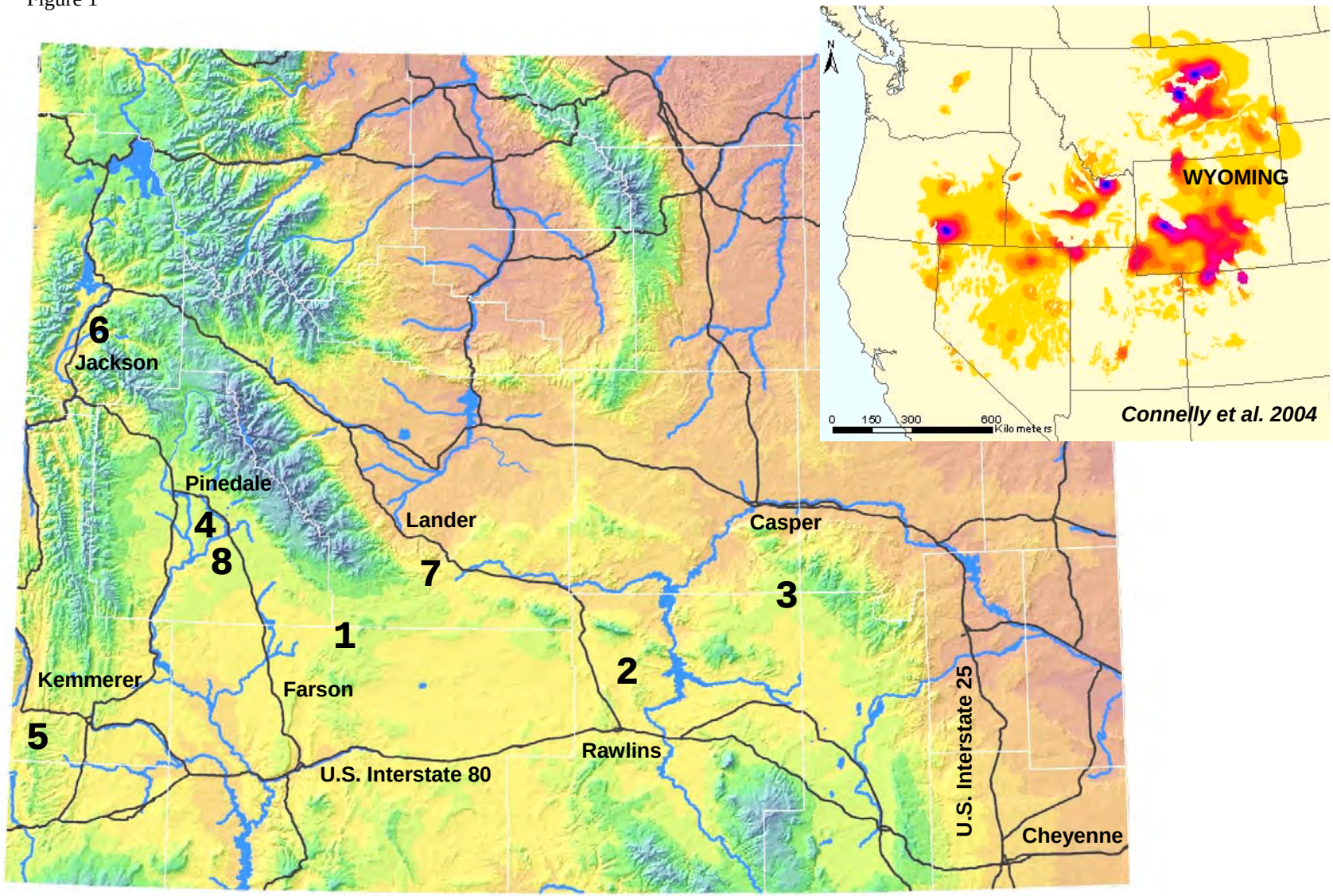
| Study Area | Year | n[a] | Nesting Propensity | Nesting Success | Brooding Success | Chicks per Female[b] |
|---|---|---|---|---|---|---|
| Farson | 1994 | 29 | 24/29 (83%) | 9/24 (38%) | 4/9 (44%) | 8/29 (0.28) |
| | 1995 | 41 | 33/37 (89%) | 9/36 (25%) | 8/9 (89%) | 24/37 (0.65) |
| | 1996 | 25 | 21/24 (88%) | 11/23 (48%) | 10/11 (91%) | 38/24 (1.58) |
| Rawlins | 1996 | 24 | 19/23 (83%) | 15/19 (79%) | 11/15 (73%) | 38/23 (1.65) |
| | 1997 | 32 | 21/30 (70%) | 15/23 (65%) | 6/15 (40%) | 24/30 (0.80) |
| Casper | 1997 | 40 | 32/38 (84%) | 16/31 (52%) | 11/16 (69%) | 41/38 (1.08) |
| | 1998 | 55 | 50/54 (93%) | 29/43 (67%) | 16/29 (55%) | 57/54 (1.06) |
| Pinedale | 1998 | 41 | 28/31 (90%) | 14/32 (44%) | 10/13 (77%) | 27/31 (0.87) |
| | 1999 | 40 | 26/33 (79%) | 12/27 (44%) | 3/10 (30%) | 10/33 (0.30) |
| | 2000 | 37 | 17/23 (74%) | 7/16 (44%) | 5/7 (71%) | 17/23 (0.74) |
| | 2001 | 46 | 27/32 (84%) | 10/27 (37%) | 6/8 (75%) | 13/32 (0.41) |
| | 2002 | 76 | 51/60 (85%) | 21/52 (40%) | 14/20 (70%) | 33/60 (0.55) |
| | 2003 | 91 | 54/64 (84%) | 24/53 (45%) | 12/20 (60%) | 37/64 (0.58) |
| | 2004 | 97 | 59/77 (77%) | 36/57 (63%) | 25/33 (76%) | 62/77 (0.81) |
| Kemmerer | 2000 | 27 | 16/25 (64%) | 1/17 (6%) | 1/1 (100%) | 1/25 (0.04) |
| | 2001 | 45 | 29/38 (76%) | 10/30 (33%) | 5/10 (50%) | 11/38 (0.29) |
| | 2002 | 57 | 42/48 (88%) | 13/50 (26%) | 9/13 (69%) | 26/48 (0.54) |
| Jackson | 1999 | 9 | 7/8 (88%) | 4/7 (57%) | 3/4 (75%) | 7/8 (0.88) |
| | 2000 | 14 | 11/13 (85%) | 5/11 (45%) | 1/4 (25%) | 0 |
| | 2001 | 20 | 13/17 (76%) | 6/15 (40%) | 4/6 (67%) | 11/17 (0.65) |
| | 2002 | 10 | 9/10 (90%) | 4/10 (40%) | 3/4 (75%) | 8/10 (0.80) |
| Lander | 2000 | 26 | 16/23 (70%) | 7/16 (44%) | 4/7 (57%) | 9/23 (0.39) |
| | 2001 | 31 | 21/27 (78%) | 8/21 (38%) | 6/9 (67%) | 17/27 (0.63) |
| | 2002 | 24 | 23/24 (96%) | 12/23 (52%) | 9/12 (75%) | 21/14 (0.88) |
| | 2003 | 48 | 36/42 (86%) | 16/36 (44%) | 12/16 (75%) | 35/42 (0.83) |

[a] Potential breeding females (i.e., number of females alive the first 2 weeks in April).

[b] Number of chicks fledged (last 2 weeks August) divided by the total number of females that could have produced a chick (i.e., number of potentially nesting females).

Figure 1: Study area locations for greater sage-grouse research projects conducted by the Wyoming Cooperative Research Unit, 1994-2005. Consult the text for study area description corresponding to numbers present on map. Inset map (Connelly et al. 2004) outlines sage-grouse breeding population strongholds as of 2003; the darkest shades represent the greatest densities of males / $km^2$.

Figure 1


N
WYOMING
0 150 300 600
Kilo meters
Connelly et al. 2004
6
Jackson
Pinedale
4
8
Lander
7
Casper
3
1
2
Kemmerer
Farson
5
Rawlins
U.S. Interstate 80
U.S. Interstate 25
Cheyenne

# POPULATION RESPONSE OF YEARLING GREATER SAGE-GROUSE TO THE INFRASTRUCTURE OF NATURAL GAS FIELDS IN SOUTHWESTERN WYOMING

Completion Report

August 2007
U.S. Geological Survey
Wyoming Cooperative Fish and Wildlife Research Unit
Laramie, Wyoming, USA

MATTHEW J. HOLLORAN, Wyoming Wildlife Consultants, LLC., 207 West Pine Street, Pinedale, WY 82941, USA. matth@wyowildlife.com; 307 742 3253 (voice).

RUSTY C. KAISER, Bureau of Land Management, 1625 West Pine Street, Pinedale, WY 82941, USA.

WAYNE A. HUBERT, U. S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department 3166, East University Avenue, Laramie WY 82071, USA.

**ABSTRACT**

Energy development throughout the western United States has caused habitat changes resulting in local sage-grouse population declines. Sagebrush-dominated habitats in the Green River Basin of southwestern Wyoming have experienced extensive, rapid changes due to the development of natural gas fields. It is unclear whether population declines in natural gas fields are caused by avoidance or demographic impacts, and which age classes are most affected. We investigated habitat selection during the breeding season and demographics of greater sage-grouse to determine if natural gas development has influenced yearling male and yearling female populations in the Upper Green River Basin of southwestern Wyoming. Yearling males avoided leks near the infrastructure of natural gas fields when establishing breeding territories. Additionally, yearling males reared in areas influenced by infrastructure established breeding territories less often, were observed on leks during the breeding period less often, and had lower annual survival rates compared to yearling males reared in areas with no infrastructure. Yearling females avoided nesting within 930 m of the infrastructure of natural gas fields. Additionally, yearling females reared in areas influenced by infrastructure had lower annual survival rates than females reared in areas with no infrastructure. Our results suggest that development of natural gas fields will result in the loss of leks within developed areas and in the functional loss of nesting habitat within 930 m of infrastructure. Because both yearling dispersal from infrastructure and reduced demographics are contributing to abandonment of leks and nesting habitat within natural gas fields, we suggest that peripheral areas be protected from energy development and managed to sustain robust populations to ensure that greater sage-grouse may be available to re-colonize disturbed areas following reclamation.

## INTRODUCTION

Populations of greater sage-grouse (*Centrocercus urophasianus*) throughout North America are one-half to one-third the size of those during the late 1960s (Connelly et al. 2004), and the species currently occupies 56% of its pre-European settlement distribution (Schroeder et al. 2004). Throughout Wyoming, greater sage-grouse populations declined an average of 5.2% annually between 1965 and 2003, and the average number of males per lek declined by 49% over that 38-year period (Connelly et al. 2004). Although factors responsible for declines vary regionally, Braun (1998) suggested that declines are primarily a result of human-caused habitat changes. The development of gas and oil fields throughout the western United States (U.S.) has been recognized as one of several anthropogenic changes associated with reduced sage-grouse (*Centrocercus* spp.) populations (U.S. Fish and Wildlife Service 2005).

Approximately 2.7 million ha of land managed by the U.S. Bureau of Land Management (BLM) in the western U.S. are currently in production status for oil, natural gas, or geothermal energy (Knick et al. 2003). A minimum of 25-28% of the total area delineated by a 50-km buffer around the pre-settlement distribution of sage-grouse was influenced by the infrastructure of oil or natural gas developments in 2003 (Connelly et al. 2004). Extraction of oil resources in Wyoming began in the early 1880s (Salt Creek and Dallas Dome oil fields), but industry emphasis has shifted to extraction of natural gas resources since the 1960s (Braun et al. 2002, Connelly et al. 2004; E. T. Rinkes, BLM Lander, Wyoming Field Office; personal communication). Connelly et al (2004) estimated that in 2003, 6 major fields producing oil and gas in the Greater Green River Basin of southwestern Wyoming covered over 8,740 $km^2$, and active and potential wells numbered approximately 7,890. The infrastructure associated with natural gas developments in the region is expected to increase by 40% by 2015 (Connelly et al. 2004). Existing and proposed oil and gas wells in Wyoming are primarily within landscapes dominated by sagebrush (*Artemisia* spp.; Knick et al. 2003), which are essential for persistence of greater sage-grouse populations.

In southwestern Wyoming, researchers have observed that as the distances between leks and the infrastructure of natural gas fields decrease and as the level of development surrounding leks increase, declines in lek attendance by males approached 100% (Holloran 2005). Walker et al. (2007) reported that only 38% of greater sage-grouse leks active in 1997 or later within coal-bed methane (CBM) fields in the Powder River Basin (PRB) of northeastern Wyoming and

southeastern Montana were still active in 2004-2005, compared to 84% of leks outside CBM fields. Active leks in CBM fields had 46% few males per lek than leks outside the fields (Walker et al. 2007). Similarly, Braun et al. (2002) found that the average number of males on leks within 0.4 km of CBM wells was significantly lower than leks greater than 0.4 km from CBM wells. Between 1983 and 1985, 3 lek complexes in southern Canada were disturbed by oil and gas activities within 200 m, and none of these leks have been active since disturbance (Braun et al. 2002, Aldridge and Brigham 2003). In northern Colorado, the overall decline in the number of males on 4 leks near the infrastructure of coal mines was 73% from peak numbers prior to development to approximately 3 years after an increase in mining activity; declines in the number of males were significantly higher than changes witnessed on non-impacted leks (Braun 1986, Remington and Braun 1991).

Impacts of energy developments on sage-grouse can include behavioral avoidance of anthropogenic disturbance and/or increased risk of mortality (Connelly et al. 2004). Lyon and Anderson (2003) observed that female greater sage-grouse nested significantly farther from leks disturbed by roads associated with natural gas fields compared to birds on leks in undisturbed areas in southwestern Wyoming. Significantly fewer females from disturbed leks nested within 3 km of the lek where they were captured compared to birds from undisturbed leks (Lyon and Anderson 2003). Additionally, Holloran (2005) suggested that nesting females avoided areas with high densities of natural gas wells (i.e., 16 ha well spacing). In the PRB, Doherty et al. (2008) concluded that greater sage-grouse avoided CBM wells located in otherwise suitable wintering habitat. At CBM well densities of 12.3 wells/4 $km^2$ greater sage-grouse were 1.3 times more likely to occupy sagebrush habitats with no CBM wells (Doherty et al. 2008). Greater sage-grouse in Canada avoided nesting in areas with high proportion of non-natural edge habitats, and brood-rearing females avoided areas with high densities of visible wells within 1 km (Aldridge and Boyce 2007). The authors noted that avoidance of human features effectively removed nesting habitat within a 1-$km^2$ area of these structures (i.e., functional habitat loss).

In Colorado, the probability of detecting Gunnison sage-grouse (*Centrocercus minimus*) declined as sagebrush patches became smaller and were situated closer to roads (Oyler-McCance 1999). Similarly, in southwestern Kansas, lesser prairie-chickens (*Typmanuchus pallidicinctus*) avoided wells and power lines, and the presence of high densities of either type of feature in areas with otherwise suitable habitat precluded use (Hagen 2003). The odds of a power line or

road occurring within a monthly-range were 3 times and 11% less likely than in a non-use range. Additionally, lesser prairie-chickens selected nesting sites farther from wellheads, improved roads, buildings (including natural gas compressor stations), and transmission lines than was expected at random (Pitman et al. 2005). Avoidance of anthropogenic features resulted in a functional loss of 58% of the total amount of suitable lesser prairie-chicken nesting habitat (Robel et al. 2004).

Adverse impacts of energy development to demographic parameters have also been noted. Lyon and Anderson (2003) suggested that nesting propensity was significantly lower for females breeding on leks disturbed by roads associated with natural gas fields compared to females in undisturbed areas. The risk of chick mortality among greater sage-grouse increased by a factor of 1.5 for each additional well visible within 1 km of brooding locations (Aldridge and Boyce 2007). Population growth rates of greater sage-grouse and lesser prairie-chickens influenced by energy development were less than growth rates of non-impacted populations (Hagen 2003, Holloran 2005). Both authors suggested that lower population growth rates were primarily due to lower survival and nesting success in the impacted populations.

Research has suggested that energy developments can cause the loss of affected populations. Remington and Braun (1991) suggested that greater sage-grouse population declines in areas near coal mines may have been caused by displacement of yearlings to leks situated away from development. Holloran and Anderson (2004) were able to reproduce observed declines in the number of males occupying 3 natural gas development-impacted leks in southwestern Wyoming by assuming adult male tenacity and minimal yearling male recruitment. A delayed shift in nesting habitat selection away from the infrastructure has been documented in southwestern Wyoming, a pattern consistent with adult females showing nest-site fidelity and yearling females avoiding gas fields (Holloran 2005). Although these studies suggest that the elimination of populations from energy fields may have resulted from the reaction of the yearling cohorts to developments, the response of yearling greater sage-grouse to development of natural gas fields has not been quantified. It is important to determine if yearlings are being primarily displaced or if development negatively influences demographics as these scenarios suggest different mitigation alternatives.

Our objectives were to determine if natural gas development influences habitat selection and demographics of yearling male and yearling female greater sage-grouse in southwestern

Wyoming. We investigated habitat selection and demographics relative to the locations of drilling rigs, producing well pads, and main haul roads. For males, we investigated the location of leks where yearlings established breeding territories, date of territory establishment, breeding-period lek tenacity, and annual and seasonal survival probabilities for both the yearling male cohort overall and for yearlings of known maternity. For females, we investigated nesting habitat selection, nesting propensity, dates-of-nest establishment, nest success, chick productivity, and annual and seasonal survival for both the overall yearling female cohort and for yearlings of known maternity.

**STUDY AREA**

The study area (42°60′ N, 109°75′ W) encompassed 17 leks primarily within the boundaries of the Pinedale Anticline Project Area (PAPA) and portions of the Jonah II gas field in the upper Green River Basin in southwestern Wyoming (Figure 1; Bureau of Land Management 2000). The study area covered approximately 255,000 ha (2,550 $km^2$) dominated by Wyoming big sagebrush (*Artemesia tridentata wyomingensis*) shrub-steppe habitats. Elevation ranged from 2,100 to 2,350 m and annual precipitation averaged 27.3 cm (Western Regional Climate Center, Reno, NV). Natural gas development and livestock grazing were the predominant human uses of the area (Bureau of Land Management 2000).

**FIELD METHODS**

We captured female greater sage-grouse on and near leks from mid-March through April in 2004 and 2005 by spot-lighting and hoop-netting (Giesen et al. 1982, Wakkinen et al. 1992). We secured radio transmitters to females with PVC-covered wire necklaces (Advanced Telemetry Systems Inc. [ATS], Isanti, MN, USA). Transmitters weighed 19.5 g, had a battery life expectancy of 530 days, and were equipped with motion sensors (i.e., radio-transmitter pulse rate increased in response to inactivity).

We used hand-held receivers and 3-element Yagi antennas (ATS) to monitor radio-marked females at least twice weekly through pre-laying (April) and nesting (May-June). We located nests of radio-marked birds by circling the signal source until females could be directly observed. We monitored incubating females after nest identification from a distance of ≥60 m to minimize chances of human-induced nest predation or nest abandonment. We established nest

fate (successful or unsuccessful) when radio monitoring indicated that the female had left the area. We considered nests successful if ≥1 egg hatched, indicated by presence of detached eggshell membranes (Wallestad and Pyrah 1974). We monitored unsuccessful females twice weekly for 2 weeks following nest failure to detect re-nests.

We located females that nested successfully 14 days post-hatch. We considered females with ≥1 chick to have been successful through the early brood-rearing stage. We based chick existence on either visual confirmation of chick(s) or the reaction of brooding females to the presence of a potential predator (i.e., the researcher; Schroeder et al. 1999). We relocated females for which no live chicks were detected at 14 days post-hatch 2 to 4 days following the initial location to confirm brood loss.

We monitored females that successfully raised ≥1 chick through the early brood-rearing stage from ≥100 m at least twice weekly through 10 weeks post-hatch. In late summer 2004 and 2005, we captured male and female chicks (e.g., hatch-year birds) that were ≥10 weeks old by spot-lighting radio-equipped brood-rearing females. We captured chicks with the brooding females using hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992). We weighted captured chicks to ensure that radio transmitters could be safely attached (Caccamise and Hedin 1985). We sexed captured chicks based on weights or plumage and aged the birds (to ensure captured grouse were hatch-year birds) based on the shape of the outermost wing primaries (Eng 1955). We collected blood samples by clipping the middle toenail and stored blood on Whatman FTA micro cards (Whatman 2005). We secured 16- or 19.5-g radio transmitters (depending on chick weight) to chicks with PVC-covered wire necklaces (ATS). Transmitters had battery life expectancies of 500 or 530 days, respectively, and were equipped with motion-sensors. We considered radio-equipped male chicks that survived to 1 March and female chicks that survived to 1 April the spring following capture the yearling sample.

**Yearling Males**

We collected lek visitation data for yearling males using data-logger stations (ATS) situated near 17 leks throughout the study area (Figure 1). Data loggers allowed for constant monitoring of leks during the breeding season. Radio-equipped yearlings visiting a monitored lek were recorded as being on or near that lek at specific dates and times.

***Data Loggers.***--Data-logger stations consisted of 1 data logger run by 2 deep-cycle recreational vehicle (RV) gel batteries charged by solar panels; all equipment was housed in metal Knaack® boxes. We mounted omni antennas on steel casing pipe such that the top of the antenna was 3 m high. Data loggers were attenuated (i.e., calibration of data logger sensitivity) to detect the entire area utilized by strutting males, and situated to minimize detection of birds using non-strutting habitat surrounding leks. We set data loggers to scan for ATS transmitters (Model A4000) with 35 and 45 pulse per minute (PPM) signals. Due to the possible effects of cold weather on transmitter pulse rates, we allowed a tolerance of 1 (e.g., 35 PPM: 34-36 was recorded; 45 PPM: 44-46 was recorded). We directly accessed stations when leks were not occupied (e.g., non-crepuscular periods) and downloaded data loggers to a laptop computer at least twice during the breeding season. We placed reference transmitters at each data-logger station to verify logging accuracy on all downloads. We monitored leks annually from 1 April to 15 May.

***Lek Counts.***--Annual lek counts on the 17 monitored leks were conducted by personnel from the Wyoming Cooperative Fish and Wildlife Research Unit (COOP), the Wyoming Game and Fish Department (WGFD), and the Pinedale field office of the BLM. Lek counts were conducted according to standardized methods outlined by the WGFD's Sage-Grouse Technical Committee (Cheyenne, WY, USA; also see Connelly et al. 2003:19-20).

***Survival.***--We used hand-held telemetry equipment (ATS) to locate yearling males during the breeding season to assess survival. Annual survival for yearling males was assessed from 1 March through the end of February. We assessed survival directly between 1 April and 15 May by locating males weekly. From 15 May through August, we located males from long-range bi-weekly and used transmitter pulse-rates (e.g., motion sensors) to assess survival. Survival from 1 September through March was assessed using fixed-wing aircraft (Mountain Air Research, Driggs, ID, USA; Sky Aviation, Dubois, WY, USA). Flights were conducted at least bi-monthly and we used motion-sensors to evaluate whether individuals were dead or alive.

**Yearling Females**

***Demographics.***--We assessed yearling female demographics similarly to those described for the original sample of radio-equipped females. We used hand-held telemetry equipment (ATS) to locate nests by circling the signal source until females could be directly observed. We

monitored incubating females from a distance of ≥60 m to minimize abandonment risks. Nest fate (successful or unsuccessful) was established when radio monitoring indicated that the female had left the area; we considered nests successful if ≥1 egg hatched, indicated by presence of detached eggshell membranes (Wallestad and Pyrah 1974). We monitored unsuccessful yearling females twice weekly for 2 weeks following nest failure to assess re-nesting attempts.

We located yearling females that nested successfully weekly from hatch through 35 days post-hatch. We considered females with ≥1 live chick to have been successful through each brooding stage. We based chick existence during the early brooding stage (i.e., hatch through 2 weeks post-hatch) on either visual confirmation of chick(s) or the reaction of brooding females to the presence of a potential predator (i.e., the researcher; Schroeder et al. 1999). During the 2005 late-brooding stages, we obtained fledge estimates (i.e., the number of chicks per brood) by spot-light surveys conducted during trapping. In 2006, we obtained fledge estimates from spot-light surveys conducted 35 days post-hatch (Walker et al. 2006). We relocated females found without live chicks during any of these stages 2 to 4 days following the initial location to confirm brood loss.

***Survival.--***We assessed annual survival for yearling females from 1 April through March. We located all females twice weekly between 1 April and hatch (approximately 15 June), and brooding females weekly from hatch through August. We assessed survival directly from observations during these periods. We monitored barren females from long-range weekly from nest loss through June, and bi-weekly from July 1 through August; motion sensors were used to evaluate barren female survival during these stages. We assessed survival from 1 September through March for all females from fixed-wing aircraft (Mountain Air Research, Driggs, ID, USA; Sky Aviation, Dubois, WY, USA). Flights were conducted at least bi-monthly and we used the motion sensors to evaluate whether individuals were dead or alive.

## STATISTICAL METHODS

### Infrastructure of Natural Gas Fields

We mapped features of the infrastructure of natural gas fields within 5 km (Holloran and Anderson 2005) of the 17 monitored leks using ArcGIS 9 (Environmental Systems Research Institute [ESRI], Redlands, CA, USA). We mapped producing well pads, drilling rigs, and main haul roads; state highways, the Paradise Road, and the Green River Road were included as main

haul roads (Figure 1). We obtained infrastructure location, drilling activity date, and well producing date information from the Wyoming Oil and Gas Conservation Commission and verified these data using information supplied by Western Ecosystems Technology, Inc. (Cheyenne, WY, USA), Edge Environmental, Inc. (Laramie, WY, USA), individual gas companies (i.e., operators) responsible for specific wells, and through direct ground-truthing using hand-held, 12 channel, Garmin RINO 110 Global Positioning System units (Garmin International, Olathe, KS, USA). Infrastructure data were dynamic and were modified to reflect the conditions encountered seasonally. We considered well pads with multiple producing wells single active locations.

**Maternity**

We established yearling maternity using microsatellite polymerase chain reaction (PCR) analyses of DNA extracted from blood samples collected during trapping (Taylor et al. 2003, Hawk et al. 2004); 5 primers were used in the analysis (LLSD4, LLSD8, LLST1, SGCA11, and SGCTAT1; Wyoming Game and Fish Laboratory, Laramie, WY, USA). We obtained genotypes following methods described by Frantz et al. (2003). We determined maternity using program Cervus 3.0.3 (Marshall et al. 1998). The simulated population genetic structure was based on 10,000 simulations with 5,000 potential parents, 1% of the candidate parents sampled, and 25% relatedness. Candidate mothers were all females identified by the analysis with ≥80% confidence in parentage assignment. We based final maternal assignment on trap location; if a chick was trapped from the same flock as a candidate mother, maternity was assigned.

We estimated natal areas as the area within 1.9 km of natal nests. We used this distance because 1.9 km represents the mean radius of home ranges during early brood-rearing (Drut et al. 1994) and the upper 95% confidence limit of the mean distance from nest to early brood-rearing locations (Lyon 2000, Slater 2003). We defined natal treatment yearlings as any yearling whose natal area contained >1 producing well pad or >1 km of main haul road; all others were considered natal control yearlings. The inclusion of natal areas with 1 well or a short distance of main haul road in the control population was to guard against including yearlings raised in areas with isolated well pads (e.g., wildcat wells) as treatment birds.

**Greater Sage-grouse Yearling Variables**

***Survival.--***We estimated yearling male annual (March-February), yearling female annual (April-March), and monthly survival estimates and standard errors using the staggered entry Kaplan-Meier estimator (Pollock et al. 1989). We censored birds that were not found during any monthly period. We combined monthly survival estimates into sexually distinct seasonal periods: for males, breeding (Mar.-May), summer (June-Aug.) and winter (Sept.-Feb.); and for females nesting (April-June), summer (July-Aug.) and winter (Sept.-Mar.).

***Overall Lek Recruitment.--***We estimated overall lek recruitment of males annually from lek counts. We estimated the number of males recruited to a lek as the annual change in the maximum number of males minus the number of adult males expected to return to a lek the following year (37%; Zablan et al. 2003).

***Yearling Male Demographics.--***We based lekking demographics of yearling males on information from data loggers or telemetry. Logged signals consisted of the date, time, transmitter frequency, signal strength, number of pulses recorded in 15 seconds, transmitter pulse-per-minute (PPM) value, and the number of pulse matches (ATS algorithms). The steps taken for distinguishing radio-transmitter detection versus interference included: (1) signals that logged at a PPM outside the range of values set for the data-logger were discounted as interference (e.g., PPM <34, 37-43, >47). (2) Given transmitter pulse rates of either 35 or 45 PPM, the data-loggers accepting pulse rates of 36 and 46 PPM, respectively for these transmitter types, and a 15 second scan time, the number of pulses detected for 35 PPM transmitters had to be $\leq 9$ ([36 PPM/60 sec] × 15) and for 45 PPM transmitters $\leq 12$ ([46 PPM/60 sec] × 15); if the number of pulses matched was outside these ranges, logged signals were discounted as interference. Logged signals remaining were potential birds. We primarily used pulse match to pulse detected ratios (e.g., the number of matched pulses relative to the number of detected pulses) and the number of logs over a given time period to validate remaining detections as birds. We established the protocol for assessing bird probabilities using pulse match-to-detected ratios and the number of detections by evaluating data from reference collar logs. Reference collar downloads suggested a high pulse match-to-detected ratio, numerous detections, and a recorded pulse count >4 and <30 was a validated detection of a radio-transmitter and not interference. Numerous logs by the same frequency, especially numerous within the same relative time period, with high pulse match-to-detected ratios, had higher potential to be a confirmed bird detection.

We did not consider those frequencies only logged once as bird detections until compared with future data and telemetry locations. We consulted ATS experts for verification of questionable data. We considered confirmed yearling male detections between 0430 and 0730 hours daily lek visits.

The average date that radio-equipped yearling males were first documented on established leks was April 8; thus yearlings were available to be logged for 37 days. Because yearling male daily lek attendance rates in a previous study averaged 19% (Walsh et al. 2004), we considered a bird to have established on a particular lek if it had ≥7 confirmed daily lek visits during the monitoring period. We assessed lek establishment of males not detected on data-logger-monitored leks using telemetry data. A yearling male had to be detected on a lek ≥3 times during the crepuscular daily breeding period between 1 April and 15 May to verify establishment. The date of establishment was estimated as the first day yearling males were documented on the lek where established. Yearling male lek tenacity was estimated as the total number of confirmed daily lek visits on the lek where established. The number of different leks visited by yearling males was estimated as the number of leks with ≥1 confirmed daily lek visit(s), and included leks where established. We only estimated establishment dates, lek tenacity, and number of different leks visited for yearlings that visited leks monitored by data-loggers.

Distance from natal nest-to-established lek was estimated as the straight-line distance from the nest site where a yearling male hatched to the lek where he established the following spring. The probability of establishing a breeding territory on a lek was estimated as the number of yearling males with confirmed lek establishment divided by the total number of available males. Available males survived the breeding season and were those we actively attempted to document establishment leks using telemetry (i.e., those monitored during the breeding season).

***Nest Site Designations (Yearling Females).***--Females that nested within 930 m of an infrastructure feature of a natural gas field were considered to have been potentially influenced by infrastructure (i.e., nesting treatment females); those nesting outside the 930-m buffer were considered nesting control females (Figure 2). The 930-m buffer represented the upper limit of the 95% confidence interval around mean distances between consecutive year's nests and, due to nesting area fidelity, represented a female's life-time nesting area (Holloran and Anderson 2005).

Natal nesting areas were an estimate of the area around the natal nest where a yearling female will usually select a nest location. We used the upper limit of the 95% confidence interval around the mean natal nest-to-yearling nest distances for females raised in areas without the infrastructure of natural gas fields to establish the natal nesting area.

***Yearling Female Demographics.***--Nesting propensity was estimated as the number of females initiating a nest divided by the total number of yearlings intensively monitored throughout the entire nesting season. We did not include females found for the first time after 15 May annually in nesting propensity estimates (15 May represented the latest date of incubation initiation based on mean latest hatch date and 27 days to incubate a clutch [Schroeder et al. 1999]). The date of nest establishment was the first day females were documented on a nest. Apparent nest success was the number of successfully hatched nests divided by the total number of known nests. Early brood-rearing success was the number of females successfully raising ≥1 chick through 14 days post-hatch divided by the total number of successfully nesting females monitored through the early brood-rearing period. Overall brood-rearing success was the number of females successfully fledging ≥1 chick divided by the total number of successfully nesting females that were monitored throughout the entire brood-rearing period. Natal nest-to-yearling nest distances were estimated as the straight-line distance from the nest site where a yearling female hatched to her first nest the following spring.

**Yearling Male Comparisons**

We investigated overall male recruitment to monitored leks and radio-equipped yearling male lek establishment relative to the distance of leks to infrastructure of natural gas fields. We also investigated yearling male lek establishment demographics and survival relative to infrastructure impacts to natal areas.

***Overall Recruitment.***--We used Chi-square tests with continuity corrections (due to sample sizes <25 in certain instances; Dowdy and Wearden 1991) to compare overall recruitment of males among leks. Although we assumed that the number of recruited males was related to lek size, the relationship was probably not 100% correlated. Therefore, we established expected proportions using a scaled allocation of the total recruited population. Leks with ≤50 total males the preceding year were expected to recruit either 4.5 or 5%, leks with >50 and ≤100 males were expected to recruit either 7 or 8.5%, and leks with ≥100 males were expected to recruit either 9.5

or 12.25% of the total recruited population. We used different proportions annually because some of the leks changed size categories between years, and we needed the total proportion of the expected population to sum to 100%. We categorized leks as those recruiting more, less, or equal to the expected number of males. We compared categories by distance to closest active drilling rig, producing well pad, and main haul road using 95% confidence interval overlap.

***Lek Establishment.***--We generated minimum convex polygons (Kenward 1987) around all producing well pads, and categorized monitored leks as either: contained within the polygon, ≤2 km outside, between 2 and 5 km outside, or >5 km outside the polygon. We used Chi-square tests with continuity corrections (Dowdy and Wearden 1991) to compare the number of radio-equipped yearling males establishing on leks by category (i.e., observed establishment). We assumed equal availability between leks for each yearling male, thus expected proportions were based on the total number of leks within each buffer. We compared dates-of-establishment, lek tenacity, and annual and seasonal survival by buffer using 95% confidence interval overlap.

***Natal Areas.***--We compared the probability of establishing a breeding territory on a lek between natal treatment and natal control yearling males using Chi-square tests with continuity corrections (Dowdy and Wearden 1991). We determined the expected establishment rate from the control population (e.g., results suggest a difference between natal treatment and natal control groups). We compared the number of different leks visited during the breeding season, the distance from natal nest-to-established lek, dates-of-establishment, lek tenacity, and annual and seasonal survival by natal area category using 95% confidence interval overlap.

**Yearling Female Comparisons**

***General Habitat Selection.***--We investigated habitat selection of yearling females relative to infrastructure features of natural gas fields by comparing nesting treatment and nesting control females using Chi-square tests with continuity corrections (Dowdy and Wearden 1991). We estimated the expected number of nests per category as the proportion of the total area within 5 km of trapped leks (Holloran and Anderson 2005) that was within 930 m of an infrastructure variable (Figure 2). We only considered nests located within the 5-km buffer in the comparison.

We assumed suitable nesting habitats were sagebrush and desert shrub-dominated areas within 2 standard deviations of the mean roughness of nest sites located within the 5-km buffer

between 2000 and 2006 (Holloran 2005). Jensen (2006) suggested roughness (i.e., the ratio of actual surface area to planimetric area) was the terrain measure best distinguishing greater sage-grouse nests from available locations in southwestern Wyoming. We used Gap Analysis Program (GAP) landcover layers (Wyoming Geographic Information Science Center (WyGISC), University of Wyoming, Laramie, WY, USA) to identify sagebrush and desert shrub-dominated areas, and Hawth's Analysis Tools 3 (Beyer 2004) within ArcView 3 (ESRI, Redlands, CA, USA) to calculate roughness from digital elevation models (DEM; WyGISC). We compared the proportion of suitable nesting habitat within 930 m of infrastructure and outside of the 930-m buffer but within the 5-km buffer to investigate if the proportion of suitable habitat in compared areas differed.

***Overall Demographics.--***We used nesting or spring locations to categorize all yearling females as treatment (i.e., within 930 m of infrastructure) or control individuals (Figure 2). Differences in nesting propensity, apparent nest success, early brood-rearing success, and overall brood-rearing success were investigated using Chi-square tests with continuity corrections (Dowdy and Wearden 1991). We established expected proportions from the control population (e.g., results suggest a difference between treatments and controls). The date of nest establishment, and annual and seasonal survival were compared between categories using 95% confidence interval overlap.

***Natal Areas.--***We compared nesting propensity and apparent nest success between natal treatment and control yearling females using Chi-square tests with continuity corrections (Dowdy and Wearden 1991). We determined expected nesting propensity and success rates from the control population. Distances from the natal nest to the yearling's nest, date of nest initiation, and annual and seasonal survival differences between treatment and control populations were compared using 95% confidence interval overlap.

To examine nest site selection of yearling females relative to where they were raised and the existence of infrastructure features of natural gas fields, we compared the proportion of yearlings with infrastructure in the natal nesting area (i.e., the area around the natal nest where a yearling female will usually select a nest location) that nested within and beyond 930 m of infrastructure using Chi-square tests with continuity corrections (Dowdy and Wearden 1991). We used all natal nesting areas with infrastructure present in the analysis. We estimated the expected number of nests per category (i.e., within or beyond 930 m of infrastructure) as the

proportion of the total natal nesting area (i.e., all natal nesting areas with gas field infrastructure present combined) within 930 m of infrastructure.

Because of relatively small sample sizes and the possibility that single measures could disproportionately influence results, we identified influential observations and considered those when interpreting results. We performed statistical procedures with MINITAB 13.1 (Minitab Inc., State College, PA, USA). We estimated distance variables (km) using ArcGIS 9 (ESRI).

## RESULTS

We radio-tagged 64 male and 76 female chicks (45 males and 39 females during fall 2004; 19 males and 37 females during fall 2005). Between capture and yearling status designation, 41 chicks died, 7 lost the radio-transmitter (based on field sign at retrieved transmitter location), and 6 were never found. Thirty-four male and 52 female radio-equipped chicks were available as yearlings at the beginning of the breeding season monitoring periods. Maternity was confirmed for 16 male and 17 female yearlings, and breeding-season data were collected on 15 males and 16 females with known maternity.

Because of sample size constraints, we chose to use conservative statistical approaches when comparing treatment and control groups of yearlings.

### Yearling Male Comparisons

***Overall Recruitment.--***Leks that recruited fewer than expected males were significantly closer to producing well pads, and tended to be closer to main haul roads compared to leks that recruited the same number of males as expected. Generally, greater sage-grouse leks that recruited significantly less than expected numbers of males were closer to infrastructure features of natural gas fields than those that recruited equal to or significantly more males than expected. Leks that recruited more than expected males were consistently closer to infrastructure than those that recruited the same number of males as expected (Table 1; Figure 3).

***Lek Establishment.--***The proportion of radio-equipped yearling males that established on leks inside and outside the development boundaries (as designated by minimum convex polygons around producing well pads) of the natural gas field differed significantly from that expected assuming equal establishment probabilities for all leks ($\chi^2_1 = 4.54$; $P = 0.03$; Table 2). Yearling males establishing on leks within the interior (2) were less than expected (7.4), while numbers

establishing on leks outside the development boundaries (23) were more than expected (17.6). The number of radio-equipped yearling males that established on leks outside development and categorized by distance to the development boundary did not differ from expected ($\chi^2_2 = 0.12$; $P = 0.94$; Table 2).

Mean date of establishment, lek tenacity, and annual survival of yearling males did not differ inside and outside gas fields (Table 2).

***Natal Areas.***--Lek tenacity of natal treatment and natal control yearling males did not differ. However, after removing a natal treatment male (e.g., male reared in an area with infrastructure of natural gas fields present) that was documented on a lek 2.5 times as often as any other treatment male, lek tenacity of treatment males (9.3 days) was significantly less than control males (22.8 days; Table 3). Annual survival of natal treatment yearling males (52.5%) was significantly lower than natal control yearling males (100%; Table 3). Additionally, although not significantly different ($\chi^2_1 = 1.53$; $P = 0.22$), the estimated probability of natal treatment yearling males establishing on a lek was half that of natal control yearling males; 7 of 7 control yearling males and 4 of 8 treatment yearling males established breeding territories. The number of different leks visited during the breeding season, distance from natal nest-to-established lek, dates-of-establishment, and seasonal survival probabilities did not differ between natal treatment and control yearling males (Table 3).

**Yearling Female Comparisons**

***General Habitat Selection.***--The proportion of radio-equipped yearling females that selected nest locations within 930 m of an infrastructure feature of the natural gas fields and those nesting outside the 930-m buffer differed significantly from that expected assuming spatially proportional selection of nest locations ($\chi^2_1 = 4.10$; $P = 0.04$). The number of yearling female nests located within 930 m of infrastructure (6) was less than expected (11.5), while nest numbers located outside the buffer (19) were more than expected (13.5). The proportions of area assessed to be suitable nesting habitat within (75.1%) and outside (80.9%) the 930-m buffer were similar.

***Overall Demographics.***--Nesting propensity, apparent nest success, early brood-rearing success, and overall brood-rearing success did not differ between treatment (i.e., nesting within 930 m of gas field infrastructure) and control individuals ($\chi^2_1 < 0.12$; $P > 0.72$; Table 4). Date of

nest establishment and annual survival were not related to nest location treatment status (Table 4).

***Natal Areas.--***Annual survival of natal treatment yearling females (69.4%) was significantly lower than natal control yearling females (100%; Table 5). Nesting propensity and nest success probabilities were not related to natal area ($\chi^2_1 < 0.13$; $P > 0.71$; Table 5). Natal nest-to-yearling nest distances, nest initiation dates, and seasonal survival did not differ between natal treatment and control yearling females (Table 5).

The upper limit of the 95% confidence interval around the mean natal nest-to-yearling nest distances for natal control females suggested that a 4.0-km buffer around natal nesting locations represented the area around the natal nest where a yearling female typically selected a nest location (i.e., natal nesting area; Table 5). There was weak evidence that the proportion of natal yearling females reared near infrastructure that selected nest locations within 930 m of infrastructure and those that nested outside the 930-m buffer differed from that expected assuming spatially proportional selection of nest locations ($\chi^2_1 = 3.49$; $P = 0.06$). The number of yearling female nests located within 930 m of infrastructure (3) was less than expected (6.3), while nest numbers located outside the buffer (7) were more than expected (3.7).

## DISCUSSION

Energy development impacts to greater sage-grouse populations typically result from a combination of demographic and behavioral responses (i.e., cumulative effects) affecting different age classes. Our results suggest that avoidance of infrastructure by breeding yearlings, decreased yearling survival, and reduced fecundity of yearling males contribute to abandonment of leks and nesting habitat within natural gas fields.

Greater sage-grouse leks situated near the infrastructure of natural gas fields recruited fewer males than expected. Because of lek tenacity by adult males (Patterson 1952, Wiley 1973, Gibson 1992), a majority of the birds recruited were probably yearling males. There was also a tendency for leks situated on the periphery of the fields to recruit a higher proportion of yearling males than those farther from disturbance, suggesting that yearling males avoid natural gas fields and move to the periphery of the fields when establishing breeding territories. Additionally, yearling males reared in areas with infrastructure features of natural gas fields were less likely to establish a breeding territory, did not occupy leks during the breeding period as tenaciously, and

had lower annual survival than males reared in areas with no activities associated with natural gas fields. Dunn and Braun (1985) suggested that leks selected by yearling males were spatially associated to natal areas. Thus, decreased fecundity may be in response to anthropogenic activity encountered either as chicks, or in response to conditions encountered during inaugural breeding seasons. Regardless, natural gas development appeared to influence negatively both the breeding-season distribution and success of the yearling male population.

Greater sage-grouse yearling females generally avoided nesting within 930 m of the infrastructure of natural gas field. Yearling females with natural gas infrastructure present in their natal nesting area also generally avoided nesting within 930 m of infrastructure; this general avoidance results in the functional loss of at least the habitats within 930 m of infrastructure. However, distance from natal-nest to first-year-nest locations did not differ, suggesting that yearling females did not vacate natal areas but simply avoided nesting near infrastructure within natal areas. Holloran (2005) suggested that the eventual response of greater sage-grouse nesting populations will be avoidance of natural gas development, but the avoidance response would be driven by habitat selection of yearling females due to nesting-area fidelity of adult females. Further, Wiens et al. (1986) suggested that site fidelity in breeding birds could delay population response to habitat changes, and that a clear response required that most site-tenacious individuals be dead. Fidelity of adults to nesting areas and fidelity of yearlings to natal areas may delay a population-level avoidance response, and may explain time lags between the development of gas fields and the abandonment of gas fields by greater sage-grouse found in previous studies (Holloran 2005, Walker et al. 2007).

Yearling females reared in areas with natural gas infrastructure had lower annual survival rates than females reared in areas without infrastructure. However, we detected no negative effects of natal-area condition on productivity. These results are similar to analyses investigating population growth differences between anthropogenically disturbed and undisturbed populations that attributed differences in population growth to lower female annual survival in impacted populations (Hagen 2003, Holloran 2005). Natural gas development appeared to influence negatively both the nesting-season distribution and annual survival of the yearling female population.

## MANAGEMENT IMPLICATIONS

The results from this study suggest that dispersal of yearling greater sage-grouse from the infrastructure of natural gas fields and demographic impacts are contributing to abandonment of leks and nesting habitat within natural gas fields. This implies that developing a natural gas field reduces the extent of the landscape used by sage-grouse populations. Sage-grouse populations typically inhabit large, unbroken expanses of sagebrush and are characterized as a landscape-scale species (Patterson 1952, Connelly et al. 2004). Thus, preserving sagebrush-dominated areas within an impacted landscape as refugia may be necessary to maintain remnant sage-grouse populations. To ensure that viable populations are conserved, we recommend managers rely on seasonal habitat selection and movement information collected from individual sage-grouse residing in proposed refugia to determine appropriate refugia size and configuration. Additionally, if impacts continue through the gas field production phases as suggested by Aldridge and Brigham (2003) and Walker et al. (2007), refugia will have to be maintained until developed areas are re-occupied by sustainable sage-grouse populations (gas well life-expectancy estimated at 25 to 40 years for the types of formations encountered in the PAPA; Wyoming Oil and Gas Conservation Commission, personal communication 2005).

Dispersal corridors may be needed to ensure the maintenance of the genetic diversity of sage-grouse populations potentially isolated into refugia, and to allow for immigration if a stochastic natural event (i.e., drought, fire, disease outbreak) eliminates a protected population. Sage-grouse can disperse long distances between seasonal ranges (Connelly et al. 2000*b*), and are physically capable of traversing natural gas fields. However, because of strong adult fidelity to breeding sites (Patterson 1952, Wiley 1973, Gibson 1992, Fischer et al. 1993, Schroeder and Robb 2003, Holloran and Anderson 2005) and the propensity of yearling females to nest near natal areas, large-scale movements of individuals does not necessarily equate to the dispersal of genetic material nor the functional immigration of individuals. If genetic diversity is maintained through the dispersal of yearling males, and yearlings tend to establish breeding territories on leks near natal areas, the abandonment of leks situated between distinct population segments may genetically isolate those segments. We recommend research investigating the mechanisms responsible for the dispersal of greater sage-grouse genetic information throughout a landscape.

Sage-grouse survival and fecundity have been linked to sagebrush-steppe habitat quality, and the dependence of the species on sagebrush through all seasonal periods has been well

documented (see Connelly et al. 2004 for review). Sagebrush habitat enhancements typically entail manipulation of shrub overstories in an attempt to increase herbaceous understories and improve brood survival (e.g., prescribed fire, herbicide application). However, no research to date has shown a positive response of sage-grouse populations to sagebrush treatment (Wallestad 1975, Martin 1990, Fischer et al. 1996). In fact, large-scale shrub manipulations, particularly in winter, nesting, or year-round habitats may result in population declines (Swenson et al. 1987, Connelly et al. 2000*a*, Nelle et al. 2000). We recommend that land managers exercise extreme caution in applying shrub manipulations (Connelly et al. 2000*b*, Dahlgren et al. 2006), and focus instead on management options that enhance or restore herbaceous understories within sagebrush stands (e.g., via livestock grazing management [Beck and Mitchell 2000]). The establishment of interconnected refugia managed to sustain robust populations will help ensure that greater sage-grouse are present to re-colonize natural gas fields following reclamation.

## ACKNOWLEDGMENTS

We give special recognition to Dr. S. H. Anderson. Through his tenure at the Wyoming Cooperative Fish and Wildlife Research Unit, Dr. Anderson was instrumental in initiating and sustaining greater sage-grouse research throughout Wyoming; he was the principle investigator for 11 major projects from 1994 to 2005. He provided substantial assistance during this research, and his guidance and friendship were invaluable. Financial support was provided by the Bureau of Land Management, U.S. Department of Energy, Ultra Resources, Inc., and Shell Rocky Mountain Production. We thank all the landowners in the upper Green River Basin that allowed access to private lands. Field assistance was provided by Jacob Anderson, Steve Huber, Derek Jacobson, Lee Knox, John Michalak, Tyler Parker, Steve Slater, Ryan Stewart, Jesse Swift, Jay Vick, and Dale Woolwine. Technical assistance was provided by Western EcoSystems Technology, Inc. (Cheyenne, WY, USA), Edge Environmental, Inc. (Laramie, WY, USA), BLM Pinedale field office (Pinedale, WY, USA), and the WGFD Jackson/Pinedale regional office (Pinedale, WY, USA). Telemetry flights and lek surveys were conducted with the assistance of Mountain Air Research (Driggs, ID, USA) and Sky Aviation (Dubois, WY, USA). This report was greatly improved through critical reviews by T. J. Christiansen (sage-grouse program coordinator; WGFD), D. E. Naugle (professor in the Wildlife Biology Program;

University of Montana), E. T. Rinkes (wildlife biologist; Bureau of Land Management Idaho State Office), and B. L. Walker (wildlife biologist; Colorado Division of Wildlife).

**LITERATURE CITED**

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered Greater Sage-Grouse. Ecological Applications 117:508-526.

Aldridge, C. L., and R. M. Brigham. 2003. Distribution, abundance, and status of the greater sage-grouse, *Centrocercus urophasianus*, in Canada. Canadian Field-Naturalist 117:25-34.

Beck, J. L., and D. L. Mitchell. 2000. Influences of livestock grazing on sage grouse habitat. Wildlife Society Bulletin 28:993-1002.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.

Braun, C. E. 1986. Changes in sage grouse lek counts with advent of surface coal mining. Proceedings: Issues and Technology in the Management of Impacted Western Wildlife, Thorne Ecological Institute 2:227-231.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139-156.

Braun, C. E., O. O. Oedekoven, and C. L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage grouse. Transactions North American Wildlife and Natural Resources Conference 67:337-349.

Bureau of Land Management. 2000. Record of decision, environmental impact statement for the Pinedale anticline oil and gas exploration and development project Sublette County, Wyoming. United States Bureau of Land Management, Pinedale, WY, USA.

Caccamise, D. F., and R. S. Hedin. 1985. An aerodynamic basis for selecting transmitter loads in birds. Wilson Bulletin 97:306-318.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of Greater Sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, WY, USA.

Connelly, J. W., K. P. Reese, R. A. Fischer, and W. L. Wakkinen. 2000*a*. Response of sage grouse breeding population to fire in southeastern Idaho. Wildlife Society Bulletin 28:90-95.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station publication No. 979, University of Idaho, Moscow, ID, USA.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000*b*. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:1-19.

Dahlgren, D. K., R. Chi, and T. A. Messmer. 2006. Greater sage-grouse response to sagebrush management in Utah. Wildlife Society Bulletin 34:975-985.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal Wildlife Management 72:In press.

Dowdy, S. M., and S. Wearden. 1991. Statistics for research second edition. John Wiley & Sons, Inc., New York, NY, USA.

Drut, M. S., J. A. Crawford, and M. A. Gregg. 1994. Brood habitat use by sage grouse in Oregon. Great Basin Naturalist 54:170-176.

Dunn, P.O., and C.E. Braun. 1985. Natal dispersal and lek fidelity of sage grouse. Auk 102:621-627.

Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal Wildlife Management 19:267-272.

Fischer, R. A., A. D. Apa, W. L. Wakkinen, and K. P. Reese. 1993. Nesting-area fidelity of sage grouse in southeastern Idaho. Condor 95:1038-1041.

Fischer, R. A., K. P. Reese, and J. W. Connelly. 1996. An investigation of fire effects within xeric sage grouse brood habitat. Journal Range Management 49:194-198.

Frantz, A. C., L. C. Pope, P. J. Carpenter, T. J. Roper, G. J. Wilson, R. J. Delahay, and T. Burke. 2003. Reliable microsatellite genotyping of the Eurasian badger (*Meles meles*) using faecal DNA. Molecular Ecology 12:1649-1661.

Gibson, R. M. 1992. Lek formation in sage grouse: the effect of female choice on male territorial settlement. Animal Behaviour 43:443-450.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224-231.

Hagen, C. A. 2003. A demographic analysis of Lesser Prairie-Chicken populations in southwestern Kansas: survival, population viability, and habitat use. PhD Dissertation, Kansas State University, Manhattan, KS, USA.

Hawk, D., K. Sargeant, and S. Sharpe. 2004. Wyoming Game and Fish laboratory forensic procedure manual and molecular diagnostic protocols for fish health. Wyoming Game and Fish Department, Laramie, WY, USA.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. PhD Dissertation, University of Wyoming, Laramie, WY, USA.

Holloran, M. J., and S. H. Anderson. 2004. Greater sage-grouse population response to natural gas development in western Wyoming: are regional populations affected by relatively localized disturbances? Transactions North American Wildlife and Natural Resources Conference 70:In press.

Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742-752.

Jensen, B. M. 2006. Migration, transition range and landscape use by greater sage-grouse (*Centrocercus urophasianus*). MS Thesis, University of Wyoming, Laramie, WY, USA.

Kenward, R. 1987. Wildlife Radio Tagging: Equipment, Field Techniques and Data Analysis. Academic Press, London.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634.

Lyon, A. G. 2000. The potential effects of natural gas development on sage grouse near Pinedale, Wyoming. MS Thesis, University of Wyoming, Laramie, WY, USA.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486-491.

Marshall, T. C., J. Slate, L. E. B. Kruuk, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology 7:639-655.

Martin, R. C. 1990. Sage grouse responses to wildfires in spring and summer habitats. MS Thesis, University of Idaho, Moscow, ID, USA.

Nelle, P. J., K. P. Reese, and J. W. Connelly. 2000. Long-term effect of fire on sage grouse nesting and brood-rearing habitats in the Upper Snake River Plain. Journal Range Management 53-586-591.

Oyler-McCance, S. J. 1999. Genetic and habitat factors underlying conservation strategies for Gunnison sage-grouse. PhD Dissertation, Colorado State University, Fort Collins, CO, USA.

Patterson, R. L. 1952. The Sage grouse in Wyoming. Sage Books, Inc., Denver, CO, USA.

Pitman, J. C., C. A. Hagen, R. J. Robel, T. M. Loughin, R. D. Applegate. 2005. Location and success of lesser prairie-chicken nests in relation to vegetation and human disturbance. Journal of Wildlife Management 69:1259-1269.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: The staggered entry design. Journal of Wildlife Management 53:7-15.

Remington, T. E. and C. E. Braun. 1991. How surface coal mining affects sage grouse, North Park, Colorado. Proceedings, Issues and Technology in Management of Impacted Western Wildlife. Thorne Ecological Institute 5:128-132.

Robel, R. J., J. A. Harrington Jr., C. A. Hagen, J. C. Pitman, and R. R. Reker. 2004. Effect of energy development and human activity on the use of sand sagebrush habitat by lesser prairie-chickens in southwestern Kansas. Transactions of the North American Natural Resources Conference 69:251-266.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of Sage-grouse in North America. Condor 106:363-376.

Schroeder, M. A., and L. A. Robb. 2003. Fidelity of Greater Sage-Grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildlife Biology 9:291-299.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Pages 1-28 *in* A. Pool and F. Gill [eds.], The Birds of North America, No. 425. The Birds of North America, Inc. Philadelphia, PA, USA.

Slater, S. J. 2003. Sage-grouse (*Centrocercus urophasianus*) use of different-aged burns and the effects of coyote control in southwestern Wyoming. MS Thesis, University of Wyoming, Laramie, WY, USA.

Swenson, J. E., C. A. Simmons, and C. D. Eustace. 1987. Decrease of sage grouse Centrocercus urophasianus after ploughing of sagebrush steppe. Biological Conservation 41:125-132.

Taylor, S. E., S. J. Oyler-McCance, and T. W. Quinn. 2003. Isolation and characterization of microsatellite loci in greater sage-grouse (*Centrocercus urophasianus*). Molecular Ecology Notes 3:262-264.

U.S. Fish and Wildlife Service. 2005. Endangered and threatened wildlife and plants; 12-month finding for petitions to list the greater sage-grouse as threatened or endangered; proposed rule. Federal Register 70:2244-2282.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425-426.

Walker, B. L., K. E. Doherty, and D. E. Naugle. 2006 (*abstract only*). Spotlight counts: A new method for assessing chick survival in greater sage-grouse. University of Montana, Missoula, MT, USA.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse habitat response to energy development and habitat loss. Journal Wildlife Management 51:In press.

Wallestad, R. O. 1975. Life history and habitat requirements of sage grouse in central Montana. Montana Fish and Game Department Technical Bulletin, Helena, MT, USA.

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. Journal Wildlife Management 38:630-633.

Walsh, D. P., G. C. White, T. E. Remington, and D. C. Bowden. 2004. Evaluation of the lek-count index for greater sage-grouse. Wildlife Society Bulletin 32:56-68.

Whatman. 2005. Available at www.whatman.com/products/?pageID=7.31.31.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1986. A lesson in the limitations of field experiments: shrubsteppe birds and habitat alteration. Ecology 67:365-376.

Wiley, R. H., Jr. 1973. Territoriality and non-random mating in sage grouse, *Centrocercus urophasianus*. Animal Behavior Monographs 6:85-169.

Zablan, M. A., C. E. Braun, and G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal Wildlife Management 67:144-154.

Table 1. Mean (95% confidence interval [95% CI]) distance (km) from greater sage-grouse leks to natural gas field infrastructure in southwestern Wyoming, 2005-06. Leks were categorized as recruiting significantly less than, equal to, or more than expected numbers of males based on Chi-squared analyses of annual changes in the maximum number of males documented on leks during lek count procedures. Notice that leks recruiting fewer than expected males were those relatively close to gas field infrastructure and that leks recruiting more than expected males tended to be closer to development than those recruiting the same number of males as expected (suggesting yearling dispersal to the periphery of developing energy fields).

| Relative Number of Males Recruited | n[a] | Distance Drill Rig | | Distance Well Pad | | Distance Haul Road | |
|---|---|---|---|---|---|---|---|
| | | mean | 95% CI | mean | 95% CI | mean | 95% CI |
| Less than expected | 11 | 3.6 | (2.4, 4.8) | 1.7 | (0.6, 2.7) | 2.2 | (1.0, 3.4) |
| Equal to expected | 10 | 6.1 | (4.0, 8.2) | 5.0 | (2.9, 7.1) | 4.0 | (3.2, 4.8) |
| More than expected | 9 | 5.9 | (3.8, 8.0) | 4.0 | (2.0, 5.9) | 3.6 | (2.0, 5.1) |

[a] Total number of lek years.

Table 2. Establishment locations and breeding season demographics (means and 95% confidence intervals [95% CI]) of yearling male greater sage-grouse establishing breeding territories on leks categorized by lek-to-natural gas field development distances in southwestern Wyoming, 2005-06. Notice that leks situated within the development boundaries of the natural gas fields recruited fewer yearling males than expected.

| Lek-to-Development Distance Catagories[a] | | Number of Males | | Date of Establishment[e] | | Lek Tenacity[f] | | Annual Survival[g] | |
|---|---|---|---|---|---|---|---|---|---|
| | n[b] | Established[c] | Expected[d] | mean | 95% CI | mean | 95% CI | mean | 95% CI |
| Within Development | 10 | 2 | 7.4 | 4/1 | N/A[h] | 37.5 | (24.8, 50.2) | | |
| Between 0 and 2 km of development | 10 | 11 | 7.4 | 4/9 | (4/3, 4/16) | 21.9 | (15.1, 28.7) | 83.3 | (64.8, 101.8) |
| Between 2 and 5 km of development | 4 | 3 | 2.9 | 4/11 | (3/23, 4/30) | 27.3 | (14.9, 39.7) | | |
| More than 5 km from development | 10 | 9 | 7.4 | 4/8 | (4/2, 4/14) | 19.6 | (13.5, 25.6) | 100 | N/A[h] |

[a] Development represents the area within a minimum convex polygon (Kenward 1987) around all producing well pads.

[b] Total number of lek years within buffer distance.

[c] Number of yearling males documented on a lek for at least 7 days.

[d] Number of yearling males expected on leks with the buffer based on the total number of lek years (i.e., leks equally available for establishment by yearling males).

[e] First date established yearling males documented on lek.

[f] Total number of days established yearling males documented on lek.

[g] Annual survival estimated using Kaplan-Meier estimator (Pollock et al. 1989); because of sample sizes, annual survival was not estimated for males establishing within the buffer, and males establishing on leks more than 2 km from development were combined.

[h] Standard error = 0.

Table 3. Mean (95% confidence interval [95% CI]) of breeding season demographics of yearling male greater sage-grouse reared within 1.9 km of natural gas field infrastructure (natal treatment males) compared to yearling males reared in areas with limited natural gas field infrastructure (natal control males) in southwestern Wyoming, 2005-06. Notice that lek tenacity and annual survival were lower for natal treatment yearling males.

| | Natal Treatment Males | | | Natal control Males | | |
|---|---|---|---|---|---|---|
| Male Demographic | n | mean | 95% CI | n | mean | 95% CI |
| Leks visited[a] | 7 | 1.86 | (1.3, 2.4) | 7 | 1.57 | (1.2, 2.0) |
| Natal nest-to-lek distance[b] | 4 | 4.76 | (1.2, 8.3) | 7 | 7.38 | (1.5, 13.3) |
| Natal nest-to-lek distance_2[c] | 4 | 4.76 | (1.2, 8.3) | 6 | 5.02 | (1.5, 8.5) |
| Date of establishment[d] | 4 | 4/5 | (3/28, 4/12) | 6 | 4/11 | (4/2, 4/19) |
| Lek tenacity[e] | 4 | 14.5 | (4.2, 24.8) | 6 | 22.8 | (15.1, 30.6) |
| Lek tenacity_2[f] | 3 | 9.3 | (6.5, 12.2) | 6 | 22.8 | (15.1, 30.6) |
| Annual survival[g] | 8 | 52.5 | (27.4, 77.6) | 7 | 100 | N/A[h] |

[a] Total number of leks yearling males documented visiting.

[b] Straight line distance from natal nest to lek where yearling males established.

[c] One natal control male established on a lek 2.0 times as far from the natal nest than any other male; confidence intervals were re-computed after removing that observation.

[d] First date established yearling males documented on lek.

[e] Total number of days established yearling males documented on lek.

[f] One natal treatment male was documented on a lek 2.5 times as often as any other treatment male; confidence intervals were re-computed after removing that observation.

[g] Annual survival estimated using Kaplan-Meier estimator (Pollock et al. 1989).

[h] Standard error = 0.

Table 4. Breeding demographic probabilities and means (95% confidence intervals [95% CI]) of yearling female greater sage-grouse nesting within 930 m of natural gas field infrastructure (nesting treatment females) or nesting beyond 930 m of development (nesting control females) in southwestern Wyoming, 2005-06. Notice no differences in demographic probabilities.

| | Nesting Treatment Females | | | Nesting Control Females | | |
|---|---|---|---|---|---|---|
| Female Demographic | Available[a] | Documented[b] | 95% CI | Available[a] | Documented[b] | 95% CI |
| Nesting propensity[c] | 12 | 8 | | 31 | 22 | |
| Nesting success[d] | 8 | 4 | | 21 | 10 | |
| Early brood success[e] | 4 | 3 | | 9 | 8 | |
| Overall brood success[f] | 4 | 1 | | 8 | 4 | |
| Nest establishment date[g] | 8 | 5/6 | (5/1, 5/12) | 21 | 5/7 | (5/4, 5/9) |
| Annual survival (%)[h] | 8 | 80.0 | (55.2, 104.8) | 21 | 61.8 | (45.5, 78.1) |

[a] Total number of yearling females available for the demographic (e.g., the denominator for estimating demographic probability).

[b] Total number of yearling females documented successful (e.g., the numerator).

[c] Number of females documented nesting versus the number monitored during the nesting season.

[d] Number of females hatching at least 1 egg versus the total number initiating a nest

[e] Number of successfully nesting females with at least 1 chick to 2 weeks post-hatch.

[f] Number of successfully nesting females with at least 1 chick 35 days or 10 weeks post-hatch (see methods).

[g] Date females first documented on nest.

[h] Annual survival estimated using Kaplan-Meier estimator (Pollock et al. 1989).

Table 5. Breeding demographic probabilities and means (95% confidence intervals [95% CI]) of yearling female greater sage-grouse reared within 1.9 km of natural gas field infrastructure (natal treatment females) compared to yearling females reared in areas with limited natural gas field infrastructure (natal control females) in southwestern Wyoming, 2005-06. Notice that annual survival of natal treatment yearling females was lower than natal control yearlings.

| | Natal Treatment Females | | | Natal Control Females | | |
|---|---|---|---|---|---|---|
| Female Demographic | Available[a] | Documented[b] | 95% CI | Available[a] | Documented[b] | 95% CI |
| Nesting propensity[c] | 9 | 5 | | 7 | 5 | |
| Nesting success[d] | 4 | 1 | | 6 | 2 | |
| Natal nest-to-yearling nest distance (km)[e] | 5 | 3.33 | (1.1, 5.6) | 6 | 2.83 | (1.6, 4.0) |
| Nest establishment date[f] | 5 | 5/6 | (5/1, 5/10) | 6 | 5/8 | (5/1, 5/16) |
| Annual survival (%)[g] | 9 | 69.4 | (44.4, 94.5) | 7 | 100 | N/A[h] |

[a] Total number of yearling females available for the demographic (e.g., the denominator for estimating demographic probability).

[b] Total number of yearling females documented successful (e.g., the numerator).

[c] Number of females documented nesting versus the number monitored during the nesting season.

[d] Number of females hatching at least 1 egg versus the total number initiating a nest

[e] Straight line distance from natal nest to yearling female nest.

[f] Date females first documented on nest.

[g] Annual survival estimated using Kaplan-Meier estimator (Pollock et al. 1989).

[h] Standard error = 0.

Figure 1. Yearling greater sage-grouse study location in southwestern Wyoming, 2005-06. The figure illustrates producing well pads and main haul roads present during the breeding seasons of 2005 and 2006; well pads within 5 km of trapped leks are included.

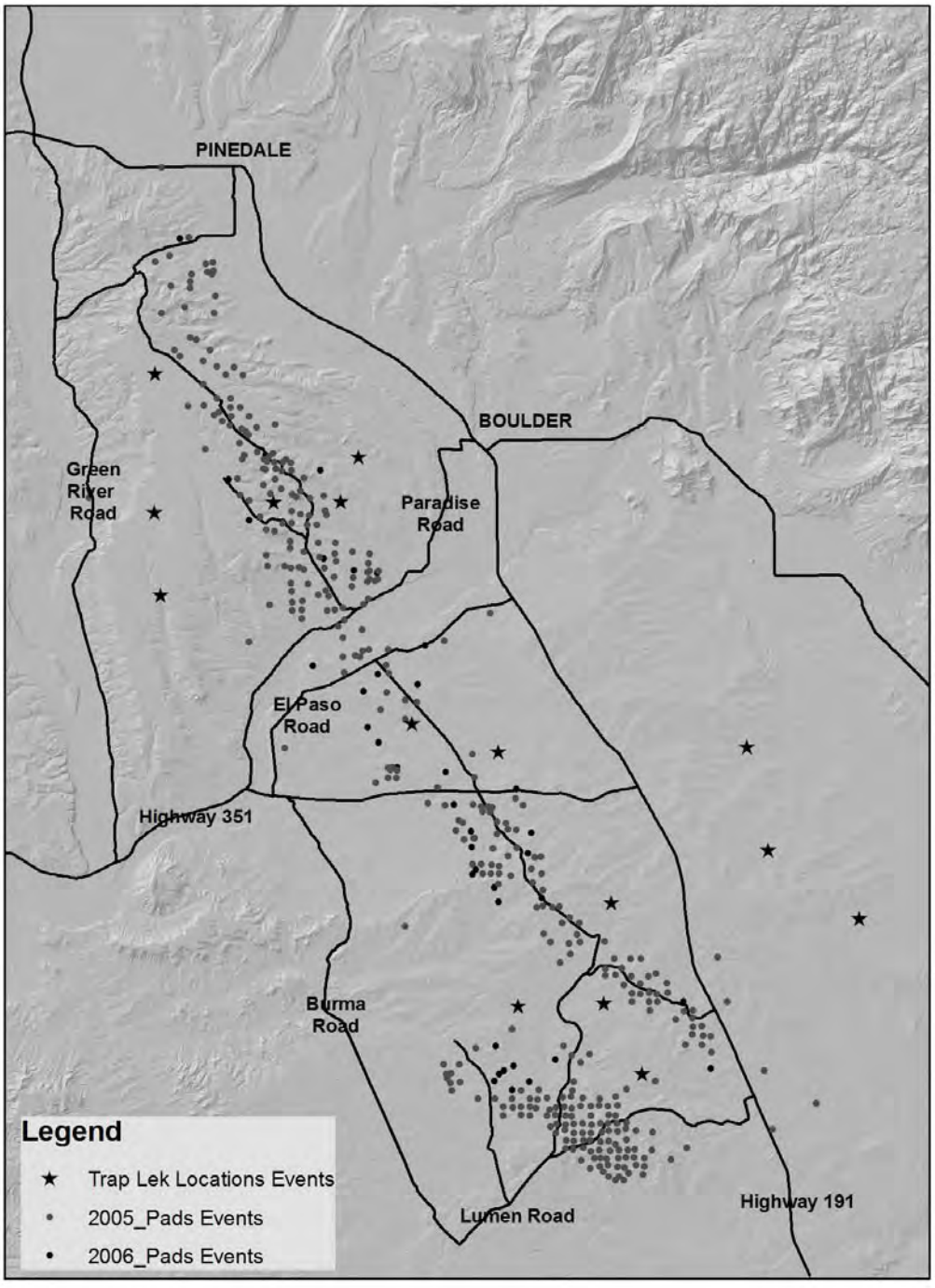


Figure 2. Yearling greater sage-grouse study location in southwestern Wyoming, 2005-06. The figure illustrates producing well pads and main haul roads present during the breeding seasons of 2005 and 2006; well pads within 5 km of trapped leks are included. Natural gas field infrastructure were buffered by 930 m (hatched areas) to determine areas of potential influence to nesting yearling females within the area of interest (i.e., within 5 km of trapped leks).

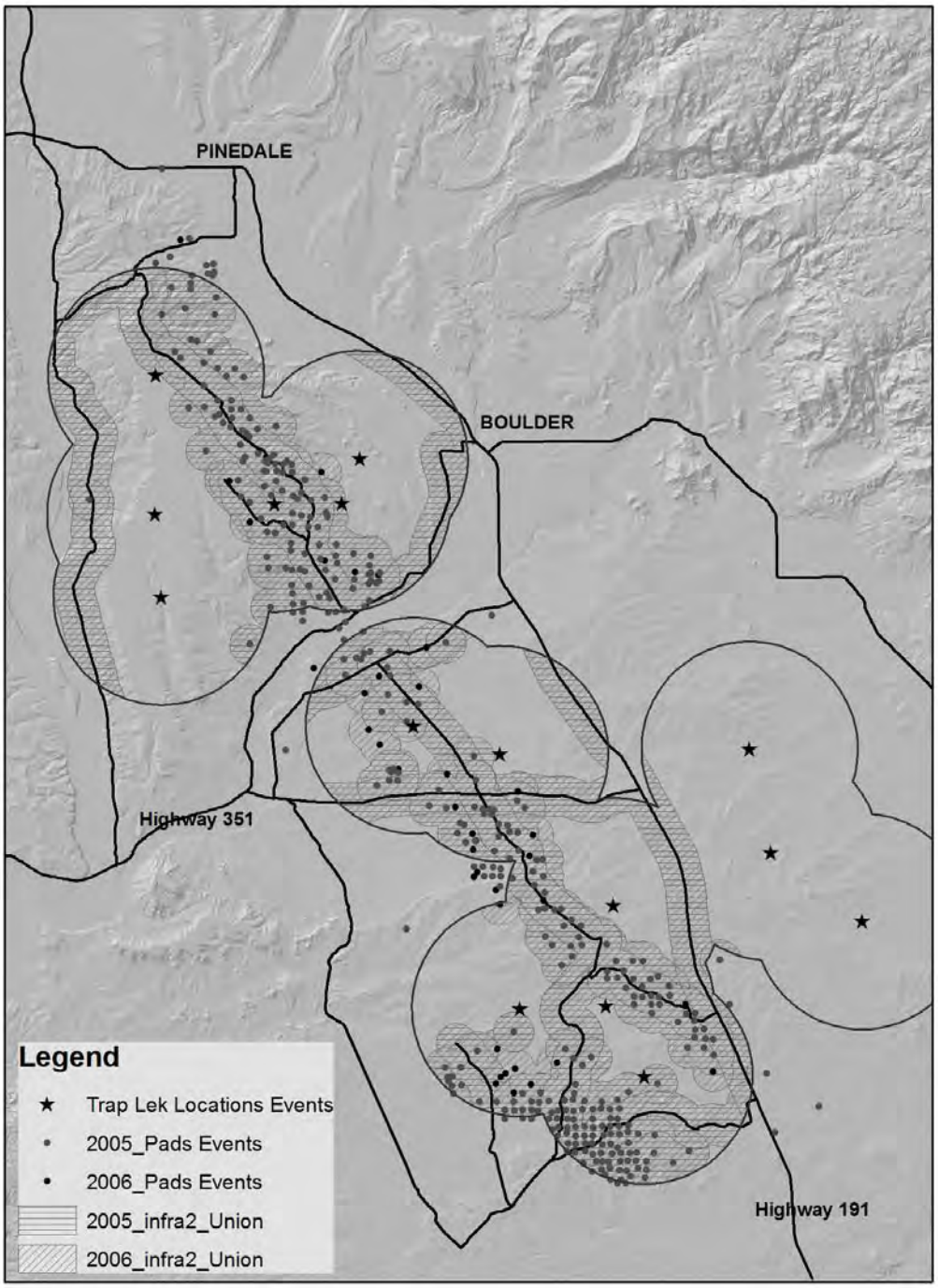
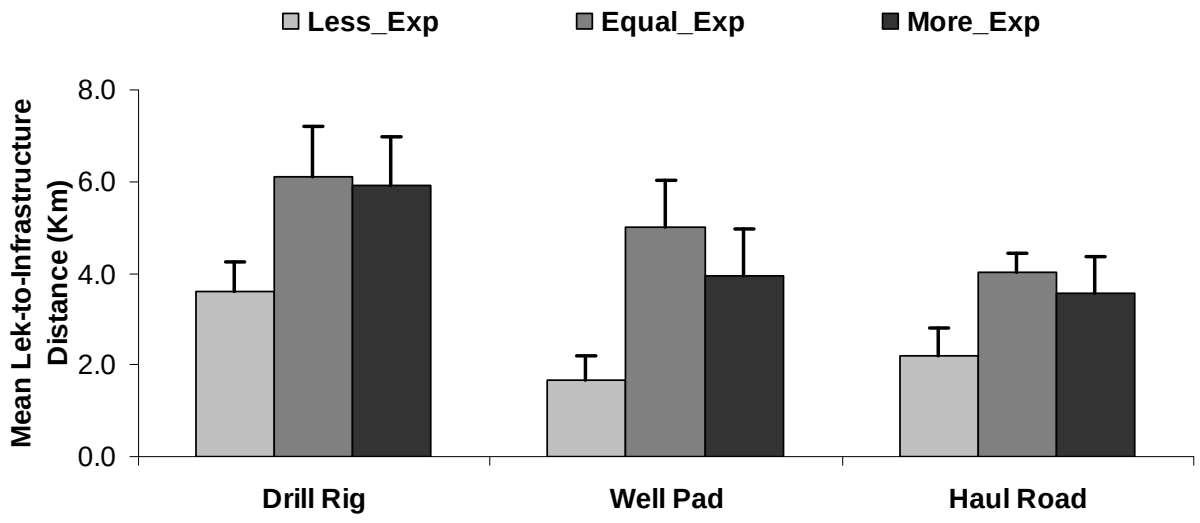


Figure 3. Mean (standard error) distances (km) from greater sage-grouse leks to natural gas field infrastructure in southwestern Wyoming, 2005-06. Leks were categorized as recruiting significantly less than, equal to, or more than expected numbers of males based on Chi-squared analyses of annual changes in the maximum number of males documented on leks during lek count procedures.



The Journal of Wildlife Management 79(4):630–640; 2015; DOI: 10.1002/jwmg.877

*Research Article*

# Winter Habitat Use of Greater Sage-Grouse Relative to Activity Levels at Natural Gas Well Pads

**MATTHEW J. HOLLORAN,**[1] *Wyoming Wildlife Consultants, LLC, 5 East Magnolia Street, Pinedale, WY 82941, USA*
**BRADLEY C. FEDY,** *Department of Environment and Resource Studies, University of Waterloo, Waterloo, ON, Canada N2L 3G1*
**JOHN DAHLKE,** *Wyoming Wildlife Consultants, LLC, 5 East Magnolia Street, Pinedale, WY 82941, USA*

**ABSTRACT** Energy development in western North America has been shown to negatively influence greater sage-grouse (*Centrocercus urophasianus*) populations. No effective methods of reducing on-site impacts of energy development to greater sage-grouse are known. We investigated greater sage-grouse use of wintering habitats relative to distances to infrastructure, densities of infrastructure, and activity levels associated with infrastructure of a natural gas field over 5 years in southwestern Wyoming. We compared year-long drilling locations, locations of conventional well pads, locations of well pads with off-site condensate and produced water gathering systems (LGS), and plowed main haul roads to the number of and time associated with greater sage-grouse visits to continually monitored, distinct patches of habitat. Liquid gathering systems reduced human activity levels at producing well pads approximately 53%. We used data loggers to monitor distinct patches of habitat throughout the 2005–2006 to 2009–2010 winters and used the number of times and the amount of time individuals from a sample of greater sage-grouse ($n = 236$) were detected at data logger stations to model frequency and time of occurrence as functions of anthropogenic and habitat variables. Greater sage-grouse avoided suitable winter habitats in areas with high well pad densities regardless of differences in activity levels associated with well pads. Our results further suggested that greater sage-grouse avoidance of conventional well pads was stronger than LGS well pads. We found relatively consistent positive relationships between distance to infrastructure with high levels of human activity and average hours greater sage-grouse spent in an area. Greater sage-grouse avoidance of natural gas field infrastructure during the winter may be explained mechanistically as movements of individuals from areas close to high levels of activity—movements that may occur at the time human activity is experienced—followed by a lack of movement back into these areas. Minimizing the densities of well pads may reduce on-site impacts of energy development on wintering greater sage-grouse. Our study, additionally, indicated that reducing anthropogenic activity levels associated with energy developments may reduce the temporal scale of indirect greater sage-grouse winter habitat loss. © 2015 The Wildlife Society.

**KEY WORDS** *Centrocercus urophasianus*, gas development, greater sage-grouse, liquids gathering system, mitigation, sage-grouse, winter habitat use, Wyoming.

Important wildlife habitats and abundant energy resources coincide in many landscapes. This overlap leads to complex management issues, particularly in light of decreasing wildlife populations and increasing energy demands. The National Environmental Policy Act (NEPA) outlines a process intended to limit impacts of energy development on sensitive wildlife species (Kiesecker et al. 2011). One option for NEPA users is to implement approaches to development that reduce impacts to wildlife (U.S. Department of Interior 2000). However, development stipulations designed to minimize on-site impacts provide limited protection as currently implemented for some species (Holloran 2005, Sawyer et al. 2006, Walker et al. 2007). Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) are a species of conservation concern that can be negatively affected by energy development (see Naugle et al. 2011). Methods of effectively reducing on-site impacts of energy development to sage-grouse are unknown.

Sage-grouse populations are influenced by multiple natural and anthropogenic factors that fragment and alter the sagebrush (*Artemisia* spp.)-dominated landscapes the species requires (Connelly et al. 2011*a*). Gas and oil field development throughout the sagebrush-dominated regions of western North America is often associated with sage-grouse population declines (Naugle et al. 2011). Sage-grouse are influenced by proximity and density of the infrastructure of natural gas fields during the winter (Doherty et al. 2008, Carpenter et al. 2010, Dzialak et al. 2012, Smith et al. 2014). Wintering sage-grouse avoided areas with high densities of

Received: 28 January 2013; Accepted: 2 March 2015
Published: 3 April 2015

[1]*E-mail: matth@wyowildlife.com*

coal-bed methane wells located in otherwise suitable habitats in the Powder River Basin of northeastern Wyoming (Doherty et al. 2008). In central Wyoming, sage-grouse at the scale of a home range avoided natural gas wells during the winter; at the scale of the population, avoidance of haul roads associated with natural gas development was observed (Dzialak et al. 2012). Sage-grouse avoided areas with higher levels of surface disturbance associated with energy development and human dwellings during the winter in south-central Wyoming (Smith et al. 2014). Additionally, the probability of sage-grouse using winter habitat in southern Alberta, Canada declined when these habitats were within 1,900 m of oil or natural gas wells (Carpenter et al. 2010). Disturbance to wintering sage-grouse from energy development are likely also related to anthropogenic activity levels (Dzialak et al. 2012).

Sage-grouse avoidance, or lack thereof, of the infrastructure of a natural gas field could be manifested in multiple ways: 1) the likelihood of sage-grouse in a population using a given location may be influenced by infrastructure, 2) habitats used by individual sage-grouse may exhibit patterns relative to infrastructure, or 3) the amount of time a sage-grouse remains within an area may be related to the infrastructure present within the area. Likewise, different characteristics of the distribution or types of infrastructure may have different impacts. We investigated sage-grouse use of wintering habitats relative to distances to infrastructure, densities of infrastructure, and activity levels associated with infrastructure of a natural gas field in southwestern Wyoming. We considered whether population-level use of a location, the habitat use patterns of individuals, or the amount of time individuals spent in a location were influenced by these differing natural gas field characteristics. Our primary objective was to estimate differences in responses by wintering sage-grouse between infrastructures in a natural gas field with different levels of recurring human activity, and thereby empirically investigate a potential option for reducing on-site impacts of energy development to the species.

## STUDY AREA

We conducted our study on the northern half of the Pinedale Anticline Project Area (PAPA) in the Upper Green River Basin of central Sublette County, Wyoming (42°45'N, 109°55'W; Fig. 1). The study area was bordered by Wyoming State Highway 191 to the north and east, the Green River to the west, and the New Fork River to the south. The study area encompassed approximately 41,700 ha of predominantly federal lands administered by the Bureau of Land Management (approx. 75%) and private lands (approx. 22%). Vegetation was dominated by big sagebrush (*Artemesia tridentata* spp.)-steppe habitats; Wyoming big sagebrush (*A. t. wyomingensis*) was the dominant shrub species important for wintering sage-grouse. Terrain was predominantly flat with breaks occurring toward the edges of the study area, elevations ranged from 2,120 m to 2,330 m, and precipitation averaged 27 cm annually (Western Regional Climate Center, Reno, NV). The Wyoming Game and Fish Department had documented large numbers of sage-grouse wintering throughout the study area (Lyon 2000, T. Christiansen, Wyoming Game and Fish Department, personal communication). Natural gas development and cattle grazing were the predominant anthropogenic uses of the area (USDI 2000). Other than direct habitat loss as a result of the building of well pads and roads associated with natural gas development, no large-scale losses of sagebrush habitat occurred on the study area during the study.

During the 2005–2006 through 2009–2010 winters, 3 categories of well pads existed on the PAPA (Table 1): 1) well pads with active drilling rigs, 2) conventional producing well pads, and 3) producing well pads with liquid gathering systems (LGS; Bureau of Land Management 2004). Conventional well pads were those where condensate and produced water collected as by-products of natural gas recovery were stored in tanks on-site and removed regularly via tanker truck. Well pads with LGS had less human activity associated with them during production phases of development because condensate and produced water were transported off-site via underground pipelines alleviating the need to visit pads for removal of these liquids (Sawyer et al. 2009). The LGS were designed to mitigate for multiple project impacts, including air quality (reduced vehicle engine emissions and particulate matter), wildlife (reduced wildlife-vehicle collisions), traffic safety (reduced traffic hazards), and human presence (reduced wildlife avoidance and displacement; http://www.papaoperators.com/Liquids-Gathering-Systems.php, accessed 30 Mar 2012). Multiple wells were directionally drilled from single pad locations for most of the well pads located in the study area.

Sawyer et al. (2009) used active infrared sensors to monitor vehicle traffic and quantify differences in activity levels associated with various well pad infrastructures on the PAPA. Well pads with active drilling rigs had the highest mean daily traffic volumes with 112 (SE = 17.3) and 85 (SE = 2.9) vehicle passes per day in 2005–2006 and 2006–2007 winters, respectively; conventional well pads had mean daily traffic volumes of 7 (SE = 0.6) and 8 (SE = 1.2) and LGS well pads had 3 (SE = 0.3) and 4 (SE = 0.5) vehicle passes per day in 2005–2006 and 2006–2007 winters, respectively (Sawyer et al. 2009).

## METHODS

### Field Methods

We captured sage-grouse by spot-lighting and hoop-netting during April and/or August annually (Giesen et al. 1982, Wakkinen et al. 1992). We focused capture efforts in areas known to support sage-grouse that used the study area during the winter. For each captured sage-grouse, we recorded sex based on plumage, and age (hatch-year, yearling, or adult) based on shape or length of outermost wing primaries (Eng 1955). We secured very high frequency (VHF) radio transmitters to captured sage-grouse with a polyvinyl chloride (PVC)-covered wire necklace (Advanced Telemetry Systems Inc. [ATS], Isanti, MN). Transmitters weighed 16, 19.5, 21, or 25.5 g and had a battery life

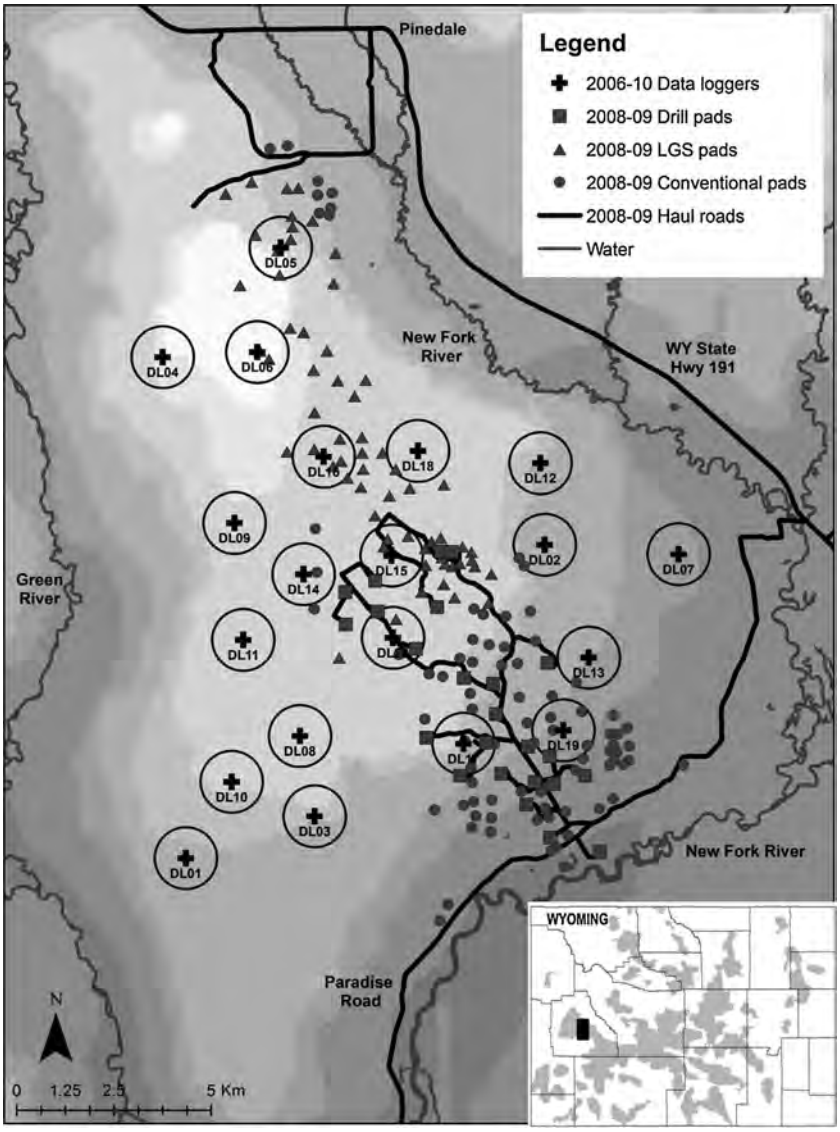



**Figure 1.** Data logger station locations and 0.8-km radius buffers generally delineating the area monitored by each station for radio-equipped greater sage-grouse on the Pinedale Mesa in Sublette County, Wyoming, 2005–2006 through 2009–2010 winters. Natural gas field infrastructure, including well pads with active drilling rigs (drill pads), conventional producing well pads (conventional pads), and producing well pads with liquid gathering systems (LGS pads), corresponds to that present during the 2008–2009 winter and is relatively representative of infrastructure present on the study area during the study. Haul roads include roads accessing drilling rigs, county roads, and state highways. Shading represents elevation at 30-m intervals (darkest areas represent elevation 2,090–2,120 m and lightest areas represent elevation 2,300–2,330 m). Inset map includes county lines, location of study area (black shading) and volume 3 of sage-grouse core areas in Wyoming (gray shading).

**Table 1.** Number of well pads with infrastructure summarized by winter and by infrastructure category on the Pinedale Mesa in Sublette County, Wyoming, 2005–2006 through 2009–2010 winters.

| Winter | Drill pads[a] | Conventional pads[b] | LGS pads[c] |
|---|---|---|---|
| 2005–2006 | 6 | 80 | 55 |
| 2006–2007 | 4 | 87 | 57 |
| 2007–2008 | 6 | 87 | 62 |
| 2008–2009 | 24 | 83 | 62 |
| 2009–2010 | 20 | 51 | 99 |

[a] Well pads with drilling rig active on pad during the winter.
[b] Well pads where condensate and produced water were stored in tanks on-site and removed regularly via tanker truck.
[c] Well pads with liquid gathering systems (LGS) where condensate and produced water were transported off-site via underground pipelines alleviating the need to visit pads for removal of these liquids which reduced human activity associated with pads.

expectancy of 500, 530, 789, or 610 days, respectively. We weighed hatch-year sage-grouse to ensure radio transmitters did not exceed 2% of body weight (Caccamise and Hedin 1985). Our study sample size was bolstered by including sage-grouse that could potentially use the area but were radio-marked as part of 3 additional studies conducted by The Wyoming Cooperative Fish and Wildlife Research Unit, Wyoming Wildlife Consultants, LLC, or the Department of Ecosystem Science and Management at the University of Wyoming. We used monthly telemetry flights to monitor and verify presence of radio-equipped sage-grouse in the study area during each winter (Mountain Air Research, Driggs, ID and Sky Aviation, Dubois, WY). We captured and handled sage-grouse in accordance with Wyoming Game and Fish Department standards under

Chapter 33 Permit for scientific research, educational/display, or species purposes no. 572.

We collected winter habitat use data for radio-equipped sage-grouse over 5 seasons using 20 data logger (telemetry receiver; ATS) stations situated throughout the study area (Fig. 1). We generated a minimum convex polygon around all producing well pads present on the study area in 2005, and situated 10 data logger stations randomly within the polygon and 10 randomly outside the polygon but within the study area. We placed data logger stations at least 2 km apart. Each station was attenuated (i.e., calibration of the sensitivity to control signal strength received by data loggers) to only detect transmitters within 0.8 km. We followed attenuation recommendations proposed by Breck et al. (2006:114) to increase the reliability of accurately detecting transmitter presence. Because the ability of a receiver to detect a transmitter is influenced by topography, we generated viewsheds in a geographic information system (GIS; ArcGIS 9, ESRI, Redlands, CA) to estimate the amount of area within 0.8 km of a data logger station a transmitter would reliably be detected (i.e., areas within 0.8 km of a data logger that were in direct line-of-site with receiver antenna). We adjusted station locations based on mean total area (ha) where a transmitter would reliably be detected within 0.8 km to ensure a similar amount of area was monitored by all stations; this typically involved moving a data logger location up or down a slope such that more or less area was in direct line-of-site of the antenna. Although we assigned general locations of stations randomly, specific sites were based on viewsheds and therefore were not random. We moved 3 data logger stations between the 2005–2006 and 2006–2007 winters to better standardize monitored area between stations. Final placement of data loggers resulted in a distribution of winter-monitored locations (standardized to the amount of area monitored) across the study area. We placed data logger stations in the same locations annually following the initial adjustments described above.

Data loggers provided constant monitoring for radio-equipped sage-grouse of distinct patches of habitat. Data logger stations consisted of 1 data logger run by 2 deep-cycle recreational vehicle gel batteries charged by solar panels. All equipment was housed in metal Knaack® tool boxes (Crystal Lake, IL). We mounted omni antennas on PVC pipe so the top of the antenna was 3 m above ground. During the 2007–2008 winter, we experienced excessive moisture accumulation in Knaack® boxes due to high winds and drifting snow; the moisture resulted in corrosion of electronic components of some data loggers. We resolved moisture accumulation issues in subsequent years by improving sealing methods (e.g., taping around lids) and adding desiccant to Knaack® boxes. We omitted from all analyses data loggers that malfunctioned for $\geq$14 days through a given winter. We set data loggers to scan for 35 and 45 pulse per minute (PPM) transmitters (ATS Model A4000). Cold weather may cause transmitters to pulse differently than the programmed pulse rate; therefore, we allowed for a tolerance of 1 for all pulse rates (e.g., for 35 PPM transmitters, pulse rates 34 and 36 were also recorded). We placed reference transmitters at each data logger station to verify logging accuracy on all downloads.

We monitored sage-grouse winter habitat use annually between 15 November and 15 March. During the 2005–2006 winter, we directly accessed data logger stations and downloaded data to a laptop computer twice monthly. During the 2006–2010 winters, we accessed data logger stations remotely and downloaded data using FreeWave® radio equipment (Boulder, CO). To minimize disturbance to wildlife wintering on the study area, we accessed stations situated >250 m from a plowed road with horses.

**Data Preparation**

The radio-transmitter detections downloaded from the data loggers each contained the date, time, transmitter frequency, signal strength, number of pulses recorded in 15 seconds, transmitter pulses-per-minute (PPM), and number of pulse matches (determined by ATS algorithms). We distinguished true radio-transmitter detections (vs. interference) recorded by data loggers from an accumulation of evidence. Initially, signal diagnostics (i.e., transmitter PPM values and number of pulse matches) had to match those possible for the radio transmitters active within each year. We used pulse match to pulse detected ratios (i.e., the number of matched pulses relative to the number of detected pulses) and the number of logs over a given time period to further diagnose true signal detections; we established these protocols by evaluating data from reference transmitter logs. Numerous logs by the same frequency, especially numerous within the same relative time period, with high pulse match-to-detected ratios had higher potential to be a confirmed sage-grouse detection. We used telemetry data as the final log verification. If a logged frequency corresponded to a sage-grouse documented on the study area $\geq$1 times through telemetry flights, we considered the logged signals of that frequency verified. We consulted ATS experts for verification of questionable detections. Following these accumulation of evidence procedures, we established a list of confirmed sage-grouse log events, or confirmed visits by individual sage-grouse to a data logger station-monitored area.

Independent log events for a given sage-grouse frequency were log events separated by $\geq$10 hours. We assumed that if an individual sage-grouse was not logged for 10 hours, it had left the data logger station's monitored area; thus, we considered logs separated by 10 hours independent visits to the area monitored by a particular station. For example, sage-grouse often shift locations from day-use to night-roost areas (Dzialak et al. 2012), and we assumed that if an individual used a given area during the day, moved to roost in a different location during the night, and then returned to the same day-use location the following day, that represented 2 independent visits to the location. Total time per independent log event was the time between the first logged detection and the last logged detection that were separated by <10 hours. For single log events (i.e., a frequency logged once and not logged again for $\geq$10 hours), we assumed the individual spent 15 minutes in the data logger coverage area. This time unit was the time it took data logger stations to cycle through 150

frequencies, the approximate number of available radio-equipped sage-grouse annually. Rarefication of raw data resulted in a list of the number of independent log events (i.e., the number of times a sage-grouse visited the area monitored by a data logger station) and the amount of time for each independent log event (i.e., the amount of time per visit a sage-grouse spent within the area monitored by a data logger station) for each data logger station for each individual sage-grouse recorded.

### Model Covariates

Infrastructure covariates included distance from data logger station to plowed main haul roads and natural gas well pads by category, and the number of well pads by category within 2.8 km of the data logger station (Table 2). Because a confirmed sage-grouse log event established that an individual sage-grouse was somewhere within a 0.8-km buffer of the data logger, we chose to summarize well density metrics within 2.8 km of data logger stations. This distance represented the impact distances of infrastructure to wintering sage-grouse, which have been estimated at approximately 2 km (Carpenter et al. 2010), while taking into account the scale of a log event (sage-grouse presence within a 0.8-km radius area). We obtained gas field infrastructure information from the Wyoming Oil and Gas Conservation Commission and supplemented it with information supplied by Western Ecosystems Technology, Inc. (Cheyenne, WY), Edge Environmental, Inc. (Laramie, WY), and through direct ground-truthing using hand-held, 12-channel global positioning systems (Garmin RINO 110; Garmin International, Olathe, KS). Industry representatives verified final infrastructure layers directly. Gas field infrastructure data varied annually and we updated the data yearly to reflect the conditions encountered during each winter. We estimated distances to infrastructure to the center of well pads in kilometers using ArcGIS 9. We considered well pads with multiple wells to be single active locations. We considered plowed main haul roads to be those used to access active drilling rigs. Habitat covariates included shrub height, sagebrush cover, and topography (Doherty et al. 2008, Connelly et al. 2011*b*; Table 2) and we estimated habitat covariates as the mean of values associated with the viewshed within 0.8 km of each data logger (i.e., habitat values of monitored areas). We used sagebrush canopy cover and shrub height vegetation layers developed for Wyoming by Homer et al. (2012). We calculated a topographic roughness index using nearest neighbor analysis in ArcGIS Spatial Analyst (ESRI) from 30-m digital elevation grids (DEM; Wyoming Geographic Information Science Center, Laramie, WY); we calculated this metric by dividing the actual surface area of a $3 \times 3$-pixel region by the planimetric area.

### Analysis at the Level of Locations

We estimated the influence of infrastructure on the relative probability of sage-grouse in a population using a given location by investigating differences in the total number of radio-equipped sage-grouse and the total number of log events (e.g., the number of sage-grouse visits) summarized for each data logger station each year. We analyzed these data using mixed-effects Poisson models (xtmepoisson procedure STATA 10.1; StataCorp 2007). Poisson regression is generally used to analyze data represented by counts of occurrences of some event over time and space, without definite upper bounds (Ramsey and Schafer 2002, Millspaugh et al. 2006). These analyses were focused toward our primary objective of estimating differential effects of conventional and LGS well pads.

A mixed-effects modeling approach allowed us to account for the hierarchical nature of the data through the inclusion of random effects in model estimation. We used this approach to account for intracluster correlation; for example, the response variables (numbers of sage-grouse and numbers of log events) were nested within the year. We included random intercepts for each year. We developed 4 model sets that represented combination of the 2 different response variables and the 2 different metrics of well pads (density and distance). Within each of the 4 model sets, we additionally included the other covariates of interest (Table 2); we allowed habitat covariates to be additive with anthropogenic covariates. We examined all covariates for correlations prior to estimating models to avoid issues of multicollinearity. When variables were highly correlated (Pearson's $r \geq |0.60|$; Sawyer et al. 2006) we included the most relevant variable. For example, distance to closest conventional well pad and

**Table 2.** Infrastructure and habitat covariates summarized for each data logger station, including mean (SD) of range on the Pinedale Mesa in Sublette County, Wyoming, 2005–2006 through 2009–2010 winters.

| Covariate | Description | Mean (SD) |
|---|---|---|
| Conventional distance | Distance from data logger location to closest producing well pad where liquids were conventionally stored on-site and removed via tanker truck | 2.7 (1.8) km |
| LGS distance | Distance from data logger location to closest producing well pad with off-site liquid gathering systems (LGS; liquids piped off-site) | 2.5 (2.1) km |
| Drill distance | Distance from data logger location to closest drilling rig active during winter | 3.8 (2.4) km |
| Road distance | Distance from data logger location to closest point along plowed main haul roads (state highways and the Paradise Road included as plowed main haul roads [Fig. 1]) | 2.9 (2.0) km |
| Conventional density | Number of conventional well pads within 2.8 km buffer of data logger location | 6.9 (12.9) no. of well pads |
| LGS density | Number of LGS well pads within 2.8 km buffer of data logger location | 8.3 (10.3) no. of well pads |
| Sage height | Mean sagebrush height in data logger-monitored area | 26.1 (4.1) cm |
| Sage cover | Mean sagebrush canopy cover in data logger-monitored area | 15.6 (2.4) % |
| Roughness | Mean roughness (ratio of surface to planimetric area) in data logger-monitored area | 1.4 (0.9) unitless |

distance to closest drilling rig active during winter (Table 2) were correlated at $r = 0.67$ and because we were interested in the relative influence of conventional versus LGS well pads, we retained distance to closest conventional well pad in the distance models. In addition to removing highly correlated variables, we further considered issues of multicollinearity through the calculation and consideration of tolerance values and variance inflation factors (VIF) for all variables included in the models; VIF values >10 suggest potential issues with collinearity (O'Brian 2007). We included all potential covariates as fixed effects when issues of collinearity were not present. We included metrics representing the different well categories for the 2 different types of wells (i.e., LGS and conventional) in every model. These 2 variables represented the base model in both the density and distance model sets. We then determined the inclusion of additional non-correlated covariates based on Akaike's Information Criterion adjusted for small sample sizes ($AIC_c$). We included covariates that improved model fit by >2 $\Delta AIC_c$ in final models.

We defined an exposure variable as an expected rate and, in effect, specified a linear model for the log of the ratio of observed to expected sage-grouse based on the reference population of all radio-equipped sage-grouse (i.e., the number of individuals that could be detected by the data logger stations). In other words, the exposure variable (number of radio-equipped sage-grouse) reflected the amount of exposure over which the dependent variables (number of grouse or log events recorded) were observed. We reported fixed effect coefficients as incident rate ratios (i.e., e(b) rather than b; IRR) which allowed us to interpret results as an increase or decrease in the number of grouse or events as distance from data logger stations to well pads increased by 1 km and as the number of well pads within 2.8 km of data logger stations increased by 1. We evaluated residual plots to assess adherence to assumptions of normality and homogeneity of variance; both assumptions were met for all models. We also evaluated and ranked models for each response variable based on $AIC_c$.

**Analysis at the Level of Individuals**

To investigate habitat-use patterns of individuals relative to infrastructure of natural gas fields, we estimated relative probabilities of use of individual sage-grouse and combined parameter estimates from these individual-based models by year. We treated each winter period separately to account for changing environmental conditions (e.g., category of well pads) through time, and treated radio-equipped sage-grouse as the experimental unit to avoid pseudo-replication (i.e., spatial and temporal autocorrelation among locations of an individual) while allowing for population-level inference (Sawyer et al. 2006, 2009). We summed the number of independent log events per data logger station for each sage-grouse and modeled the total number of independent log events (i.e., response variable) for each grouse logged at ≥4 data logger stations. We assumed all 20 data logger station locations were available to each sage-grouse because 42% of individuals logged at ≥4 stations traversed gas development infrastructure (reference Results Section). We investigated all 1-, 2-, and 3-predictor covariate combinations and fit the same series of 55 or 57 models to each individual each year; the same models are required for each individual within a winter to allow for coefficient combination across sage-grouse within a year (Sawyer et al. 2006). We allowed habitat covariates to be additive with anthropogenic covariates. We did not include covariates correlated by Pearson's $r \geq |0.60|$ in the same model.

We used an extension of Poisson regression based on the negative binomial distribution to generate individual grouse models (White and Bennetts 1996) because the count data used in analyses were over-dispersed (i.e., variance larger than mean, predominantly because of the large number of 0 visits to data-logger locations per sage-grouse). The approach modeled relative probability of use as a function of covariates (Manly et al. 2002). We conducted analyses using the generalized linear model (GLM) procedure in the MASS library of program R version 2.5.0 (Dalgaard 2002, R Core Team 2007). We investigated non-linear relationships, but inclusion of non-linear terms resulted in substantial model instability (i.e., modeling algorithms [R Core Team 2007] did not converge). We therefore modeled linear relationships only.

We used $AIC_c$ to generate a weighted global model for each sage-grouse. We conducted weighted averaging over all models considered (Burnham and Anderson 2002:150–152). We generated weighted-average estimates of model parameters and made inferences on averaged models because employing a weighted averaging procedure reduces model selection bias effects on coefficient estimates in all-subsets model selection in situations with high model selection uncertainty (Burnham and Anderson 2002). If the negative binomial modeling algorithm did not converge for an individual grouse model, we did not include that covariate combination in model averaging across all grouse for that year.

We generated a single model for each year by averaging the parameter estimates of the covariates from the sage-grouse models for that year. We estimated the variance of each coefficient in by-year models using the variation among individual grouse and equations provided in Sawyer et al. (2009:1055). We established confidence intervals (95% CI) for each coefficient as the 2.5 and 97.5 percentiles of 10,000 replicates randomly selected from a normal distribution of the derived estimates and variances. We additionally extracted the proportion of each distribution that intersected 0.

We used an analysis of log duration to assess influences of infrastructure on the amount of time a sage-grouse spent in an area given the area was used. We averaged time (hours) of separate log events by sage-grouse by data logger station and modeled average time (i.e., response variable) with the covariates of interest (Table 2). We used linear regression to generate weighted average time models by year. We conducted weighted averaging with Akaike weights generated over all models considered (Burnham and Anderson 2002). We estimated unconditional variance of each coefficient in by-year models following Burnham and Anderson (2002:162). We investigated all 1-, 2-, and 3-predictor covariate combinations

by year and did not include covariates correlated by Pearson's $r \geq |0.60|$ in the same model. As before, we established confidence intervals (95% CI) for each coefficient as the 2.5 and 97.5 percentiles of 10,000 replicates randomly selected from a normal distribution of the derived estimates and variances. We additionally extracted the proportion of each distribution that intersected 0. We conducted analyses using the linear model function in the MASS library of program R version 2.5.0 (Dalgaard 2002, R Core Team 2007). We initially assessed outlying time values subjectively from scatter plots; suspected outliers were those that differed substantially from the remainder of the data (e.g., >5 standard deviations from the mean). We statistically assessed those values we suspected of being outliers using the Grubbs test statistic ($Z$; Sokal and Rohlf 1995) and removed significant outliers from analyses.

## RESULTS

We documented 312 individual sage-grouse on the study area during the winter through telemetry flights among the 5 years of study. We confirmed 4,171 log events of 236 individual sage-grouse. We considered data logger 16 (Fig. 1) unavailable during the 2007–2008 winter because it malfunctioned for ≥14 days during that winter. Over 5 years with 20 stations minus the station inoperable for winter 2007–2008, we had 99 station × year summaries. Over all years, we recorded an average of 8.5 (SE = 0.8) sage-grouse at data logger stations and the mean number of log events per station was 42.1 (SE = 8.1). We logged 103 individual sage-grouse at ≥4 data logger stations (2005–2006, $n = 6$; 2006–2007, $n = 33$; 2007–2008, $n = 16$; 2008–2009, $n = 32$; 2009–2010, $n = 16$). The mean number of data logger stations visited by individuals logged at ≥4 data logger stations was 4.3 (SE = 0.2) and ranged from 4 to 12; the mean number of logs per sage-grouse per data logger station was 5.6 (SE = 0.2) and ranged from 1 to 36. We logged 43 (42%) of the 103 sage-grouse used for the individual-based modeling at stations situated both east and west of the center of gas development infrastructure (Fig. 1) indicating that all stations were available to individuals spending at least portions of a winter on the study area. These documented movements also suggested that results were not biased by capture location (e.g., sage-grouse captured east of the study area were not restricted to data logger stations east of infrastructure). We used 807 time of log event estimates for log duration analysis. Mean time of visits over the 5 years was 8.0 (SE = 0.3) hours and ranged from 0.25 to 98.4 hours.

### Analysis at the Level of Locations

Our analysis of tolerance values and variance inflation factors (VIF) suggested that collinearity was not an issue in any of our models. Tolerance estimates ranged from 0.44 to 0.86 for the well density model variables and from 0.73 to 0.96 for the well distance model variables. Our VIF estimates ranged from 1.16 to 2.28 for the well density model variables and from 1.04 to 1.37 for the well distance model variables.

Comparisons between density and distance models indicated well pad density was a better predictor of both the total number of sage-grouse and the total number of log events occurring at data logger stations than distance to well pads. The $AIC_c$ values for the best model including density were 123.4 and 1,645 points lower compared to the best model including distance for the number of sage-grouse logged and the number of events, respectively. Both of the most parsimonious density models investigating the number of sage-grouse and the number of events included LGS pad density, conventional pad density, distance to roads, roughness, and sagebrush height, with $AIC_c$ values = 574.4 and 2,575.9 and Akaike weights ($w_i$) = 1 and 1, respectively. Both of the most parsimonious distance models investigating the number of sage-grouse and the number of events included distance to LGS pad, distance to conventional pad, and roughness, with $AIC_c$ values = 697.7 and 4,220.9 and $w_i = 1$ and 1, respectively. All additional covariate combinations investigated had $\Delta AIC_c$ values ≥24.0 and $w_i < 0.01$. As the number of well pads within 2.8 km of a data logger station increased, the number of sage-grouse and the number of events decreased (Table 3; Fig. 2). For each additional conventional well pad within 2.8 km, the number of sage-grouse logged decreased by 1 and the number of events decreased by 2; and for each additional LGS well pad within 2.8 km, the number of sage-grouse logged decreased by 4 and the number of events decreased by 6.

**Table 3.** Incident rate ratios (IRR) and confidence intervals (CI) for the fixed-effects components of the mixed-effects Poisson models investigating the total number of sage-grouse logged (Logs) and the total number of independent log events (Events) by data logger station relative to distance to and density of natural gas field infrastructure on the Pinedale Mesa in Sublette County, Wyoming, 2005–2006 through 2009–2010 winters.

| | Density models | | | Distance models | | |
|---|---|---|---|---|---|---|
| **Response** | **Covariate** | **IRR** | **CI** | **Covariate** | **IRR** | **CI** |
| Logs | LGS[a] density | 0.96 | 0.95–0.97 | LGS[a] distance | 1.13 | 1.08–1.18 |
| | Conventional density | 0.99 | 0.98–0.99 | Conventional distance | 1.17 | 1.12–1.23 |
| | Road distance | 1.07 | 1.03–1.12 | Roughness | 0.92 | 0.84–0.99 |
| | Sage height | 1.08 | 1.05–1.11 | | | |
| | Roughness | 0.98 | 0.89–1.06 | | | |
| Events | LGS[a] density | 0.94 | 0.93–0.94 | LGS[a] distance | 1.12 | 1.10–1.15 |
| | Conventional density | 0.98 | 0.98–0.99 | Conventional distance | 1.48 | 1.44–1.52 |
| | Road distance | 1.09 | 1.07–1.11 | Roughness | 1.16 | 1.11–1.21 |
| | Sage height | 1.25 | 1.24–1.27 | | | |
| | Roughness | 1.32 | 1.27–1.38 | | | |

[a] Well pads with liquid gathering systems (LGS) where liquids were transported off-site via underground pipelines.

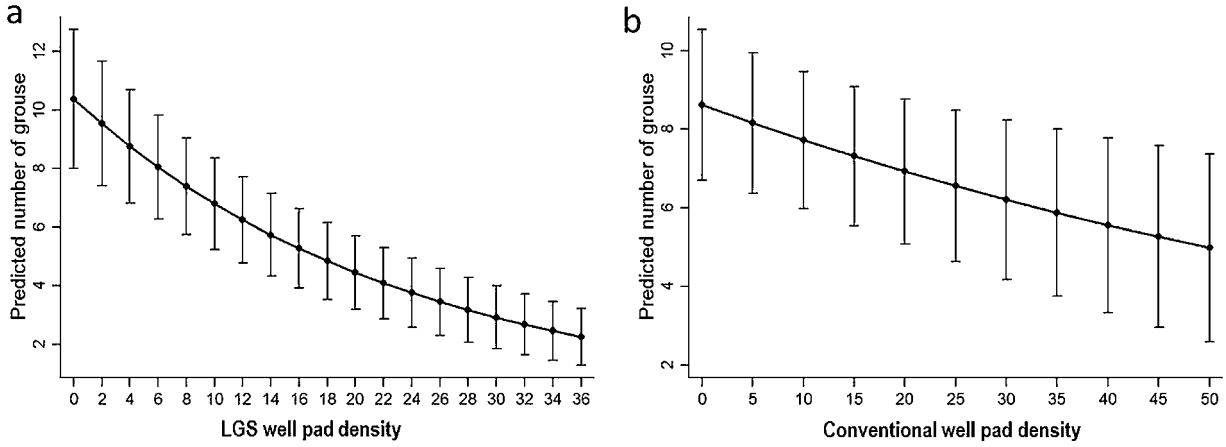



**Figure 2.** Predicted marginal effects (95% CI) of the density (no. of well pads within a 2.8-km radius of data logger stations) of a) well pads with off-site liquid gathering systems (LGS) and b) well pads with liquids gathered conventionally on the predicted number of sage-grouse visiting a location on the Pinedale Mesa in Sublette County, Wyoming, 2005–2006 through 2009–2010 winters. We estimated predictive margins using the most parsimonious mixed-effects models that were developed to estimate the total number of sage-grouse visiting each station location. Both models predict a decline in the number of sage-grouse visiting areas with increasing well density.

The mixed-effect models suggested that numbers of sage-grouse and log events increased as distance from well pads increased. For each 1-km increase in distance from a given location to a conventional well pad and LGS well pad the number of sage-grouse increased by 17 and 13, and the number of events increased by 48 and 12, respectively (Table 3). We also found a consistently positive relationship between the number of sage-grouse and the number of log events and distance to a plowed main haul road and sagebrush height (Table 3).

### Analysis at the Level of Individuals

Models generated from the log histories of individuals indicated sage-grouse were avoiding areas close to conventional well pads relatively consistently (Table 4). No other consistent relationships were apparent. The following combinations of variables did not converge (R Core Team 2007) for $\geq$1 sage-grouse: in 2006–2007, conventional pad density + LGS pad density + sagebrush height and conventional pad density + LGS distance + road distance; and in 2008–2009, conventional pad density + LGS distance + road distance and conventional pad density + LGS distance + road distance.

Sage-grouse that visited a given area (i.e., were logged) spent in general less time near infrastructure with higher levels of activity (i.e., conventional well pads, drilling rigs, and plowed main haul roads), and more time in areas with taller sagebrush (Table 5). We identified 2 time values as outliers; these values were abnormally long visits by 2 separate individuals to DL18 (Fig. 1) in 2008–2009 and 2009–2010 (77.2 hr [$Z = 7.72$; $P < 0.05$] and 98.4 hr [$Z = 7.45$; $P < 0.05$], respectively). Additionally, exclusion of these 2 time values decreased minimum $AIC_c$ values by >76 points.

## DISCUSSION

Sage-grouse avoided areas with high well pad densities during the winter regardless of differences in activity levels associated with well pads. These results are consistent with previous research that also documented avoidance of suitable

**Table 4.** The 95% confidence intervals for each average by-year model parameter estimated from weighted average by-sage-grouse models investigating the number of log events relative to natural gas field infrastructure (distance and density) on the Pinedale Mesa in Sublette County, Wyoming, 2005–2006 through 2009–2010 winters. We estimated mean parameter coefficients and unconditional variances (Sawyer et al. 2009:1055) among individual sage-grouse models by year, and established confidence intervals as the 2.5 and 97.5 percentiles of 10,000 replicates randomly selected from a normal distribution of these derived coefficients and variances. We present the percent of the distribution that overlapped 0 in parentheses.

| Covariate | 2005–2006 | 2006–2007 | 2007–2008 | 2008–2009 | 2009–2010 |
|---|---|---|---|---|---|
| *n* | 6 | 33 | 16 | 32 | 16 |
| Conventional distance | 0.0052, 0.0054 (0%) | 0.017, 0.037 (0%) | 0.0062, 0.0071 (0%) | 0.033, 0.053 (0%) | −0.001, 0.014 (3.7%) |
| Conventional density | −1.41, 0.591 (20.4%) | −0.186, −0.034 (0.3%) | −0.023, −0.016 (0%) | −1.00, 0.65 (33.4%) | −0.022, 0.000 (2.7%) |
| LGS[a] distance | 0.038, 0.069 (0%) | −0.083, 0.111 (38.9%) | −0.044, −0.021 (0%) | −0.003, 0.059 (4.1%) | 0.036, 0.046 (0%) |
| LGS[a] density | −0.481, 0.028 (4.2%) | −0.705, 0.145 (10.0%) | −0.167, −0.040 (0.05%) | −0.428, 0.047 (5.8%) | −0.786, 0.034 (3.5%) |
| Drill distance | −0.0082, −0.0062 (0%) | −0.221, 0.054 (11.5%) | −0.041, −0.012 (0.03%) | −0.027, 0.108 (13.3%) | −0.083, 0.014 (8.7%) |
| Road distance | −0.0059, −0.0047 (0%) | −0.023, 0.430 (3.9%) | −0.802, 1.15 (36.1%) | −0.396, 0.486 (42.1%) | 0.050, 0.223 (0.1%) |
| Sage height | −1.13, 0.684 (30.2%) | −0.071, 0.349 (9.9%) | −0.035, 0.221 (7.8%) | 0.022, 0.361 (1.4%) | −0.010, −0.006 (0%) |
| Roughness | −1.95, 1.54 (40.5%) | −1.48, 1.01 (34.8%) | −0.642, 0.335 (26.1%) | −1.49, 1.69 (45.9%) | −0.414, −0.081 (0.2%) |

[a] Well pads with liquid gathering systems (LGS) where liquids were transported off-site via underground pipelines.

**Table 5.** The 95% confidence intervals for each by-year model parameter estimated from an investigation of average time of independent log events relative to natural gas field infrastructure (distance and density) on the Pinedale Mesa in Sublette County, Wyoming, 2005–2006 through 2009–2010 winters. We estimated unconditional variances (Burnham and Anderson 2002:162) and established confidence intervals as the 2.5 and 97.5 percentiles of 10,000 replicates randomly selected from a normal distribution of these derived variances around modeled coefficients. We present the percent of the distribution that overlapped 0 in parentheses.

| Covariate | 2005–2006 | 2006–2007 | 2007–2008 | 2008–2009 | 2009–2010 |
|---|---|---|---|---|---|
| *n* | 50 | 226 | 136 | 238 | 155 |
| Conventional distance | −1.32, −0.023 (2.2%) | 0.150, 0.391 (0%) | 0.086, 0.411 (0.1%) | 0.173, 0.478 (0%) | 0.157, 0.476 (0%) |
| Conventional density | 0.024, 0.053 (0%) | 0.004, 0.018 (0.1%) | −0.0019, −0.0018 (0%) | −0.010, −0.005 (0%) | −0.097, −0.034 (0%) |
| LGS[a] distance | −0.224, −0.009 (1.7%) | 0.012, 0.016 (0%) | 0.023, 0.047 (0%) | −0.0003, −0.0000 (0.4%) | 0.011, 0.043 (0.04%) |
| LGS[a] density | −0.043, −0.008 (0.2%) | −0.008, 0.000 (3.3%) | 0.021, 0.079 (0.02%) | 0.024, 0.098 (0.05%) | −0.031, −0.011 (0.01%) |
| Drill distance | −0.006, −0.003 (0%) | 0.226, 0.732 (0%) | 0.0021, 0.0021 (0%) | 0.332, 0.931 (0%) | 0.171, 0.693 (0.1%) |
| Road distance | 0.032, 0.189 (0.4%) | 0.206, 0.684 (0.02%) | −0.023, −0.002 (1.3%) | 0.034, 0.041 (0%) | 0.093, 0.197 (0%) |
| Sage height | 0.240, 1.59 (0.4%) | 0.043, 0.177 (0.1%) | 0.224, 0.743 (0.02%) | 0.135, 0.630 (0.1%) | −0.011, 0.032 (18.1%) |
| Roughness | −0.166, 0.651 (12.5%) | 0.035, 2.29 (2.2%) | −0.043, 0.068 (33.7%) | −0.047, −0.022 (0%) | −0.176, 0.091 (26.6%) |

[a] Well pads with liquid gathering systems (LGS) where liquids were transported off-site via underground pipelines.

habitats with high well densities by wintering sage-grouse (Doherty et al. 2008). Additionally, in southwestern Wyoming sage-grouse avoided nesting in areas with high densities of wells, and research suggests high well densities affect sage-grouse lek attendance, lek occupancy, and chick survival (Holloran 2005, Aldridge and Boyce 2007, Walker et al. 2007, Harju et al. 2010).

Distance effects of LGS well pads on sage-grouse winter habitat use may be less than the distance effects estimated for conventional well pads, although these results are not conclusive. The annually derived confidence intervals around distance to conventional well pads did not cross 0 relatively consistently. Where the confidence interval did cross 0 (2009–2010), that interval was noticeably skewed to the right and a low proportion of the distribution intersected 0 suggesting a positive association between distance to conventional well pads and sage-grouse presence (Hosmer and Lemeshow 1989:100). In contrast, the confidence intervals around distance to LGS well pads suggest inconsistent relationships (Table 4). Additionally, incident rate ratios indicated that sage-grouse were avoiding locations farther from conventional pads compared to LGS well pads, especially when investigating the number of times sage-grouse visited a given location (Table 3). Dzialak et al. (2012) documented sage-grouse during the winter avoiding the infrastructure of a gas field during the day but not at night suggesting that avoidance was of human activity rather than the infrastructure itself. Negative relationships between the number of males occupying leks and traffic levels on haul roads associated with energy development have been documented suggesting that sage-grouse breeding near development may be influenced progressively more severely as the number of vehicles using roads increases (Remington and Braun 1991, Holloran 2005). Wintering mule deer (*Odocoileus hemionus*) have been documented selecting habitats farther from the infrastructure of an energy development with higher levels of activity (Sawyer et al. 2009).

The potential positive effects of LGS may not be realized until future generations of sage-grouse occupy the study area. Over 44% of the LGS well pads studied were the result of the transition of conventional to LGS systems during the time of study (Table 1). As noted, LGS reduced daily traffic volumes to well pads by approximately 2.1 times on average (from approx. 7.5 to 3.5 vehicle passes/day; Sawyer et al. 2009); therefore, we predicted less avoidance of LGS than conventional well locations. However, sage-grouse avoided areas with high LGS well pad densities as well as areas close to LGS well pads, at least when investigating the influence of infrastructure on the relative probability of sage-grouse using a given location (Table 3). Sage-grouse exhibit strong philopatry to seasonal ranges (Fischer et al. 1993, Schroeder and Robb 2003, Holloran and Anderson 2005), which may have influenced continued avoidance of areas near well pads recently equipped with LGS.

Sage-grouse habitat use in the winter is strongly related to availability of sagebrush above snow (see Connelly et al. 2011*b*), which can be influenced by sagebrush height, sagebrush canopy cover, and topography. Shrub height and sagebrush canopy cover were highly correlated ($r = 0.70$), as were roughness and sagebrush canopy cover ($r = -0.62$). We elected to include the GIS shrub height variable (Homer et al. 2012) and topographic roughness in our analyses as representing our best proxy for sagebrush availability above snow. We recognize that other habitat attributes can influence winter habitat selection in sage-grouse, especially sagebrush nutrient and secondary metabolite concentrations (Remington and Braun 1985, Frye et al. 2013). However, the inclusion of habitat measures not readily available was beyond the scope of our study. Shrub height was highly correlated with distance to conventional well pads ($r = 0.63$); we found lower shrub heights on average at data logger stations closer to conventional well pads. Additionally, the relative probability of a location being used by sage-grouse and the amount of time sage-grouse spent in an area were related positively to sagebrush height. Habitat condition in terms of lower average shrub heights may have partially explained the documented lack of use of sites near conventional well pads by sage-grouse. However, average shrub heights at all but 1 data logger station were within 1 standard deviation of the average height of all stations, and average sagebrush cover at all stations was within 1 standard deviation of the mean for all stations. Thus, correlations between habitat attributes and infrastructure may lack biological importance.

Population-level avoidance of energy development infrastructure by sage-grouse during the winter may be a result of

relatively high anthropogenic activity levels. Given that an individual sage-grouse selected a site, distance to infrastructure with higher activity levels (i.e., conventional well pads, drilling rigs, and plowed main haul roads) was positively related to average hours spent in an area relatively consistently. Further, we found inconsistent relationships between distance to drilling rig and distance to main haul road and relative probability of use (Table 4). This suggests that sage-grouse were visiting areas near high activity sites but were spending less time in those areas possibly encountering stimuli (e.g., human activity) resulting in movement from these areas more quickly than movement from areas near infrastructure with lower levels of activity.

Results indicate that sage-grouse moving from an area typically did not return to that area, at least within the timeframe of a working radio-transmitter (i.e., 2-year battery life). We found consistently stronger relationships between the number of events (or visits to the area monitored by a data logger) compared to the number of sage-grouse visiting a location (Table 3). This indicates a higher relative proportion of total visits by sage-grouse to locations away from infrastructure. In other words, sage-grouse were visiting locations near infrastructure but not often (i.e., multiple individual sage-grouse logged but relatively few independent log events), whereas areas removed from infrastructure were visited repeatedly. This type of pattern is consistent with individuals being and then remaining displaced.

The displacement mechanism of individuals moving from anthropogenic activity followed by a lack of movement back into vacated areas may explain the relative lack of reaction to LGS observed. If displacement is occurring primarily during drilling phases of development and individuals are not inclined to return to a site once displaced, then use of habitats near producing well pads—regardless of anthropogenic activity levels associated with the pads—may not occur for several years following a pad entering production phases of development. In terms of an inconsistent distance effect of LGS, our results may be suggesting that sage-grouse displaced by activity are moving back into areas near well pads with less human activity more quickly than areas near conventional well pads. Thus, reduced activity during production phases of development may influence more temporal aspects versus spatial aspects of impact.

Copeland et al. (2011) predicted that currently proposed and existing energy developments could affect over 41 million hectares (24%) of shrubland habitats in the western United States and Canada. This may be a conservative estimate of impact for species sensitive to anthropogenic activity where energy development results in large-scale indirect habitat loss. The NEPA process of managing energy developments emphasizes prediction and prevention of environmental damage with reduction of impacts being a key stage of implementation of the process (Kiesecker et al. 2011). Our results indicate that reducing well pad densities within a developed energy field represents a potential on-site option for reducing the effects of energy development on wintering sage-grouse. Additionally, although distance effect results were not unequivocal, our results imply that decreased human activity levels around important sage-grouse winter areas may reduce on-site effects of energy development.

## MANAGEMENT IMPLICATIONS

Minimizing the densities of well pads may reduce on-site impacts of energy development on wintering sage-grouse. We suggest that implementing efforts to decrease anthropogenic activity levels associated with infrastructure of natural gas fields during both drilling and production phases of development may also help reduce effects of the infrastructure on wintering sage-grouse. We suggest designing future developments such that well densities and anthropogenic activity levels are minimized. Additionally, retroactively implementing activity-reducing efforts in existing energy development fields may reduce the spatial effects of infrastructure during production phases of development by reducing the amount of time sage-grouse avoid a producing well pad. Implementation of these measures may reduce impacts of energy development to sage-grouse during the winter relative to conventional development, but impacts will not likely be eliminated, nor immediately observed. Results from our study are specific to wintering sage-grouse, and thus may not be applicable to other seasonal habitats (e.g., breeding, nesting, brood-rearing). Additional research is required to establish effects of LGS during other seasonal periods, and to determine if demographic consequences of energy development (Lyon and Anderson 2003, Aldridge and Boyce 2007, Holloran et al. 2010, Dzialak et al. 2011) are influenced by LGS.

## ACKNOWLEDGMENTS

Financial support was provided by Shell Rocky Mountain Production (reorganized as SWEPI, LP), QEP Energy Company, Ultra Resources Inc., and the Pinedale Field Office of the Bureau of Land Management. Sage-grouse that used the study area for wintering but were radio-equipped for other projects were used within the analysis. Financial supporters for these projects included the Tom Thorne Sage-grouse Conservation Fund, Upper Green River Basin Sage-grouse Local Working Group (the Office of the Governor of Wyoming through the Wyoming Sage-grouse Conservation Fund), the North American Grouse Partnership, and the Department of Ecosystem Science and Management at the University of Wyoming. We thank all the landowners in the Upper Green River Basin that allowed access to private lands. Field assistance was provided by R. Everett, T. Lingle, J. Michalak, G. Shedd, C. Skinner, and D. Woolwine. Technical assistance was provided by R. M. Nielson and H. Sawyer with Western EcoSystems Technology Inc. (Cheyenne, WY), BLM Pinedale Field Office (Pinedale, WY), and the Wyoming Game and Fish Department Jackson/Pinedale Regional Office (Pinedale, WY). Telemetry flights were conducted with the assistance of Mountain Air Research (Driggs, ID) and Sky Aviation (Dubois, WY). No conflicts of interest to disclose. We thank the following reviewers for improving the manuscript: J. L. Beck, P. S. Coates, A. Davison, P. Guernsey, C. McKee, E. Tokarz, and 1 anonymous reviewer.

# LITERATURE CITED


Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 117:508–526.

Breck, S. W., N. Lance, and J. Bourassa. 2006. Limitations of receiver/data loggers for monitoring radiocollared animals. Wildlife Society Bulletin 34:111–115.

Bureau of Land Management. 2004. Finding of no significant impact, decision record and environmental assessment for Questar year-round drilling proposal, Sublette County, Wyoming. WY-100-EA06-043, Pinedale Field Office, Pinedale, Wyoming, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Caccamise, D. F., and R. S. Hedin. 1985. An aerodynamic basis for selecting transmitter loads in birds. Wilson Bulletin 97:306–318.

Carpenter, J., C. Aldridge, and M. S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 74:1806–1814.

Connelly, J. W., S. T. Knick, C. E. Braun, W. L. Baker, E. A. Beever, T. Christiansen, K. E. Doherty, E. O. Garton, S. E. Hanser, D. H. Johnson, M. Leu, R. F. Miller, D. E. Naugle, S. J. Oyler-McCance, D. A. Pyke, K. P. Reese, M. A. Schroeder, S. J. Stiver, B. L. Walker, and M. J. Wisdom. 2011*a* Conservation of greater sage-grouse: a synthesis of current trends and future management. Pages 549–563 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology (vol. 38) University of California Press, Berkeley, USA.

Connelly, J. W., E. T. Rinkes, and C. E. Braun. 2011*b* Characteristics of greater sage-grouse habitats: a landscape species at micro and macro scales. Pages 69–84 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology (vol. 38) University of California Press, Berkeley, USA.

Copeland, H. E., A. Pocewicz, and J. M. Kiesecker. 2011. Geography of energy development in western North America: potential impacts on terrestrial ecosystems. Pages 7–25 *in* D. E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

Dalgaard, P. 2002. Introductory statistics with R. Springer Science + Business Media, New York, New York, USA.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187–195.

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, J. P. Mudd, J. B. Winstead, and L. D. Hayden-Wing. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. PLoS ONE 6:e26273.

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, and J. B. Winstead. 2012. Temporal and hierarchical spatial components of animal occurrence: conserving seasonal habitat for greater sage-grouse. Ecosphere 3:30.

Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal Wildlife Management 19:267–272.

Fischer, R. A., A. D. Apa, W. L. Wakkinen, K. P. Reese, and J. W. Connelly. 1993. Nesting-area fidelity of sage grouse in southeastern Idaho. Condor 95:1038–1041.

Frye, G. G., J. W. Connelly, D. D. Musil, and J. S. Forbey. 2013. Phytochemistry predicts habitat selection by an avian herbivore at multiple spatial scales. Ecology 94:308–314.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Harju, S. M., M. R. Dzialak, R. C. Taylor, L. D. Hayden-Wing, and J. B. Winstead. 2010. Thresholds and time lags in effects of energy development on greater sage-grouse populations. Journal of Wildlife Management 74:437–448.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Homer, C. G., C. L. Aldridge, D. K. Meyer, and S. J. Schell. 2012. Multi-scale remote sensing sagebrush characterization with regression trees over Wyoming, USA: laying a foundation for monitoring. International Journal of Applied Earth Observation and Geoinformation 14:233–244.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Kiesecker, J. M., H. E. Copeland, B. A. McKenney, A. Pocewicz, and K. E. Doherty. 2011. Energy by design: making mitigation work for conservation and development. Pages 159–181 *in* D. E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

Lyon, A. G. 2000. The potential effects of natural gas development on sage grouse near Pinedale, Wyoming. Thesis, University of Wyoming, Laramie, USA.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486–491.

Manly, B. F., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Norwell, Massachusetts, USA.

Millspaugh, J. J., R. M. Nielson, L. McDonald, J. M. Marzluff, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. Journal of Wildlife Management 70:384–395.

Naugle, D. E., K. E. Doherty, B. L. Walker, H. E. Copeland, M. J. Holloran, and J. D. Tack. 2011. Sage-grouse and cumulative impacts of energy development. Pages 55–70 *in* D. E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

O'Brian, R. M. 2007. A caution regarding rules of thumb for variance inflation factors. Quality & Quantity 41:673–690.

R Core Team. 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Ramsey, F. L., and D. W. Schafer. 2002. The statistical sleuth: a course in methods of data analysis second edition. Duxbury, Pacific Grove, California, USA.

Remington, T. E., and C. E. Braun. 1985. Sage grouse food selection in winter, North Park, Colorado. Journal Wildlife Management 49:1055–1061.

Remington, T. E., and C. E. Braun. 1991. How surface coal mining affects sage grouse, North Park, Colorado. Proceedings, Issues and Technology in Management of Impacted Western Wildlife. Thorne Ecological Institute 5:128–132.

Sawyer, H., M. J. Kauffman, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052–1061.

Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.

Schroeder, M. A., and L. A. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildlife Biology 9:291–299.

Smith, K. T., C. P. Kirol, J. L. Beck, and F. C. Blomquist. 2014. Prioritizing winter habitat quality for greater sage-grouse in a landscape influenced by energy development. Ecosphere 5:15.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practices of statistics in biological research third edition. W. H. Freeman and Company, New York, New York, USA.

StataCorp. 2007. Stata: release 10. Statistical Software. Stata Press, College Station, Texas, USA.

U.S. Department of Interior. 2000. Record of decision, environmental impact statement for the Pinedale anticline oil and gas exploration and development project Sublette County, Wyoming. United States Bureau of Land Management, RODEIS-00-018, Pinedale, Wyoming, USA.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

White, G. C., and R. E. Bennetts. 1996. Analysis of frequency count data using the negative binomial distribution. Ecology 77:2549–2557.


*Associate Editor: Peter Coates.*

CHAPTER EIGHT

# Nesting Success and Resource Selection of Greater Sage-Grouse

*Nicholas W. Kaczor, Kent C. Jensen, Robert W. Klaver, Mark A. Rumble, Katie M. Herman-Brunson, and Christopher C. Swanson*

*Abstract*. Declines of Greater Sage-Grouse (*Centrocercus urophasianus*) in South Dakota are a concern because further population declines may lead to isolation from populations in Wyoming and Montana. Furthermore, little information exists about reproductive ecology and resource selection of sage grouse on the eastern edge of their distribution. We investigated Greater Sage-Grouse nesting success and resource selection in South Dakota during 2006–2007. Radio-marked females were tracked to estimate nesting rates, nest success, and habitat resources selected for nesting. Nest initiation was 98.0%, with a maximum likelihood estimate of nest success of 45.6 ± 5.3%. Females selected nest sites that had greater sagebrush canopy cover and visual obstruction of the nest bowl compared to random sites. Nest survival models indicated that taller grass surrounding nests increased nest survival. Tall grass may supplement the low sagebrush cover in this area in providing suitable nest sites for Greater Sage-Grouse. Land managers on the eastern edge of Greater Sage-Grouse range could focus on increasing sagebrush density while maintaining tall grass by developing range management practices that accomplish this goal. To achieve nest survival rates similar to other populations, predictions from our models suggest 26 cm grass height would result in approximately 50% nest survival. Optimal conditions could be accomplished by adjusting livestock grazing systems and stocking rates.

*Key Words: Centrocercus urophasianus*, Greater Sage-Grouse, nest initiation, nest success, renesting, resource selection, sagebrush, South Dakota.

Kaczor, N. W., K. C. Jensen, R. W. Klaver, M. A. Rumble, K. M. Herman-Brunson, and C. C. Swanson. 2011. Nesting success and resource selection of Greater Sage-Grouse. Pp. 107–118 *in* B. K. Sandercock, K. Martin, and G. Segelbacher (editors). Ecology, conservation, and management of grouse. Studies in Avian Biology (no. 39), University of California Press, Berkeley, CA.

Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter sage grouse) are a sensitive species for state and federal resource management agencies due to declining populations and degradation and loss of nesting habitat (Aldridge and Brigham 2001, Connelly et al. 2004, Schroeder et al. 2004). Estimated trends of male sage grouse lek counts in South Dakota declined steadily from 1973 to 1997. From 1997 to 2004, sage grouse populations may have increased slightly (Connelly et al. 2004). Isolation from populations in neighboring states raises additional concerns for sage grouse persistence in South Dakota (Aldridge et al. 2008).

Declines in sage grouse populations have resulted in several petitions to list sage grouse under the Endangered Species Act (ESA) of 1973 (Connelly et al. 2004). Currently, federal land management agencies are responsible for approximately 66% of the sagebrush landscape in the United States. Federal agencies such as the U.S. Bureau of Land Management (BLM) and U.S. Forest Service (USFS) are directed by administrative policy to manage public lands for sustained multiple use under the Federal Land Policy and Management Act (1976) and the Public Rangelands Improvement Act (1978). Currently, sage grouse are managed as a sensitive species by BLM and USFS, and their management should not result in further population declines of sage grouse, which could lead to listing under ESA. The South Dakota Department of Game, Fish, and Parks has identified sage grouse as a species of special concern (South Dakota Department of Game, Fish, and Parks 2006). Listing of sage grouse under the ESA could have major ramifications on the use and management of public lands in the western United States (Knick et al. 2003).

Nest success is one factor that can determine whether sage grouse populations increase or decrease (Braun 1998, Schroeder et al. 1999, Dinsmore and Johnson 2005). Yet information is lacking on the ecological requirements of nesting sage grouse in western South Dakota. The objectives of this study were to develop an understanding on the nesting ecology, success, and resource selection of sage grouse at the eastern edge of their range.

## STUDY AREA

The study was conducted within a 3,500 km$^2$ area in Butte and Harding counties, South Dakota; Crook County, Wyoming; and Carter County, Montana (44°44′ N to 45°20′ N, 103°15′ W to 104°21′ W; Fig. 8.1). Approximately 75% of the area was privately owned. The remaining 25% of the study area was managed by the BLM and State of South Dakota School and Public Lands Division. The area was predominately used for grazing, although small grain production also occurred. Open-pit mining for bentonite occurred at the south end of the study site on Pierre soils (C. Berdan, pers. comm.).

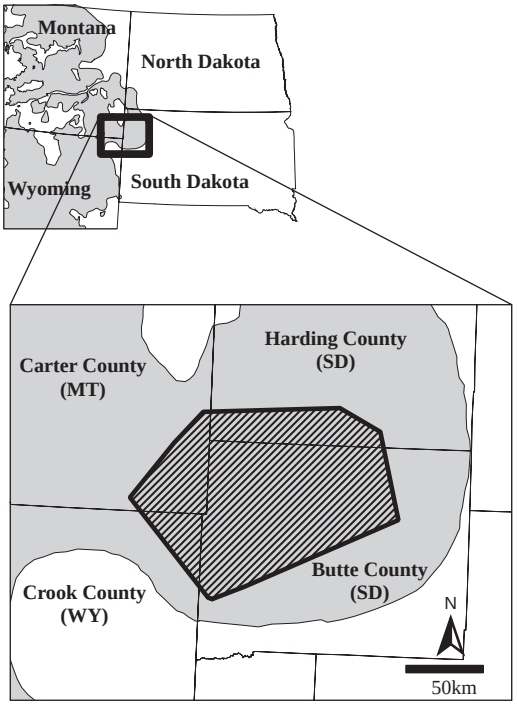



Figure 8.1. Location of study area for Greater Sage-Grouse in Butte, Carter, Crook, and Harding counties, 2006–2007. The hatched area encompasses all locations; the gray area is the current range of Greater Sage-Grouse (Schroeder et al. 2004).

Vegetation consisted of short shrubs, mostly Wyoming big sagebrush (*Artemisia tridentata* spp.) and plains silver sagebrush (*A. cana* spp.). Other shrubs included broom snakeweed (*Gutierrezia sarothrae*), greasewood (*Sarcobatus vermiculatus*), and saltbushes (*Atriplex* spp.) (Johnson and Larson 1999). Common grasses included western wheatgrass (*Pascopyrum smithii*), Junegrass (*Koeleria macrantha*), bluegrass species (*Poa* spp.), green needle-grass (*Nassella viridula*), and Japanese brome (*Bromus japonicus*). Common forbs included western yarrow (*Achillea millefolium*), common dandelion (*Taraxacum officinale*), pepperweed (*Lepidium*

*densiflorum*), and field pennycress (*Thlaspi arvense*) (Johnson and Larson 1999).

Temperatures in summer (May–August) averaged 20.1°C but can reach highs of 43.3°C (South Dakota State Climate Office 2007). During the months of March through June 2006 and 2007, the study area received approximately 14 cm and 22 cm of precipitation, 33% less and 5% more than the 58-year average of 21 cm (1956–2007; South Dakota State Climate Office 2007). Elevation ranges from 840 to 1,225 m above sea level with nearly level to moderately steep clayey soils over clay shale (Johnson 1976).

## METHODS

### Data Collection

We captured female sage grouse at or near six leks using large nets and spotlighting them from all-terrain vehicles each year between March and mid-April 2006 and 2007 (Giesen et al. 1982, Wakkinen et al. 1992). Females were weighed and equipped with a 22-g necklace-style transmitter; transmitters were approximately 1.4% of mean female sage grouse body mass and had a life expectancy of 434 days. Transmitters could be detected from a distance of approximately 2–5 km from the ground and were equipped with an 8-hour mortality switch. Females were classified as yearlings (<1 yr old) or adults (>1 yr old) based on primary wing feather characteristics (Eng 1955, Crunden 1963). The South Dakota State University Institutional Animal Care and Use Committee approved trapping and handling techniques, as well as study design (Protocol #07-A032).

We located radio-marked female sage grouse twice each week during the breeding, laying, and incubation periods. In the event we could not locate an individual from the ground, we searched the study area from a fixed-wing aircraft to obtain an approximate location. Once a female was believed to be incubating, we recorded four coordinates approximately 15 m away from the nest in the four cardinal directions with a Global Positioning System (GPS) receiver. We confirmed nest presence/absence during the subsequent visit. If a female was present on the second visit, we flushed her to determine clutch size. Our use of this method did not decrease nest survival for the immediate interval after the female was flushed from the nest. Nests were considered successful if ≥1 egg hatched. We calculated distances from nearest active display ground to nests, renests, and previous nests by the same bird using Hawth's Analysis Tool (Beyer 2004).

We characterized vegetation at nest sites after their fate was determined. Four 50-m transects were established radiating in the four cardinal directions from the nest bowl and four additional 5 m transects were established at the 45° intervals. A modified Robel pole was used to estimate visual obstruction (VOR) and maximum grass height at 1-m intervals from 0 m to 5 m ($n = 21$), and at 10-m intervals out to 50 m ($n = 20$) along each 50 m transect (Robel et al. 1970, Benkobi et al. 2000). We estimated sagebrush (*A. tridentata* spp. and *A. cana* spp.) density and height at 10-m intervals ($n = 80$) using the point-centered quarter method (Cottam and Curtis 1956). Vegetation canopy cover was estimated using a 0.10 $m^2$ quadrat at 1-m intervals to 5 m ($n = 44$) and at 2-m intervals along the long transects to 30 m ($n = 52$). We estimated percent canopy cover for total vegetation, grass, forb, shrub, litter, bare ground, and individual shrub and grass species (Daubenmire 1959). This method is amenable to collecting data on windy days and yields data that are similar (<3% difference for sagebrush) to the line-intercept method, but may provide more accurate estimates of cover (Floyd and Anderson 1987, Booth et al. 2006).

We measured an equal number of random sites within a 3-km buffer of capture leks to estimate resource selection. We navigated to the coordinates of random sites with a GPS and located the center of the transects over the nearest sagebrush because sage grouse usually nest beneath a shrub.

### Data Analyses

#### *Nesting Parameters*

We used the multi-response permutation procedure (MRPP; Mielke and Berry 2001) to test the null hypothesis that there were no differences between mass of female age-classes, clutch size of female age-classes, clutch size between first nests and renests, nest initiation date between years, distance among nests within a year, distance between nests between years (nest site fidelity), and distance to display grounds between years and age-classes of females. To avoid biasing estimates of nesting and renesting rates, we randomly

selected one observation for females that nested both years. Chi-square goodness-of-fit tests were used to test for differences in nest initiation rates between years and between age-classes of females. Statistical significance was set at $\alpha \leq 0.05$. Egg hatchability was the proportion of eggs hatching from successful clutches.

Average grass height and VOR were calculated for each 1-m interval away from the nest to 5 m, at 10-m intervals from 10 to 50 m, and for the site at 0 to 50 m. We used a maximum likelihood estimator to estimate sagebrush density (Pollard 1971). We calculated average sagebrush height for each site from the sagebrush plants that were measured to estimate density. Canopy coverage values were recoded to midpoint values of categories, and these were summarized to an average for 0 to 5 m, 6 to 30 m, and for the site at 0 to 30 m (Daubenmire 1959). To reduce the number of variables in the vegetative dataset to a manageable level and identify biologically important variables to carry forward in the analyses, we used MRPP to identify variables that exhibited differences ($\alpha \leq 0.15$) between nest and random sites, and again between successful and failed nests (Boyce et al. 2002, Stephens et al. 2005). Two separate screen processes were conducted as some variables could be important for nest selection but may not have a measurable effect on nest success.

### *Resource Selection*

We identified ten habitat variables from the nest site selection MRPP analyses (Table 8.1). We used these and a year effect to investigate sage grouse nesting resource selection. Variables included: percent total vegetation cover, grass cover, sagebrush cover, and litter; site averages for sagebrush height, grass height, and visual obstruction; grass height 0–5 m from the nest; visual obstruction at the nest; and visual obstruction 1 m from nest.

Year was included as a design variable in all resource selection candidate models. To reduce potential variable interaction in our models, variables that were correlated to one another ($r > 0.70$) were not included in the same model (e.g., total vegetation cover plus grass cover). We used an information theoretic approach with logistic regression to estimate the support for models evaluating resource selection at nest sites (Burnham and Anderson 2002, SAS Institute Inc. 2007). Due to a small sample size with respect to the number of parameters estimated ($n/K < 40$); we used the small-sample adjustment for Akaike's Information Criterion ($AIC_c$) to evaluate models (Burnham and Anderson 2002). We ranked our models based on differences between $AIC_c$ for each model and the minimum $AIC_c$ model ($\Delta AIC_c$), and Akaike weights ($w_i$) to assess the weight of evidence in favor of each model and the sum $AIC_c$ weight for each variable (Beck et al. 2006). In addition, we investigated the slope of the coefficient estimates ($\beta$) to determine variable effect. We evaluated the predictive strength of our models using a receiver operation characteristic curve (ROC); values between 0.7 and 0.8 were considered acceptable predictive discrimination and values higher than 0.8 were considered excellent predictive discrimination. Model goodness-of-fit was determined using a Hosmer–Lemeshow test (Hosmer and Lemeshow 2000).

### *Nest Success*

We used the nest survival procedure in program MARK to evaluate environmental and biological factors that might influence nest survival (White and Burnham 1999, Dinsmore et al. 2002). We standardized nesting dates among years by using the earliest date we discovered a nest as the first day of the nesting season. We monitored nests over a 59-day period beginning 23 April and ending 20 June, which comprised 58 daily intervals of observations to be used in estimating daily survival rate (DSR) for the 27-day incubation period. We identified four variables from the MRPP analyses of nest success as having potential to impact nest success. These variables included: grass height at the site level, visual obstruction at the site level, litter cover at the site level, and forb cover at the nest bowl. The variables were then combined with daily precipitation, daily minimum temperature, bird age, stage of incubation, and year. We did not model nest survival associated with nesting attempt because of a small number of renests ($n = 10$), although they were included in the analysis to test for seasonal variation. Daily weather variables were obtained from the nearest daily weather station located at Nisland, South Dakota, ~50 km from the center of the study area (South Dakota State Climate Office 2007). To reduce the effect of variable interaction in our models, variables that were correlated ($r > 0.70$) were not included in the same model.

TABLE 8.1

*Mean vegetation characteristics of nest sites and random sites between years for Greater Sage-Grouse in northwestern South Dakota, 2006–2007.*

| | Nest | | | Random | | | Pooled | | |
|---|---|---|---|---|---|---|---|---|---|
| Variable | 2006 ($n$ = 34) | 2007 ($n$ = 39) | $P \leq$ | 2006 ($n$ = 35) | 2007 ($n$ = 39) | $P \leq$ | Nest ($n$ = 73) | Random ($n$ = 74) | $P \leq$ |
| Total cover (%)[1] | 61.1 (2.3) | 75.1(2.0) | 0.01 | 55.8 (2.4) | 66.1 (2.4) | 0.01 | 68.6 (1.7) | 61.2 (1.8) | 0.01 |
| Litter (%) | 7.6 (0.8) | 7.1 (0.6) | 0.79 | 6.5 (0.7) | 6.1 (0.4) | 0.88 | 7.4 (0.5) | 6.3 (0.4) | 0.01 |
| Grass cover (%)[1] | 24.2 (1.9) | 31.4 (1.8) | 0.01 | 21.1 (1.9) | 25.8 (2.0) | 0.21 | 28.1 (1.4) | 23.6 (1.4) | 0.01 |
| Max grass hgt. (cm)[2] | 23.4 (0.9) | 29.5 (1.6) | 0.01 | 20.4 (0.8) | 25.0 (1.1) | 0.01 | 26.7 (1.0) | 22.8 (0.7) | 0.01 |
| Max grass hgt. 0–5 m (cm)[2] | 25.7 (0.9) | 30.9 (2.0) | 0.02 | 20.3 (0.8) | 24.3 (1.1) | 0.01 | 28.5 (1.2) | 22.4 (0.8) | 0.01 |
| Visual obstruction (cm) | 5.5 (0.6) | 11.1 (1.0) | 0.01 | 3.7 (0.4) | 5.1 (0.6) | 0.14 | 8.5 (0.7) | 4.4 (0.4) | 0.01 |
| Visual obstruction 0 m (cm)[3] | 20.8 (1.7) | 29.4 (1.8) | 0.01 | 10.5 (1.1) | 8.9 (1.0) | 0.13 | 25.4 (1.3) | 9.6 (0.7) | 0.01 |
| Visual obstruction 1 m (cm)[3] | 7.3 (0.9) | 13.7 (1.7) | 0.01 | 3.7 (0.5) | 4.1 (0.6) | 0.45 | 10.7 (1.0) | 3.9 (0.4) | 0.01 |
| Sagebrush cover (%) | 10.3 (0.8) | 10.1 (0.8) | 0.75 | 6.3 (0.8) | 6.3 (0.7) | 0.98 | 10.2 (0.6) | 6.2 (0.5) | 0.01 |
| Sagebrush hgt. (cm) | 25.8 (1.2) | 29.7 (1.6) | 0.04 | 23.8 (1.0) | 24.0 (1.0) | 0.97 | 27.9 (1.7) | 23.9 (1.3) | 0.01 |

NOTE: All values are reported as $\bar{x} \pm$ (SE). Variables with the same superscript number were correlated ($r > 0.70$) and not modeled together.

We used an information theoretic approach to evaluate support for models that influenced DSR (Burnham and Anderson 2002). We began by developing base models that included female age-classes, year, and constant survival. From these base models, we further explored the degree to which habitat and weather variables improved model fit. We used back-transformed estimates of DSR to estimate effects of variables on nest survival for the best supported models (Dinsmore et al. 2002). We then plotted DSR versus simulated values of variables to determine the effect of variables independently from one another. Estimated standard error for nest survival over the 27-day nesting cycle was calculated using the delta method (Seber 1982).

## RESULTS

### Nesting Parameters

We captured and attached transmitters to 53 female sage grouse (28 yearlings and 25 adults); 29 individuals were included both years for the resource selection analyses. Adults weighed (1,664 ± 14 g, $\bar{x}$ ± SE; $n = 43$) more than yearlings (1,524 ± 16, $n = 24$; $P < 0.01$). There were no differences in female mass between years ($P = 0.20$; $n = 67$). Nest initiation rate for all females was 98.0% and did not differ significantly between years ($P = 0.96$; $n = 67$) or with female age-class ($P = 0.92$; $n = 67$). Renest initiation rate was 25.8% (8/31) and did not differ significantly between years ($P = 0.19$; $n = 31$) or female age-class ($P = 0.62$; $n = 31$). Females were more likely to renest if their first nest was lost early in the incubation period ($P = 0.02$; $n = 31$). The number of nest observation days for first nests was 7.9 ± 1.3 SE days ($n = 8$) for females that renested and 14.6 ± 1.8 SE ($n = 23$) days for females that did not renest.

Average date of nest initiation for successful first nests was 24 April ± 1.6 SE ($n = 30$) days, with adults initiating egg laying approximately 6.7 days earlier than yearlings ($P = 0.02$; $n = 30$). Average hatch date for first nests was 31 May ± 1.5 SE ($n = 30$) days. Average date of renest initiation was approximately 15 days later (9 May ± 2.6 SE days; $n = 8$) than first nests, with hatch date occurring 14 June ± 2.0 SE days. Clutch size differed between nesting attempts (first nests: 8.3 ± 0.2 SE eggs; renests: 6.4 ± 0.6 SE; $P < 0.01$; $n = 64$), but not by nest fate ($P = 0.83$), female age-class ($P = 0.98$), or year ($P = 0.10$).

One adult female in 2007 nested approximately 30.3 km from lek of capture but most females nested close to leks. In 2006, successful nests were significantly closer to an active lek ($P = 0.04$; $n = 40$) than failed nests (1.5 ± 0.3 km vs. 2.9 ± 0.5 km, $\bar{x}$ ± SE); however, there was no difference in 2007 (2.5 ± 0.5 km vs. 3.2 ± 0.7 km, $P = 0.70$; $n = 39$), or when both years were combined (2.1 ± 0.3 km vs. 3.0 ± 0.4 km, $P = 0.13$; $n = 79$). The distance that adults and yearlings nested from the nearest active lek did not differ significantly (2.2 ± 0.3 km vs. 3.3 ± 0.5 km, $P = 0.08$; $n = 79$). Sixty-eight percent of nests were within 3 km of a documented active lek, and 97% of nests were within 7 km.

Average distance between an individual's nest in 2006 to its nest in 2007 was 1.08 ± 0.40 SE km ($n = 21$). There was no difference in nest site fidelity between adults and yearlings ($P = 0.65$; $n = 21$) or between nests that either failed or were successful the first year ($P = 0.47$; $n = 21$). Mean distance between failed first nests and subsequent renests was 1.85 ± 0.55 SE km ($n = 8$). Successful renests (0.95 ± 0.36 SE km) were not significantly closer to first nests than failed renests (2.03 ± 0.91 SE km, $P = 0.17$; $n = 8$).

### Resource Selection

Distribution of total cover, grass cover, grass height, visual obstruction, and sagebrush height differed between nest sites in 2006 and 2007 ($P < 0.05$; Table 8.1). In addition, all screened vegetative characteristics differed between nests and random sites (Table 8.1). The minimum $AIC_c$ model ($AIC_c$ weight = 0.39; Table 8.2) of nest site selection included sagebrush canopy coverage at the site level ($\beta = 0.20$, SE = 0.06) and visual obstruction at the nest ($\beta = 0.22$, SE = 0.04; Table 8.2). Increasing sagebrush cover by 5% increased the odds of use approximately 6.1 times. Increasing visual obstruction at the nest by 2.54 cm increased the odds of use 3.2 times. Predictive ability of the top model (ROC values) was excellent at 0.93 and the Hosmer–Lemeshow goodness-of-fit test was nonsignificant ($P = 0.14$), indicating acceptable model fit.

A second model including sagebrush canopy coverage, visual obstruction at the nest, and average

TABLE 8.2

*Selected models from logistic regression analysis (n = 39 models) predicting Greater Sage-Grouse nest sites (n = 73) versus random sites (n = 74) in northwestern South Dakota, 2006–2007.*

| Model[a] | Log(*L*) | *K*[b] | Δ AICc[c] | $w_i$[d] |
|---|---|---|---|---|
| Sagebrush cover + visual obstruction 0 m | −50.80 | 5 | 0.00 | 0.52 |
| Sagebrush cover + visual obstruction 0 m + max grass hgt. 0–5 m | −49.82 | 6 | 0.22 | 0.47 |
| Visual obstruction 0 m | −57.50 | 4 | 11.26 | 0.00 |
| Sagebrush cover | −89.14 | 4 | 74.54 | 0.00 |
| Intercept only | −101.89 | 2 | 95.85 | 0.00 |
| Year | −101.89 | 3 | 97.92 | 0.00 |

[a] For ease of interpretation, year variable was excluded from model column. See Kaczor (2008) for full model set.
[b] Number of habitat parameters plus intercept, SE, and year.
[c] Change in $AIC_c$ value.
[d] Model weight.

TABLE 8.3

*Selected models for daily nest survival of Greater Sage-Grouse in northwestern South Dakota, 2006–2007.*

| Model[a] | *K*[b] | $AIC_c$ | Δ $AIC_c$[c] | $w_i$[d] |
|---|---|---|---|---|
| Max grass hgt. + litter | 3 | 225.79 | 0.00 | 0.23 |
| Max grass hgt. + litter + daily precip. + precip. lag | 5 | 226.75 | 0.96 | 0.15 |
| Max grass hgt. + litter + daily precip. | 4 | 227.37 | 1.60 | 0.11 |
| Max grass hgt. + litter + bird age | 4 | 227.77 | 1.98 | 0.09 |
| Constant | 1 | 252.71 | 26.92 | 0.00 |

[a] See Kaczor (2008) for full model set.
[b] Number of variables plus intercept.
[c] Change in $AIC_c$ value.
[d] Model weight.

grass height within 5 m also had strong support ($AIC_c$ weight = 0.35). Sagebrush canopy coverage and visual obstruction at the nest obtained the highest summed $AIC_c$ weights of 0.99. The combined model of sagebrush canopy cover and visual obstruction at the nest had the greatest support, but there was less support for a single-factor model, although beta estimates for the two variables were similar ($\Delta\beta = 0.03$).

## Nest Success

Most nests were located under Wyoming big sagebrush (90%) or silver sagebrush (7%; $n = 79$). One nest was against a large boulder, and another was in a dense stand of prairie cordgrass (*Spartina pectinata*). Egg hatchability averaged 78.3 ± 2.1 SE % ($n = 513$). Constant nest survival rates with no covariates were 45.6 ± 5.3 SE %, but that was a poor model of DSR. The best model for DSR ($AIC_c$ weight = 0.23) included grass height and litter cover (Table 8.3). Three other models were $\Delta AIC_c \leq 2$ units of the top model. Grass height had a positive association with DSR ($\beta = 0.15$, SE = 0.03; Fig. 8.2), whereas percent litter cover had a negative association on DSR ($\beta = -0.08$, SE = 0.03); both factors were present in all of models with $\Delta AIC_c < 2.0$.

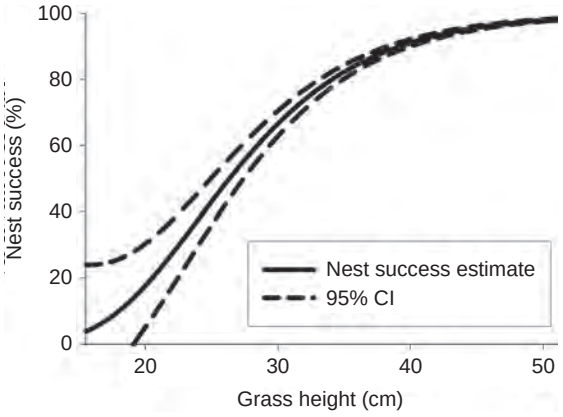



Figure 8.2. Effect of grass height on nest success of Greater Sage-Grouse in northwestern South Dakota, 2006–2007. Nest success estimates were derived from back-transformed beta estimates included in top model. Confidence intervals estimated from the delta method (Seber 1982).

The second-ranked model ($AIC_c$ weight = 0.15) included grass height, litter, daily precipitation, and a 1-day lag of precipitation. Daily precipitation had a positive association with DSR ($\beta$ = 29.5, SE = 40.4) and the 1-day lag of precipitation was negatively associated with DSR ($\beta$ = –1.89, SE = 0.77). These variables were only included in supported models when combined with grass height and litter. The third- and fourth-ranked models both included grass height and litter along with the variables daily precipitation and bird age, respectively. Nest success differed between years from 37.7 ± 7.3 SE % in 2006 to 52.5 ± 7.2 SE % in 2007. However, adding a year effect to the top model did not improve model fit.

## DISCUSSION

Our study of Greater Sage-Grouse on the easternmost portion of their range in South Dakota identified interesting aspects of sage grouse ecology that have not previously been documented. Female body condition was above average and nesting initiation rates were also high. Similar to other studies, sagebrush cover was an important variable in nest site selection, but at a much lower density than expected. Grass structure, which far exceeded range-wide estimates, played an important role in providing increased cover for successful nests (Connelly et al. 2004). Overall, nest success was within range-wide estimates, suggesting certain features of the habitat condition in South Dakota are productive for sage grouse.

### Nesting Parameters

Nest initiation rates for sage grouse are generally low compared to other prairie grouse (Bergerud 1988). However, estimates of nesting initiation based on telemetry are probably underestimated in the literature, as follicular development indicated that at least 98.2% of females laid eggs the previous spring in Idaho (Dalke et al. 1963, Schroeder et al. 1999). Nonetheless, nest initiation rates were high in this study relative to range-wide estimates (Connelly et al. 2004). Females in our study were approximately 63 g (~4%) heavier than the average for 673 individuals in eight other studies (Schroeder et al. 1999). Heavier body mass in female Wild Turkeys (*Meleagris gallopavo*) increased the likelihood of breeding (Porter et al. 1983, Hoffman et al. 1996). Sage grouse exhibit considerable temporal variation in nest initiation rates between years, which may be related to nutrition before and during the breeding season (Hungerford 1964, Barnett and Crawford 1994, Moynahan et al. 2007). High rates of initiation suggest that habitat conditions in our study site were above average.

Renesting rates in sage grouse are highly variable (0–87%), and are linked to environmental effects and habitat quality (Schroeder 1997, Moynahan et al. 2007). Low renesting rates may be related to low primary productivity in the arid and semiarid environments occupied by sage grouse (Schroeder and Robb 2003). For example, Moynahan et al. (2007) found no renesting by sage grouse in dry years with little vegetative growth. In North Dakota, Herman-Brunson et al. (2009) reported 9.5% renesting in sage grouse. The relatively high proportion of renesting females in our study and greater female mass suggest that nesting habitat in South Dakota is of higher quality than elsewhere in sage grouse range. The inverse relationship between length of incubation and renesting propensity suggests that the condition of the female may decline as

incubation progresses. An inverse relationship between the duration of incubation and renesting has also been shown elsewhere (Aldridge and Brigham 2001, Herman-Brunson 2009, Martin et al., this volume, chapter 17).

### Nest Success

Sage grouse in South Dakota selected nest sites with higher sagebrush cover and placed their nests beneath sagebrush plants with greater horizontal cover (VOR) than random sites. Shrub density (correlated with sagebrush cover) and nest-bowl VOR were important predictors of sage grouse nest sites in North Dakota (Herman-Brunson et al. 2009). Connelly et al. (2000) recommended 15–25% sagebrush canopy coverage for nesting sage grouse, and this recommendation has been confirmed with a range-wide meta-analysis (Hagen et al. 2007). In South Dakota, nesting sage grouse selected for sagebrush with the highest densities and protective cover, but that was less than recommended values. In contrast to sagebrush, grass structure in South Dakota exceeds both management recommendations and range-wide averages (Connelly et al. 2000, Hagen et al. 2007). Western South Dakota forms a transition zone between the northern wheatgrass–needlegrass prairie that dominates most of the Dakotas and the big sagebrush plains of Wyoming (Johnson and Larson 1999). Thus, while South Dakota had less than expected sagebrush cover for sage grouse, the grass structure likely compensated for the low sagebrush densities in providing cover for nests. Grass structure is highly correlated with annual precipitation; therefore, periodic drought may reduce nest cover for sage grouse. Poor grazing management in areas with low sagebrush cover could reduce grass structure, which may have detrimental effects on sage grouse nesting.

Sage grouse nest success varies widely across the range, from 14.5% (Gregg 1991) to 70.6% (Chi 2004), and is generally believed to be related to habitat conditions (Connelly et al. 1991, Aldridge and Brigham 2002, Hagen et al. 2007). Our estimate of nest success was similar to that of other sage grouse studies (48%; Connelly et al. 2004), despite the fact that available sagebrush canopy coverage was less than other areas. Successful nests in our study had taller grass structures than failed nests. Thus, tall grass differentiated not only suitable nest sites, but also nesting success. Nesting cover also increased nest success in Alberta, and was suggested to provide ample nest concealment in both sagebrush and non-sagebrush overstories in Washington (Sveum et al. 1998, Aldridge and Brigham 2002). Although litter cover entered our models as being an important predictive variable for nest success, the impact litter actually has on nest success is unknown. Litter may be greater after productive growing seasons, or be lower after intensive grazing pressure (Hart et al. 1988, Naeth et al. 1991).

Our results suggest that some aspects of sage grouse habitat in our study area were conducive to maintaining sage grouse populations despite being outside of current management recommendations (Connelly et al. 2000). Although management recommendations were based on existing knowledge, our habitat also provided the necessary requirements for the nesting period, which may be an important consideration for land managers elsewhere in sage grouse ranges.

### Management Implications

If sage grouse populations continue to decrease or remain listed as a sensitive species, sagebrush conservation and enhancement could be a top priority for land management agencies to enable sage grouse persistence in western South Dakota. Management for greater grass and sagebrush cover and height, and reduced conversion to tillage agriculture, could be encouraged to protect remaining habitats. Grazing by domestic sheep (*Ovis aries*) can reduce sagebrush cover (Baker et al. 1976), thereby reducing habitat quality for sage grouse. Domestic sheep grazing is not widespread in South Dakota, but was common on both private and public lands in our study area.

Range management practices that could increase sagebrush and grass cover and height include: rest-rotation grazing, where the rested pasture is not grazed until early July to allow for undisturbed nesting, or reduced grazing intensities or seasons of use to reduce impacts on sagebrush and grass growth (Adams et al. 2004). Land managers could develop grazing plans that leave or maintain grass heights $\geq$26 cm to try to maintain 50% nest success. In addition, we suggest annual grazing utilization not exceed 35% in order to improve rangeland conditions, particularly sagebrush cover (Holechek et al. 1999).

Wyoming big sagebrush typically recovers from a fire in 50–120 years (Baker 2006), and because of the restricted distribution and limited cover of sagebrush in South Dakota, we suggest limited use of prescribed fire or herbicides in areas with sagebrush.

## ACKNOWLEDGMENTS

Funding for this study was provided by the Bureau of Land Management (ESA000013), U.S. Forest Service Rocky Mountain Research Station (05-JV-11221609-127), U.S. Forest Service Dakota Prairie National Grasslands (05-CS-11011800-022), and support from South Dakota State University. Field assistance was provided by C. Berdan, T. Berdan, B. Eastman, B. Hauser, T. Juntti, J. Nathan, S. Harrelson, and T. Zachmeier. A number of volunteers assisted during capture and radio-collaring of females and chicks. A. Apa assisted with training on trapping techniques. We also acknowledge and appreciate those land owners who granted us permission to conduct this study on their private lands. We thank D. Turner, J. Sedinger, and an anonymous reviewer for their comments on prior versions of this manuscript. Any mention of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. government.

## LITERATURE CITED

Adams, B. W., J. Carlson, D. Milner, T. Hood, B. Cairns, and P. Herzog. 2004. Beneficial grazing management practices for sage-grouse (*Centrocercus urophasianus*) and ecology of silver sagebrush (*Artemisia cana*) in southeastern Alberta. Technical Report, Public Lands and Forests Division, Alberta Sustainable Resource Development. Pub. No. T/049.

Aldridge, C. L., and R. M. Brigham. 2001. Nesting and reproductive activities of Greater Sage-Grouse in a declining northern fringe population. Condor 103:537–543.

Aldridge, C. L., and R. M. Brigham. 2002. Sage-grouse nesting and brood-rearing habitat use in southern Canada. Journal of Wildlife Management 66: 433–444.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of Greater Sage-Grouse persistence. Diversity and Distributions 14:983–994.

Baker, M. F., R. L. Eng, J. S. Gashwiler, M. H. Schroeder, and C. E. Braun. 1976. Conservation committee report on the effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin 88:165–170.

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin 34:177–185.

Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of sage-grouse hens in Oregon. Journal of Range Management 47:114–118.

Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile Greater Sage-Grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070–1078.

Benkobi, L., D. W. Uresk, G. Schenbeck, and R. M. King. 2000. Protocol for monitoring standing crop in grasslands using visual obstruction. Journal of Range Management 53:627–633.

Bergerud, A. T. 1988. Population ecology of North American grouse. Pp. 578–685 *in* A. T. Bergerud and M. W. Gratson (editors), Adaptive strategies and population ecology of northern grouse. Wildlife Management Institute, Minneapolis, MN.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. <http://www.spatialecology.com/htools> (10 January 2006).

Booth, D. T., S. E. Cox, T. W. Meikle, and C. Fitzgerald. 2006. The accuracy of ground-cover measurements. Rangeland Ecology and Management 59:179–188.

Boyce, M. S., P. R. Vernier, S. E. Nielson, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modeling 157:281–300.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of Fish and Wildlife Agencies 78:139–156.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information theoretic approach. 2nd ed. Springer-Verlag, New York, NY.

Chi, R. Y. 2004. Greater Sage-Grouse on Parker Mountain, Utah. M.S. thesis, Utah State University, Logan, UT.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, WY.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage-grouse use of nest sites in southeastern Idaho. Journal of Wildlife Management 55:521–524.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451–460.

Crunden, C. W. 1963. Age and sex of sage grouse from wings. Journal of Wildlife Management 27:846–849.

Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. Journal of Wildlife Management 27:811–841.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33:43–64.

Dinsmore, S. J., and D. H. Johnson. 2005. Population analysis in wildlife biology. Pp. 154–184 *in* C. E. Braun (editor), Techniques for wildlife investigations and management. 6th ed. The Wildlife Society, Bethesda, MD.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal of Wildlife Management 19:267–272.

Floyd, D. A., and Anderson, J. E. 1987. A comparison of three methods for estimating plant cover. Journal of Ecology 75:221–228.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Gregg, M. A. 1991. Use and selection of nesting habitat by sage-grouse in Oregon. M.S. thesis, Oregon State University, Corvallis, OR.

Hagen, C. A., J. W. Connelly, and M. A. Schroeder. 2007. A meta-analysis of Greater Sage-Grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. Wildlife Biology 13(Supplement): 42–50.

Hart, R. H., M. J. Samuel, P. S. Test, and M. A. Smith. 1988. Cattle, vegetation, and economic responses to grazing systems and grazing pressure. Journal of Range Management 41:282–286.

Herman-Brunson, K. H., K. C. Jensen, N. W. Kaczor, C. C. Swanson, M. A. Rumble, and R. W. Klaver. 2009. Nesting ecology of Greater Sage-Grouse *Centrocercus urophasianus* at the eastern edge of their historic distribution. Wildlife Biology 15:237–246.

Hoffman, R. W., M. P. Luttrell, and W. R. Davidson. 1996. Reproductive performance of Merriam's Wild Turkeys with suspected *Mycoplasma* infection. Proceedings of National Wild Turkey Symposium 7:145–151.

Holechek, J. L., H. Gomez, F. Molinar, and D. Galt. 1999. Grazing studies: what we've learned. Rangelands 21:12–16.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. 2nd ed. John Wiley and Sons Inc., New York, NY.

Hungerford, C. R. 1964. Vitamin A and productivity in Gambel's Quail. Journal of Wildlife Management 28:141–147.

Johnson, J. R., and G. E. Larson. 1999. Grassland plants of South Dakota and the northern Great Plains. South Dakota State University. Brookings, SD.

Johnson, P. R. 1976. Soil survey of Butte County, South Dakota. U.S. Department of Agriculture, South Dakota Agricultural Experiment Station, Brookings, SD.

Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection Greater Sage-Grouse in northwestern South Dakota. M.S. thesis, South Dakota State University, Brookings, SD.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late: conservation and research issues for avifauna of sagebrush habitats. Condor 105:611–634.

Mielke, P. W., and K. J. Berry. 2001. Permutation methods: A distance function approach. Springer-Verlag, New York, NY.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of Greater Sage-Grouse in northcentral Montana. Journal of Wildlife Management 71:1773–1783.

Naeth, M. A., A. W. Bailey, D. J. Pluth, D. S. Chanasyk, and R. T. Hardon. 1991. Grazing impacts on litter and soil organic matter in mixed prairie and fescue grassland ecosystems in Alberta. Journal of Range Management 44:7–12.

Pollard, J. H. 1971. On distance estimators of density in randomly distributed forests. Biometrics 27:991–1002.

Porter, W. F., G. C. Nelson, and K. Mattson. 1983. Effects of winter conditions on reproduction in a northern Wild Turkey population. Journal of Wildlife Management 47:281–290.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–298.

SAS Institute Inc. 2007. JMP version 7. Cary, NC.

Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99:933–941.

Schroeder, M. A., and L. A. Robb. 2003. Fidelity of Greater Sage-Grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildlife Biology 9:291–299.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). A. Poole and F. Gill, (editors), The Birds of North America No. 425. The Birds of North America, Inc., Philadelphia, PA.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd ed. Charles Griffin and Company Ltd., London.

South Dakota Department of Game, Fish, and Parks. 2006. South Dakota comprehensive wildlife conservation plan. South Dakota Department of Game, Fish, and Parks, Wildlife Division Report 2006-08, Pierre, SD.

South Dakota State Climate Office. 2007. Office of the State Climatologist. <http://climate.sdstate.edu> (15 December 2007).

Stephens, P. A., S. W. Buskirk, G. D. Hayward, and C. M. Del Rio. 2005. Information theory and hypothesis testing: a call for pluralism. Journal of Applied Ecology 42:4–12.

Sveum, C. M., W. D. Edge, and J. A. Crawford. 1998. Nesting habitat selection by sage-grouse in south-central Washington. Journal of Range Management 51:265–269.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120–138.

# NESTING AND BROOD-REARING SUCCESS AND RESOURCE SELECTION OF GREATER SAGE-GROUSE IN NORTHWESTERN SOUTH DAKOTA

**BY**

**NICHOLAS W. KACZOR**

A thesis submitted in partial fulfillment of the requirements for the

Master of Science

Wildlife and Fisheries Sciences

South Dakota State University

2008

**NESTING AND BROOD-REARING SUCCESS AND RESOURCE SELECTION OF GREATER SAGE-GROUSE IN NORTHWESTERN SOUTH DAKOTA**

This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

14 April 2008

Dr. Kent C. Jensen — Date
Major Advisor

4/14/08

Dr. David W. Willis — Date
Head, Department of Wildlife
and Fisheries Sciences

## ACKNOWLEDGEMENTS

This research would not have been possible without the funding and logistic support of the following organizations: Bureau of Land Management (South Dakota, North Dakota, and Miles City, MT field offices), United States Forest Service Rocky Mountain Research Station, South Dakota Game, Fish, and Parks, North Dakota Game and Fish Department, United States Geological Service EROS, and South Dakota State University.

I would like to thank Dr. Kent C. Jensen for providing me with this wonderful opportunity to conduct research on sage-grouse, and other upland game species. The past three years have provided me with insight into many different aspects of wildlife I would not have received anywhere else. Thank you for answering and listening to my many questions and ideas, and then guiding me in the right direction. This was truly an enjoyable experience and I can never thank you enough.

I would like to recognize the members of my graduate committee: Drs. Kent C. Jensen, Mark A. Rumble, Robert W. Klaver, Kenneth H. Higgins, and George H. Hamer. Thank you for taking time out of your tremendously busy schedules to critique my work and make it the best is could be. Mark Rumble deserves a special thank you for helping with all aspects of the study; from design, to providing field assistance, to data analysis; Mark was always willing to help out. In addition, I would like to thank Bob Klaver for his assistance with Program MARK.

I am forever indebted to Thomas Berdan for being a stand up technician both years of the research; his determination and willingness to capture chicks at night after

tracking birds all day will not be forgotten. I also want to thank my other technicians, Sarah Nelson-Harrelson, Tom Juntti, and Ben Hauser for helping with the tedious habitat sampling. Other volunteers were Ryan Williamson, Heidi Jacobsen, Dawn Gardner, Ashly Steinke, Adam Giegle, and Rocky Ruzicka. Thank you to Bill Eastman, Rudy King, Tom Kirschenmann, Jerry Kobriger, Stan Kohn, Kent Undlin, Greg Wolbrink, John Wrede, and Tim Zachmeier for either lending an ATV, capturing chicks, helping with statistical analyses or any other aspect of the project. In addition, I want to thank Tony Apa for showing me my first sage-grouse, and the techniques to capture and radio-mark them. Two individuals who helped prepare me for this research were Bill Vodehnal and Greg Schenbeck. Thank you for taking a chance on me and providing me with my first work experience in the wildlife field.

A big thank you is necessary to the other graduate students researching sage-grouse in the Dakotas. Katie Herman-Brunson provided an outstanding motivation and drive that could not be matched. Her dedication to sage-grouse and their conservation is truly unique. Thank you for being there at all hours of the day, helping me catch up when I was behind, and being a friend I can always rely upon. I also want to thank Chris Swanson for his contribution to the project. Without him, this research would not have been as successful as it was.

The support staff at South Dakota State University is second to none. Di Drake, Carol Jacobson, and Terri Symens helped with everything from credit card receipts to providing me with many great laughs. I also want to thank all the other graduate students at SDSU. Over the past three years I have become friends with many of you, and will be

leaving with some unforgettable memories. I wish each and every one of you the best of luck in your future careers.

This project would not have been possible without the cooperation of the many landowners who graciously allowed me to track the unpredictable sage-grouse, fed me lunch, and made me feel welcome in their homes. Thank you to the following individuals and their families: C. Blake, J. Burke, P. Burke, R. Bush, K. Carlsen, R. Carver, D. Conner, T. Costello, J. Courtney, B. Crago, Cl. Crago, C. Davis, R. Delzer, K. Deschamps, D. Dobesh, G. Erk, P. Erk, J. Fortner, R. Fox, J. Hughes, Indian Butte Ranch LLP, G. Johnson, J. Johnson, D. Junek, T. Kudlock, C. Kukuchka, J. McCoy, K. McFarland, R. Meyer, M. Miller, L. Moncur, Moreau Grazing Association, L. Nelson, W. Newland, PCS LLC, J. Rosencranz, O. Rumph, C. Schmidt, G. Shy, R. Steineke, D. Turbiville, A. VanKley, and L. Vroman.

Finally I want to thank my own family. I came into this project with a wonderful family that has provided me with about anything a kid could ever ask for. Thank you Mom and Dad for helping me get through 7 years of college, allowing me to pursue my dreams, and motivating me during the low times. I want to thank my sister Jen and her entire family for giving me a good laugh when I needed it and the willingness to try and track down the sheriff; it will never be forgotten. During the project however, I feel as I gained another family, the Berdan's. Chuck and Marilyn provided not only home-cooked meals, but a sense of belonging that made my field work much more enjoyable. Thank you Chuck for taking me under your wing to show me the lay of land, spending many nights looking through binoculars, and for all the memorable visits in your drive way.

# ABSTRACT


## NESTING AND BROOD-REARING SUCCESS AND RESOURCE SELECTION OF GREATER SAGE-GROUSE IN NORTHWESTERN SOUTH DAKOTA

Nicholas W. Kaczor

May 2008

Understanding population dynamics and resource selection is crucial in developing wildlife resource management plans, particularly for sensitive species. Greater sage-grouse (*Centrocercus urophasianus*) populations have declined range-wide at a rate of 2% per year from 1965 to 2003. In South Dakota, populations have generally declined. Reasons for the decline are mostly attributed to human-induced factors such as sagebrush degradation and removal, improper range management practices, oil and gas exploration, and West Nile virus infection. Sage-grouse occupy habitats at the eastern edge of their range in western South Dakota. We conducted a 2-year study to investigate the nesting and brood-rearing ecology of sage-grouse in northwestern South Dakota.

Female sage-grouse were captured and radio-marked ($n$ = 53) on traditional display grounds. Radio-marked hens were tracked to estimate nesting effort, nest success, and associated habitats. Nest initiation was 95.9%, with an overall nest success of 45.6 ± 5.3%. Hens selected habitats with greater sagebrush canopy cover and nest bowl visual obstruction compared to random sites. Nest success models developed in Program MARK indicated taller grass structures increased nest success.

Chick survivorship to seven weeks post hatch ranged from 31 to 43% over the two year period and recruitment of chicks into the breeding population (1 March) was estimated to be between 5 and 10%. Between 12 July and 31 September, West Nile virus accounted for 7 to 21% of the mortality incurred by chicks, however WNv reduced recruitment by 2 to 4%. Sage-grouse selected brood-rearing habitats that provided increased visual obstruction and bluegrass (*Poa spp.*) cover. More herbaceous vegetation at these sites may provide increased invertebrate abundance, which is necessary in the diets of sage-grouse chicks.

Management of sage-grouse nesting habitat on the eastern edge of their range should focus on increasing levels of sagebrush density and canopy cover while maintaining cover and height of grasses. We recommend that land managers maintain maximum grass heights of 26 cm. For brood-rearing sites, managers should maintain high vegetation biomass (visual obstruction) for protective cover and increased invertebrate abundance. We recommended that land managers strive to attain >10% chick recruitment into the breeding season.

# TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS ..... iii

ABSTRACT ..... vi

TABLE OF CONTENTS ..... viii

LIST OF TABLES ..... x

LIST OF FIGURES ..... xii

LIST OF APPENDICES ..... xiv

GENERAL INTRODUCTION ..... 1

Study Area ..... 4

Literature Cited ..... 7

CHAPTER 1 – NESTING SUCCESS AND RESOURCE SELECTION

Introduction ..... 11

Methods ..... 12

Results ..... 16

Discussion ..... 20

Management Implications ..... 25

Literature Cited ..... 41

CHAPTER 2 – BROOD-REARING SUCCESS AND RESOURCE SELECTION

Introduction ..... 56

Methods ..... 58

Results ..... 62

Discussion ..... 64

Management Implications ..... 68

Literature Cited ..... 78

# LIST OF TABLES

Table Page

1. Mean vegetation characteristics of nest sites and random sites between years for greater sage-grouse used in logistic regression models in northwestern South Dakota, USA, using MRPP (Mielke and Berry 2001), 2006-2007. ....28

2. Observed mean values for habitat variables between greater sage-grouse successful and failed nests used in nest success models in northwestern South Dakota, USA, using MRPP (Mielke and Berry 2001) 2006-2007. ....29

3. Nest initiation rates of radio-marked adult and yearling greater sage-grouse in northwestern South Dakota, USA, 2006-2007. ....30

4. Average clutch size and average hatch dates for first nests and renests of greater sage-grouse in northwestern South Dakota, USA, 2006-2007. ....31

5. Results from logistic regression models predicting greater sage-grouse nest sites ($n$ = 73) versus random sites ($n$ = 74) in northwestern South Dakota, USA, 2006-2007. ....32

6. Parameter Estimates, odds ratios, and corresponding confidence intervals for the best-approximating model of greater sage-grouse nests sites versus random sites in northwestern South Dakota, 2006-2007. ....33

7. Summary of model selection results for nest survival between year and age of greater sage-grouse in northwestern South Dakota, USA, 2006-2007. ....34

8. Observed mean values for habitat variables between greater sage-grouse brood-rearing and random sites, and between years used in logistic regression in northwestern South Dakota, USA, using MRPP (Mielke and Berry 2001)2006-2007. ....70

9. Apparent greater sage-grouse chick survival to 7 weeks post hatch, and recruitment as of 1 March using a Kaplan-Meier product-limit method (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989) in northwestern South Dakota, USA, 2006-2008. Estimated survival rates given as mean (95% CI). ....71

Table Page

10. West Nile virus (WNv) mortality rates and testing for greater sage-grouse chicks during the peak WNv transmission period (12 July – 31 September) in northwestern South Dakota, USA, 2006-2007. Estimated minimum and maximum mortality given as mean (95% CI) after Walker et al. (2007). .....72

11. Results from logistic regression models predicting greater sage-grouse brood-rearing sites ($n$ = 119) versus random sites ($n$ = 116) in northwestern South Dakota, USA, 2006-2007. .....73

12. Parameter Estimates, odds ratios, and corresponding confidence intervals for the best-approximating model of greater sage-grouse brood-rearing sites versus random sites in northwestern South Dakota, 2006-2007.....74

## LIST OF FIGURES

Figure Page

1. Study area of Butte, Carter, Crook, and Harding counties where we researched greater sage-grouse during 2006-2007. The dashed area encompasses all locations collected and the grayed area is current sage-grouse range (Schroeder et al. 2004).....6

2. Mean distances plus one standard error (SE) of successful and failed greater sage-grouse nests to nearest documented active lek for greater sage-grouse in northwestern South Dakota, USA, 2006-2007. .....35

3. Distribution of successful and failed nests to nearest documented lek distances for greater sage-grouse in northwestern South Dakota, USA, 2006-2007. .....36

4. Monthly precipitation received during the breeding and nesting periods in 2006 – 2007 compared to the 58-year mean from the nearest daily weather station (Nisland, SD). .....37

5. Effect of grass height on greater sage-grouse nest success in northwestern South Dakota, USA, 2006-2007. Nest success estimate derived from back-transformed beta estimates included in top model. Confidence intervals estimated from the delta method (Seber 1982). .....38

6. Effect of grass height and litter canopy coverage on greater sage-grouse nest success in northwestern South Dakota, USA, 2006-2007. Nest success estimate derived from back-transformed beta estimates included in top model. .....39

7. Effect of litter canopy coverage on greater sage-grouse nest success in northwestern South Dakota, USA, 2006-2007. Nest success estimate derived from back-transformed beta estimates included in top model. Confidence intervals estimated from the delta method (Seber 1982).....40

8. Greater sage-grouse apparent chick survival to 7 weeks post hatch (dashed area), and recruitment as of 1 March 2007 using a Kaplan-Meier product-limit method (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989) in northwestern South Dakota, USA, 2006-2007. A sample size of $n = 31$, was used in the Kaplan-Meier analysis.....75

Figure Page

9. Greater sage-grouse apparent chick survival to 7 weeks post hatch (dashed area), and recruitment as of 1 March 2008 using a Kaplan-Meier product-limit method (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989) in northwestern South Dakota, USA, 2007-2008. A sample size of $n = 24$, was used in the Kaplan-Meier analysis.....76

10. Effect of visual obstruction and bluegrass cover on greater sage-grouse brood-rearing habitat selection in northwestern South Dakota, USA, 2006-2007. Probability of use derived from parameter estimates in best approximated model (visual obstruction + bluegrass cover). .....77

## LIST OF APPENDICES

Appendix Page

1. Complete results from logistic regression models predicting greater sage-grouse nest sites ($n$ = 73) versus random sites ($n$ = 74) in northwestern South Dakota, USA, 2006-2007. .....49

2. Complete summary of model selection results for nest survival between year and age of greater sage-grouse in northwestern South Dakota, USA, 2006-2007.....50

3. Demographic information for all greater sage-grouse captured in northwestern South Dakota, USA, 2006-2007. .....52

4. Complete results from logistic regression models predicting greater sage-grouse brood-rearing sites ($n$ = 119) versus random sites ($n$ = 116) in northwestern South Dakota, USA, 2006-2007. .....85

## GENERAL INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*) populations have declined range-wide at a rate of 2% per year from 1965 to 2003 (Connelly et al. 2004). These declines have been attributed to many factors, mostly human-induced (Connelly and Braun 1997). Factors for decline include, but are not limited to: sagebrush (*Artemisia spp.*) degradation and removal (Knick et al. 2003, Wisdom et al. 2005), livestock grazing (Beck and Mitchell 2000), fire (Baker 2006), construction of highways, fences, and power lines, (Braun 1998, Schroeder et al. 1999, Aldridge and Brigham 2001) oil and gas development (Lyon and Anderson 2003), and increased mortality due to West Nile virus infections (Naugle et al. 2005).

Further declines in sage-grouse populations are a concern to many stakeholders in the western United States landscape, as several petitions have been filed for sage-grouse to be listed under the Endangered Species Act (ESA) of 1973 (Connelly et al. 2004). Currently, Federal land management agencies are responsible for approximately 66% of the sagebrush landscape in the United States (Connelly et al. 2004). Federal agencies such as the Bureau of Land Management (BLM) and U.S. Forest Service (USFS) are directed by administrative policy to manage public lands for sustained multiple use under the Federal Land Policy and Management Act (1976), and Public Rangelands Improvement Act (1978). In addition, sage-grouse are a considered a sensitive species for the BLM and USFS. Listing of sage-grouse under the ESA could have major ramifications on the use and management of public lands in of the western United States (Knick et al. 2003).

It has been widely documented that sage-grouse are sagebrush obligates during winter and depend heavily upon it throughout their annual life cycle (Patterson 1952, Connelly and Braun 1997, Schroeder et al. 1999, Connelly et al. 2004, Moynahan et al. 2007). Sagebrush provides food resources, nesting cover, and protection from predators (Schroeder et al. 1999). Since the arrival of European settlers, sagebrush habitats have undergone numerous alterations and degradations (Patterson 1952). Sagebrush has been lost to tillage agricultural (Swenson et al. 1987), energy development (Braun 1998, Walker et al. 2007, Doherty et al. 2008), and urban expansion, reservoirs, and roads (Braun 1998, Aldridge and Brigham 2001). Furthermore, degradation and fragmentation of sagebrush has occurred from chemical and mechanical treatments of sagebrush, livestock grazing (Knick et al. 2003, Wisdom et al. 2005), construction of fences and powerlines (Braun 1998), and the introduction of invasive species (Knick et al. 2003).

Current guidelines for sage-grouse management (Connelly et al. 2000) are based on extensive studies in core sage-grouse range (e.g., Wyoming and Montana). These studies typically focused on varying aspects of sage-grouse ecology; particularly nesting and brood-rearing ecology. However, little research has been conducted on the eastern limit of sage-grouse distribution. Western South Dakota forms a transitional zone between the northern wheatgrass-needlegrass prairie that dominates most of the Dakotas and the big sagebrush plains of Wyoming (Johnson and Larson 1999). In South Dakota, sage-grouse are imperiled because of rarity or some factor(s) making them very vulnerable to extinction within the state (South Dakota Department of Game, Fish, and Parks 2006). Smith et al. (2004) reported steady declines in South Dakota sage-grouse

populations since 1972 that were possibly the result of sagebrush removal through cultivation and herbicides (Smith et al. 2005). No study has been conducted in western South Dakota investigating sage-grouse nesting and brood-rearing success and associated habitats.

The objectives of this study were to (1) determine and quantify nesting and brood-rearing resource selection of radio-marked sage-grouse, (2) estimate nest success and evaluate cause and timing of nest failures, and (3) estimate chick survival and recruitment. This study will complement previous and concurrent research conducted on sage-grouse in the Dakotas, thus providing regional land managers with baseline ecology of sage-grouse. Furthermore, management recommendations produced from this research will aid in resource management plans and coordination efforts to enhance sage-grouse habitats.

This thesis is designed as two chapters dealing with the nesting and brood-rearing aspects of sage-grouse in western South Dakota. It is the intent to publish these papers in the Journal of Wildlife Management (JWM) or a similar type of peer-reviewed journal. Therefore, publication style will follow JWM guidelines unless otherwise noted. This research was a team approach, including multiple authors on publications so I have substituted the pronoun “I” for “We”. Data will be archived at the U.S. Forest Service Rocky Mountain Research Station, Fort Collins, CO.

## STUDY AREA

The study was conducted within a 3,500-km$^2$ area in Butte and Harding counties, South Dakota; Crook County, Wyoming; and Carter County, Montana (44°44'N to 45°20'N, 103°15'W to 104°21'W; Figure 1). Approximately 75% of the area was privately owned and we conducted research on 40 private ranches. The remaining 25% of the study area was managed by the United States Bureau of Land Management (BLM), and State of South Dakota School and Public Lands Division (SDSPL). The area is predominately used for grazing purposes although small grain production is evident. Open-pit mining for bentonite occurs at the south end of the study site on Pierre soils (Charles Berdan, BLM, Belle Fourche, South Dakota, personal communication).

Vegetation consists of short shrubs, mostly Wyoming big sagebrush (*Artemisia tridentata spp.*) and plains silver sagebrush (*A. cana spp.*). Other shrubs include broom snakeweed (*Gutierrezia sarothrae*), greasewood (*Sarcobatus vermiculatus*), and saltbushes (*Atriplex spp.*) (Johnson and Larson 1999). Common grasses include western wheatgrass (*Pascopyrum smithii*), Junegrass (*Koeleria macrantha*), bluegrass species (*Poa spp.*), green needle-grass (*Nassella viridula*), and Japanese brome (*Bromus japonicus*). Common forbs include western yarrow (*Achillea millefolium*), common dandelion (*Taraxacum officinale*), pepperweed (*Lepidium densiflorum*), and pennycress (*Thlaspi arvense*) (Johnson and Larson 1999).

Temperatures in summer (May-August) average 20.1° C but can reach up to 43.3°C (South Dakota State Climate Office 2007). Mean annual precipitation is 35.3 cm, with a majority occurring during the months of April through July (South Dakota State

Climate Office 2007). Elevation ranges from 840 – 1225 m above sea level with nearly level to moderately steep clayey soils over clay shale (Johnson 1976).

Common predators included red fox (*Vulpes vulpes*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), badger (*Taxidea taxus*), raccoon (*Procyon lotor*), golden eagle (*Aquila chrysaetos*), ferruginous hawk (*Buteo regalis*), American crow (*Corvus brachyrhynchos*), long-tailed weasel (*Mustela frenata*), and red-tailed hawks (*Buteo jamaicensis*).

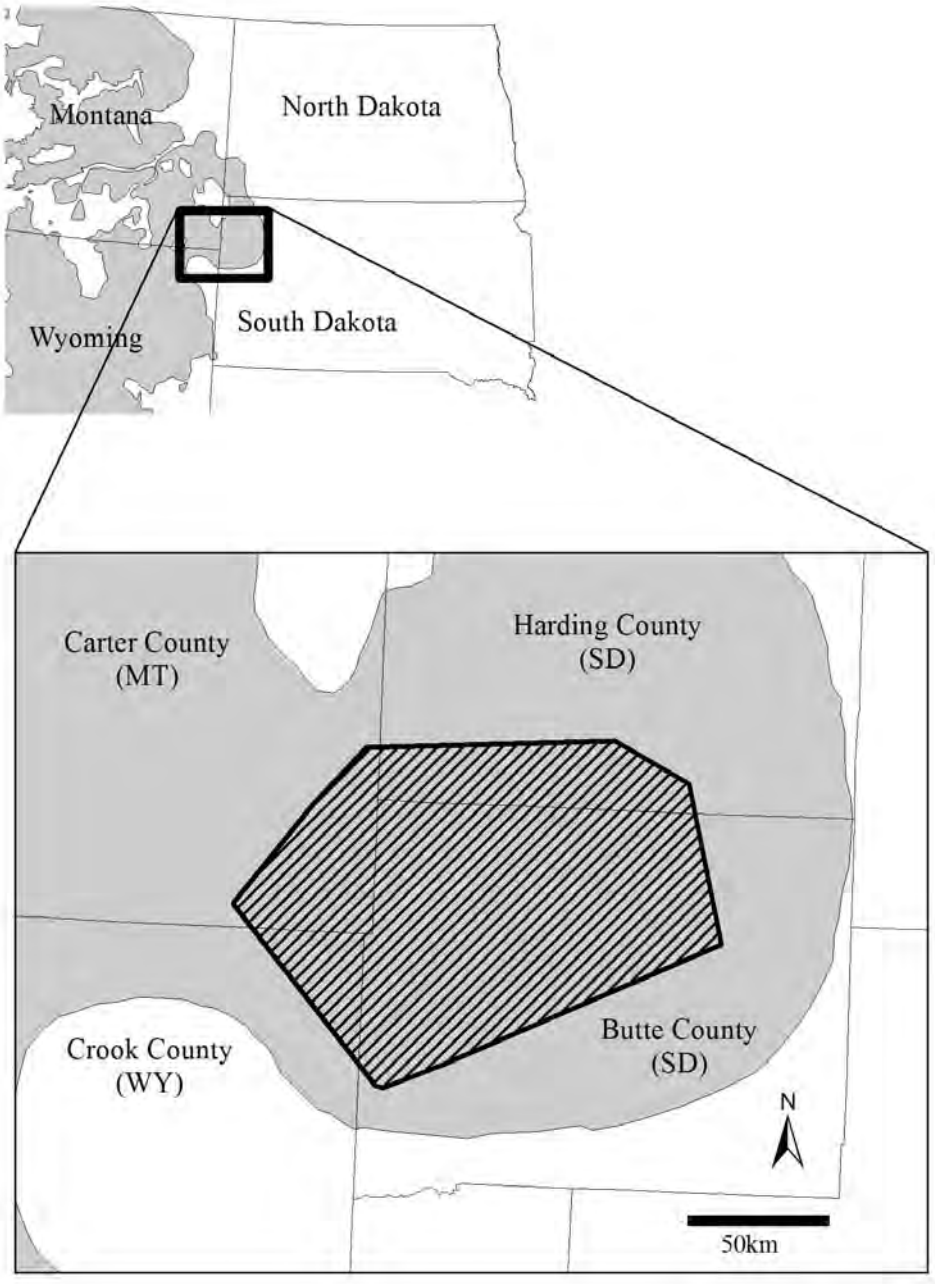



Figure 1. Study area of Butte, Carter, Crook, and Harding counties where we researched greater sage-grouse during 2006-2007. The dashed area encompasses all locations and the grayed area is current sage-grouse range (Schroeder et al. 2004).

## LITERATURE CITED

Aldridge, C. L. and R. M. Brigham. 2001. Nesting and reproductive activities of greater sage-grouse in a declining northern fringe population. Condor 103:537-543.

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin 34:177-185.

Beck, J. L., and D. L. Mitchell. 2000. Influences of livestock grazing on sage-grouse habitat. Wildlife Society Bulletin 28:993-1002.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association State Fish and Wildlife Agencies 78:139-156.

Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* in western North America. Wildlife Biology 3:229-234.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187-195.

Johnson, J. R., and G. E. Larson. 1999. Grassland plants of South Dakota ant the northern Great Plains. South Dakota State University. Brookings, South Dakota, USA.

Johnson, P. R., 1976. Soil survey of Butte County, South Dakota. U.S. Department of Agriculture, South Dakota Agricultural Experiment Station, Brookings, South Dakota, USA.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C.Van Riper III. 2003. Teetering of the edge or too late: conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486-491.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of Greater sage-grouse in northcentral Montana. Journal of Wildlife Management 71:1773-1783.

Naugle, D. E., C. L. Aldridge, B. L. Walker, K. E. Doherty, M. R. Matchett, J. McIntosh, T. E. Cornish, and M. S. Boyce. 2005. West Nile virus and sage-grouse: What more have we learned? Wildlife Society Bulletin 33:616-623.

Patterson, R. L. 1952. The sage grouse in Wyoming. Sage Books, Inc., Denver, CO.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. Condor 106:363-376.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Account No. 425 *in* A. Poole. And F. Gill, editors. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.

Smith, J. T., L. D. Flake, K. F. Higgins, and G. D. Kobriger. 2004. History of greater sage-grouse in the Dakotas: Distribution and population trends. Prairie Naturalist 36:213-230.

Smith, J. T., L. D. Flake, K. F. Higgins, G. D. Kobriger, and C. G. Homer. 2005. Evaluating lek occupancy of greater sage-grouse in relation to landscape cultivation in the Dakotas. Western North American Naturalist 65:310-320.

South Dakota Department of Game, Fish, and Parks. 2006. South Dakota comprehensive wildlife conservation plan. South Dakota Dept. of Game, Fish, and Parks, Pierre, Wildlife Division Report 2006-08.

South Dakota State Climate Office. 2007. Office of the State Climatologist. http://climate.sdstate.edu. Accessed on 12 October 2007.

Swenson, J. E., C. A. Simmons, and C. D. Eustace. 1987. Decrease of sage grouse, *Centrocercus urophasianus*, after ploughing of sagebrush steppe. Biological Conservation 41:125-132.

Walker, B. L., D. E. Naugle, K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644-2654.

Wisdom, M. J., M. M. Rowland, and L. H. Suring, editors. 2005. Habitat threats in the sagebrush ecosystem: methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, Kansas, USA.

# CHAPTER 1 – NESTING SUCCESS AND RESOURCE SELECTION OF GREATER SAGE-GROUSE IN NORTHWESTERN SOUTH DAKOTA.

## INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) were once distributed in parts of at least 12 states and 3 provinces, but have been extirpated from Nebraska and British Columbia (Schroeder et al. 2004). Furthermore, sage-grouse currently inhabit only 56% of their pre-settlement potential habitat (Schroeder et al. 2004) and populations have declined at an estimated rate of 2.0% per year from 1965 to 2003 (Connelly et al. 2004). Greater sage-grouse have become a sensitive species due to decreases in populations, (Aldridge and Brigham 2001, Connelly et al. 2004) and degradation of quality nesting habitat (Braun 1998, Connelly et al. 2004). Populations in South Dakota declined steadily from 1973 to 1997, and then recovered from 1997 to 2002 (Smith 2003, Connelly et al. 2004). However, in South Dakota, population indices from lek-counts were inconsistent over these time periods and meaningful assessments are lacking (Connelly et al. 2004). Nest fate and what factors determine nest success are of particular interest to biologists as it has been shown that nest success has the potential to limit population growth of sage-grouse (Schroeder 1997, Braun 1998, Schroeder et al. 1999, Dinsmore and Johnson 2005). Yet, information is lacking on the ecological requirements of nesting sage-grouse in western South Dakota. The objectives of this study were to develop an understanding on the nesting ecology, success, and resource selection of sage-grouse on the eastern edge of their range.

## METHODS

### Data Collection

*Female Capture* – We identified six active sage-grouse leks for which we had landowner cooperation for trapping. We captured female sage-grouse with large nets by spotlighting them from all-terrain vehicles between March 2006-2007 and mid-April 2006-2007 (Giesen et al. 1982). Females were weighed and equipped with a 22-g necklace-style transmitter, which were ~1.4% of mean female sage-grouse body mass and a life-expectancy of 434 days. Transmitters could be detected from approximately 2.0 to 5.0 km from the ground and were equipped with an 8-hour mortality switch. Females were classified as adults (≥2 yr old) or yearlings (<1 yr old) based upon primary wing feather characteristics (Eng 1955, Crunden 1963). The South Dakota State University Institutional Animal Care and Use Committee approved trapping and handling techniques, and study design (Approval #07-A032).

*Locating and Monitoring Nests* – We located radio-marked female sage-grouse twice each week during the breeding, laying, and incubation periods. In the event we could not locate an individual(s) from the ground, we searched the study-area from a fixed-wing aircraft to obtain an approximate location. Once a hen was believed to be incubating, we marked four coordinates approximately 15 m away in the four cardinal directions with a Global Positioning System (GPS) receiver (Garmin Ltd., Olathe, KS). We confirmed nest presence/absence during the subsequent visit. If a hen was present on the second visit, we flushed her to determine clutch size. This method did not cause nest abandonment as only 1 of 80 (1.3%) females abandoned their nests. Nests were checked

approximately twice each week until nest fate was determined. Nests were considered successful if ≥1 egg hatched. We documented evidence (e.g., nest bowl disturbance, eggshell remains, etc.) at the nest site to estimate predator type (i.e., mammalian or avian) (Sargeant et al. 1998). Nest distances from nearest active display ground, renests, and prior nests were calculated by Hawth's Analysis Tool (Beyer 2004) in ArcMap 9.1 (ESRI, Inc., Redlands, CA.).

*Habitat Measurements* – We characterized vegetation at nest sites after the fate was determined. Four, 50-m transects were established radiating in the 4 cardinal directions from the nest bowl. A modified Robel pole (Robel et al. 1970, Benkobi et al. 2000) was used to estimate visual obstruction readings (VOR) and maximum grass height at 1-m intervals from 0 m to 5m ($n$ = 21), and at 10-m intervals out to 50 m ($n$ = 20). We estimated sagebrush (*A. tridentata spp.* and *A. cana spp.*) density and height at 10 m intervals ($n$ = 80) using the point-centered-quarter method (Cottam and Curtis 1956). We added four, 5-m transects, radiating in the 4 ordinal directions from the nest bowl for vegetation cover measurements. Vegetation cover was estimated using a 0.10 $m^2$ quadrat (Daubenmire 1959) at 1-m intervals to 5 m ($n$ = 44) and then alternating out to 30 m ($n$ = 52). We recorded total cover, grass cover, forb cover, shrub cover, litter cover, bare ground, and individual shrub and grass species canopy cover. In addition, we measured an equal number of random sites within a 3 km buffer of capture leks to estimate resource selection. We entered the coordinates of the random sites into a GPS and navigated to the location, then located the center over the nearest sagebrush to the coordinate.

**Data Analyses**

*Nesting Parameters* – We used the multi-response permutation procedure (MRPP; Mielke and Berry 2001) to test the null hypothesis that there were no differences among weights, clutch size, nest initiation dates, nest site fidelity, and distances to display grounds between years and between ages of females. Chi-square goodness of fit test was used to test differences of nest initiation rates between years and between ages of females. For these analyses, results were considered significant at a critical value of $\alpha \leq 0.05$.

*Habitat Measurements* – Maximum grass height and VOR were summarized for each of the intervals and then averages were calculated for 0 to 5 m, 1 to 5 m, 10 to 50 m, and the site level (0 to 50 m). Sagebrush density and height was estimated from a maximum likelihood estimate (Pollard 1971) and summarized for the site. Canopy coverage values were recorded to mid-point values of categories for each species, or category. These were then summarized to an average for 0 to 5 m, 1 to 5 m, 6 to 30 m, and to the site (0 to 30 m). With over 100 variables in the data set, we then screened all variables using MRPP (Mielke and Berry 2001) to identify important variables between nest and random sites and between successful and failed nests (Boyce et al. 2002). A relaxed critical value of $\alpha \leq 0.15$ was used in the screening process to reduce the risk of excluding a potentially important variable.

*Resource Selection* – We identified 10 habitat variables (Table 1) from the screened variables along with a year effect to investigate sage-grouse nesting habitat preferences. Variables selected included: total cover, grass cover, sagebrush cover, litter cover, mean sagebrush height, maximum grass height, and visual obstruction all at the

site level. In addition, grass height 0-5 m away from the nest bowl, visual obstruction at the nest bowl, and visual obstruction 1 m away from nest bowl were included in the data set. Year was considered a design variable in all candidate models. We used an information theoretic approach (Burnham and Anderson 2002) with nominal logistic regression to estimate the importance of various *a priori* and *post-hoc* exploratory models in SAS JMP (2005 SAS Institute Inc.). Due to a small sample size with respect to the number of parameters estimated, AIC*c* (Akaike's Information Criterion) was used being derived from our log-likelihood estimate (Burnham and Anderson 2002). Model strength was estimated using a receiver operation characteristic curve (ROC) with values between 0.7 and 0.8 considered as acceptable discrimination and values higher than 0.8 were considered excellent discrimination (Hosmer and Lemeshow 2000).

*Nest Success* – We used the nest survival module in program MARK (White and Burnham 1999, Dinsmore et al. 2002) to evaluate environmental and biological factors that might influence nest success. We standardized nesting dates among years by using the earliest location date for any year as the first day of the nesting season. We monitored nests over a 59-day period beginning 23 April and ending 20 June, which comprised 58 daily intervals of observations to be used in estimating daily survival rate (DSR) for the 27 day incubation period. We identified four variables from the screen process as having a potential impact on nest success which included: grass height at the site level, visual obstruction at the site level, litter cover at the site level, and 0 m forb cover (Table 2). These variables were combined with daily precipitation, daily minimum temperature, bird age, and year. We did not model nesting attempt because of a small

number of renests ($n$ = 10), or days into incubation because we could not accurately measure them. Daily weather variables were obtained from the nearest daily weather station located at Nisland, South Dakota, approximately 50 km from the center of the study area (South Dakota State Climate Office 2007).

We used an information theoretic approach (Burnham and Anderson 2002) to evaluate support for models of DSR and variables. We began by developing base models which included bird age, year, and constant survival. From these base models we further explored the degree to which habitat and weather variables improved model fit. We used back-transformed estimates of DSR (Dinsmore et al. 2002) to determine effect of variables on nesting success for the best supported model. We plotted DSR versus simulated values of variables to determine the effect of variables independently from one another. We estimated standard error of DSR using the delta method (Seber 1982).

## RESULTS

### Nesting Parameters

*Trapping and Monitoring* – We captured 53 female sage-grouse (25 adults and 28 yearlings) and fitted them with transmitters during the study, 29 individuals were included both years. Adults weighed (1664 g, range: 1492 – 1912 g) more ($P$ <0.01) than yearlings (1524 g, range: 1332 – 1734 g), but there were no differences between years ($P$ = 0.20). We found 80 nests (41 in 2006, and 39 in 2007) and 73 were included in nest survival analyses. Seven nests were excluded because either we did not collect vegetative measurements ($n$ = 5), we felt we caused nest abandonment ($n$ = 1), or were denied access to private land ($n$ = 1).

*Nest Initiation* – Nest initiation rates (proportion of individuals initiating ≥1 nest) for all nests was 95.9% (Table 3) and did not differ between years ($P = 0.09$) or bird age ($P = 0.89$). Renest initiation rate was 28.6% (10/35) and did not differ between years ($P = 0.67$) or bird age ($P = 0.24$). Females were more likely to renest ($P = 0.02$) if their first nest was lost early into incubation with the number of first nest observation days being 7.9 ± 1.3 days for females that renested and 14.6 ± 1.8 days for females that did not renest.

Average date of nest initiation for first nests was 24 April ± 1.6 days (Table 4), with adults (≥2 years) initiating egg laying approximately 6.7 days earlier than yearlings ($P = 0.02$). No differences of nest initiation dates were detected between years for first nests ($P = 0.27$). Average hatch date for first nests was 31 May ± 1.5 days. Average renest initiation was approximately 15 days later (9 May ± 2.6 days) than first nests, with hatch date occurring 14 June ± 2.0 days. Clutch size varied between nesting attempts (first nests: 8.3 ± 0.2, renests: 6.4 ± 0.6, $P < 0.01$) (Table 4), but not between nest success ($P = 0.83$), bird age ($P = 0.98$), or year ($P = 0.10$).

*Nest Location in Relation to Leks* – Female sage-grouse visited multiple leks during the breeding season. One adult female in 2007 nested approximately 30.3 km from lek of capture. In 2006, successful nests were significantly closer to an active lek ($P = 0.04$) than failed nests (1.5 ± 0.3 km vs. 2.9 ± 0.5 km) (Figure 2), however there was no difference in 2007 (2.5 ± 0.5 km vs. 3.2 ± 0.7 km, $P = 0.70$), or when both years were combined (2.1 ± 0.3 km vs. 3.0 ± 0.4 km, $P = 0.13$). The distance that adults and yearlings nested to the nearest active lek did not differ significantly (2.2 ± 0.3 km vs.

3.3 ± 0.5 km, $P = 0.08$). Sixty-eight percent of nests were within 3 km of a documented active lek, and 97% of nests were within 7 km (Figure 3).

*Nest site Fidelity* – Mean distance between an individuals' nest in 2006 to its subsequent nest in 2007 was 1.08 ± 0.40 km ($n = 21$), but was highly variable (range: 0.07 km to 6.62 km). However, 76% of nests were within 0.70 km from a previous year's nest. There was no difference ($P = 0.65$) of nest site fidelity between adults and yearlings, or between nests that either failed or were successful the first year ($P = 0.47$). Mean distance between a failed first nest and subsequent renest was 1.85 ± 0.55 km ($n = 10$, range: 0.22 km – 5.12 km). Successful renests (0.95 ± 0.36 km, $n = 5$) were not significantly closer ($P = 0.17$) to first nests than failed renests (2.03 ± 0.91 km, $n = 5$).

*Precipitation* – During the months of March through June 2006, the study area received approximately 14 cm of precipitation (Figure 4). This was 33% less than the 58-year mean of 21 cm of precipitation. However, in 2007 the study area received approximately 22 cm, or 5% more precipitation than the 58-year mean for the same time period.

**Resource Selection**

Distributions of total cover, grass cover, grass height, visual obstruction and sagebrush height differed ($P < 0.05$) between nest sites in 2006 and 2007 (Table 1). There were also some year effects that were evident in the data for random sites, thus all logistic models included the design variable year (Table 5).

The best-approximating model (AIC*c* weight = 0.39) predicting nest sites from random sites included sagebrush canopy coverage at the site level and visual obstruction

at the nest (Table 5). Both variables positively influenced the site selected for a nest (Table 6). Increasing sagebrush cover by 5% increased the odds of use 6.1 (95% CI: 5.5 – 6.9) times. Increasing visual obstruction at the nest by 2.54 cm increased the odds of use 3.2 (95% CI: 3.0 – 3.4) times (Table 6). A second model including sagebrush canopy coverage, visual obstruction at the nest, and average grass height within 5 m was also strongly supported (AIC*c* weight = 0.35). Model discrimination (ROC values) for the top two models was excellent at 0.93 for both models. Sagebrush canopy coverage and visual obstruction at the nest had the highest summed AIC*c* weights, both achieving values of 1.0. Although the combination of sagebrush canopy coverage and visual obstruction at the nest was the strongest model, there was little evidence for a model involving them individually; visual obstruction at the nest and sagebrush canopy coverage were 11.26 and 74.54 AIC*c* units higher, respectively.

**Nest Success**

Most nests were located under Wyoming big sagebrush (90%) or silver sagebrush (7%). One nest was located under the side of a large boulder, and another was in a dense stand of prairie cordgrass (*Spartina pectinata*). Breeding success rates (proportion of females hatching ≥ 1 egg in a season) averaged 47.9%. Egg hatchability (proportion of eggs hatching from successful clutches) averaged 78.3%. Most of the eggs that did not hatch were infertile.

Constant nest survival rates (similar to Mayfield 1975) were 45.6 ± 5.3%, but constant survival was a poor model. Four models were within 2 AIC*c* units of the top model. The best model with an AIC*c* weight of 0.23, included grass height and litter

cover (Table 7) with a predicted nest success of 51.6 ± 6.3%. Grass height had a positive impact (β = 0.15 SE = 0.03) on nest success (Figures 5 & 6) and was present in all of the models considered. In contrast, litter cover negatively (β = -0.08 SE = 0.03) influenced nest success (Figures 6 & 7), but was also present in all of models considered.

The second-ranked model (AIC*c* weight = 0.15) included grass height, litter, daily precipitation, and a 1-day lag effect of precipitation. Although, daily precipitation had a positive influence on nest success (β = 29.45 SE = 40.35), and the 1-day lag effect negatively influenced nest success (β = -1.89 SE = 0.77), neither variable improved the top model and were only present due to being combined with grass height and litter. The third and fourth ranked models included daily precipitation, and bird age, respectively, but they were also combined with grass height and litter. Nest success varied 14.8% between years (37.7 ± 7.3% in 2006 compared to 52.5 ± 7.2% in 2007). However, adding a year affect to the top model did not improve model fit.

## DISCUSSION

### Nesting Parameters

*Nest Initiation* – Nest initiation rates for sage-grouse are generally believed to be lower compared to other prairie grouse species (Bergerud 1988). However, Schroeder et al. (1999) suggested that nesting attempts from telemetry based studies are probably under-represented in the literature, as follicular development indicated that at least 90.4% of females laid eggs the prior spring in three different studies. Our estimates of nest initiation in 2006 were probably influenced by a snow storm in late April (Figure 4) that hampered our tracking efforts during which we might have missed some nests. After the

storm we observed several "dumped" eggs suggesting that during the storm some individual females were unable to locate their nests and expelled those eggs. Nonetheless, nest initiation rates were high in this study relative to range-wide estimates (Connelly et al. 2004).

Females in our study were approximately 125 g greater than the average for 8 other studies (i.e., adults – 1525 g, yearlings – 1413 g, Schroeder et al. 1999). Heavier eastern wild turkey females (*Meleagris gallopavo silvestris*) were more likely to breed than lighter females (Porter et al. 1983), as were yearling Merriam's turkeys (*M. g. merriami*) (Hoffman et al. 1996). Sage-grouse exhibit considerable temporal variation in nest initiation rates (Moynahan et al. 2007) which may be related to nutrition during the breeding season (Hungerford 1964, Barnett and Crawford 1994).

Renest rates in sage-grouse are highly variable from 0 to 87% and are likely linked to environmental effects and habitat quality (Schroeder 1997, Moynahan et al. 2007). Low renesting rates may also be related to the relatively low productivity in these arid and semiarid environments as habitat productivity/quality has been suggested to regulate nesting and renesting in wild turkeys (Rumble and Hodorff 1993, Hoffman et al. 1996, Rumble et al. 2003). Moynahan et al. (2007) found no renest initiation for sage-grouse in dry years with little vegetative growth. Only 9.5% of hens renested in a population in North Dakota (Herman-Brunson 2007). Our observations suggest that hens that incubated nests for shorter periods were more likely to renest than hens that incubated longer. Other populations of sage-grouse on the edge of the range also showed

an inverse relation between length of incubation and renesting (Aldridge and Brigham 2001, Herman-Brunson 2007).

It has been suggested that sage-grouse nest later in more northern latitudes (Peterson 1980). South Dakota is further south than Washington and North Dakota, but had later hatch dates (Schroeder 1997, Herman-Brunson 2007), suggesting other variables (e.g., habitat, weather) may influence sage-grouse nesting chronology. Furthermore, hatch dates in South Dakota were comparable to what was reported for a northern sage-grouse population in Alberta (Aldridge and Brigham 2001)

We predicted age-specific variations in clutch size (Wallestad and Pyrah 1974, Peterson 1980, Moynahan et al. 2007) as adult females were significantly heavier than yearlings entering the breeding season. However, that was not observed in this study, or by Schroeder (1997), and Herman-Brunson (2007). Clutch size was lower for renests which was expected as female grouse expend substantial endogenous body reserves during the initial nesting attempt (Naylor and Bendell 1989).

*Nest Location in Relation to Leks* – Leks are the focal points of breeding and nesting conservation for non-migratory populations of sage-grouse (Connelly et al. 2000). Populations in South Dakota are believed to be non-migratory and contiguous with North Dakota and Montana populations (McCarthy and Kobriger 2005). It has been suggested that in areas with uniformly distributed habitats around leks, habitat conservation be implemented within a 3.2 km buffer (Connelly et al. 2000). However, Herman-Brunson et al. (*in review*) recommended a 5 km buffer to limit energy development and grazing

activities during the nesting period. A 5 km buffer would encompass 82% of nests in our study.

*Nest site Fidelity* – Sage-grouse, along with other grouse species, demonstrate fidelity in nesting areas from year to year (Fischer et al. 1993, Schroeder and Robb 2003). However, sage-grouse typically do not exhibit as strong of fidelity as other grouse, but usually 84% of nests are <3 km from a previous year's (Schroeder and Robb 2003). Seventy-six percent of nests in our study were within 0.70 km of the prior year's nest. Our results illustrate that sage-grouse in South Dakota may show more fidelity to nesting areas compared to other edge populations, which may be related to the availability of suitable nest areas around leks.

Fidelity to nesting areas may be advantageous as hens are able to maximize use of productive habitats and minimize the risk of predation (Greenwood and Harvey 1982). However, fidelity may lead to decreased productivity if sage-grouse hens occupy sink habitats (Aldridge and Boyce 2007), or it may indicate that the appropriate habitat is limited and clumped in distribution. Predators can key in on high densities of nests, increasing predation rates (e.g., Lariviére and Messier 1998). If predators are able to recognize high densities of sage-grouse nest locations due to fidelity, increased predation could occur.

**Resource Selection**

Sage-grouse in South Dakota selected nest sites with higher sagebrush cover and placed their nests beneath sagebrush plants with greater horizontal cover (VOR) than

random sites. In North Dakota, shrub density and nest-bowl VOR were also important predictors of sage-grouse nests (Herman-Brunson 2007).

Connelly et al. (2000) recommended 15-25% sagebrush canopy coverage for nesting sage-grouse. Meta-analysis (Hagen et al. 2007) confirmed mean sagebrush canopy coverage at sage-grouse nest sites was 21.51%. In South Dakota, sage-grouse selected the best of what was available, but that was less than the optimum. In contrast to sagebrush, grass structure in South Dakota exceeds both management recommendations (Connelly et al. 2000) and range-wide averages (Hagen et al. 2007). Western South Dakota forms a transition zone between the northern wheatgrass-needlegrass prairie that dominates most of the Dakotas and the big sagebrush plains of Wyoming (Johnson and Larson 1999). Thus, while South Dakota may have sub-optimal sagebrush cover for sage-grouse, the grass structure may be compensating the sagebrush component. However, grass structure is highly correlated with annual precipitation, and in periods of drought may not provide the necessary protection for sage-grouse nests. Poor rangeland management practices such as overgrazing will reduce grass structure which could have detrimental affects on sage-grouse populations.

**Nest Success**

Sage-grouse nest success varies widely across the range (Gregg 1991, Chi 2004), and is generally believed to be related to habitat conditions (Wallestad and Pyrah 1974, Connelly et al. 1991, Aldridge and Brigham 2002, Hagen et al. 2007). Our estimate of nest success was typical of other sage-grouse studies (48%, Connelly et al. 2004), despite the fact that available sagebrush canopy coverage was less than other areas. Grass height

in our study had a substantial impact on nest success (Figure 5) and probably provides the structural component necessary for nests. Successful nests in our study had taller grass structures than both failed nests and random sites, with failed nests being more comparable to random sites; this was also documented in Oregon (Gregg et al. 1994). Taller live and residual grass surrounding nests also increased nest success in Alberta (Aldridge and Brigham 2002), and was suggested to provide ample nest concealment in both sagebrush and non-sagebrush overstories in Washington (Sveum et al. 1998). Although litter cover entered our models as being an important predictive variable for nest success, the impact litter actually has on nest success is unknown. Litter could be considered as a measure of the prior year's herbaceous growth by being lower following less productive seasons, but it could also be lower after intensive grazing pressure (Hart et al. 1988, Naeth et al. 1991).

**MANAGEMENT IMPLICATIONS**

If sage-grouse populations continue to decrease and/or maintain sensitive status, sagebrush conservation and enhancement should be top priority for land management agencies to enable sage-grouse persistence in western South Dakota. Management for greater grass cover and height, reduced conversion to tillage agricultural, and minimizing habitat fragmentation such as energy development should be encouraged. Little information is known about the direct impacts livestock grazing has on sage-grouse habitats (Beck and Mitchell 2000) but it may be the least expensive practice to restore degraded sagebrush steppe (Braun 2006, Woodward 2006). Grazing by domestic sheep

(*Ovis aries*) has effectively controlled sagebrush (Baker et al. 1976) which could reduce sagebrush cover further in South Dakota.

Range management practices that could increase sagebrush and grass cover and height might include: rest-rotation grazing, where the rested pasture in not grazed until early July to allow for undisturbed nesting, or reduced grazing intensities and/or season of use to reduce impact on sagebrush and grass growth (Adams et al. 2004). Land managers should attempt to leave or maintain maximum grass heights ≥ 26 cm, the inflection point for 50% nest success. In addition, annual grazing utilization should not exceed 35% in order to improve rangeland conditions, particularly sagebrush cover (Holechek et al. 1999). Construction of new fences should be avoided as fences provide predator corridors, raptor perches, and pose a risk for collisions (Braun 1998). We agree with Braun (2006) and Woodward (2006) that larger pastures with fewer fences are better. Wyoming big sagebrush typically recovers from a fire in 50-120 years (Baker 2006), and because the restricted distribution and limited cover of sagebrush in South Dakota, we recommend no use of prescribed fire in areas with sagebrush.

With 75% of the study area in private ownership and the patchy network of public land; sage-grouse conservation and persistence lies in hands of private landowners. To increase sage-grouse habitats, long-term (>20 yrs) partnerships and incentives with ranchers will be imperative. This will require cooperation from state wildlife agencies, federal land management agencies, local natural resource conservation districts, and committed landowners. Forming a South Dakota sage-grouse working group may be in

order to accomplish this goal as many landowners were interested in sage-grouse conservation.

Table 1. Mean vegetation characteristics of nest sites and random sites between years for greater sage-grouse used in logistic regression models in northwestern South Dakota, USA, using MRPP (Mielke and Berry 2001), 2006-2007.

| | Nest | | | Random | | | Both Years | | |
|---|---|---|---|---|---|---|---|---|---|
| **Variable** | **2006 (*n* = 34)** | **2007 (*n* = 39)** | **P-value** | **2006 (*n* = 35)** | **2007 (*n* = 39)** | **P-value** | **Nest (*n* = 73)** | **Random (*n* = 74)** | **P-value** |
| Total Cover (%) | 61.1 | 75.1 | <0.01 | 55.8 | 66.1 | <0.01 | 68.6 | 61.2 | <0.01 |
| Litter Cover (%) | 7.6 | 7.1 | 0.79 | 6.5 | 6.1 | 0.88 | 7.4 | 6.3 | 0.04 |
| Grass Cover (%) | 24.2 | 31.4 | 0.01 | 21.1 | 25.8 | 0.21 | 28.1 | 23.6 | 0.01 |
| Max Grass Hgt. (cm) | 23.4 | 29.5 | <0.01 | 20.4 | 25.0 | <0.01 | 26.7 | 22.8 | <0.01 |
| Max Grass Hgt. 0-5m (cm) | 25.7 | 30.9 | 0.02 | 20.3 | 24.3 | 0.01 | 28.5 | 22.4 | <0.01 |
| Visual Obstruction (cm) | 5.5 | 11.1 | <0.01 | 3.7 | 5.1 | 0.14 | 8.5 | 4.4 | <0.01 |
| Visual Obstruction 0m (cm) | 20.8 | 29.4 | <0.01 | 10.5 | 8.9 | 0.13 | 25.4 | 9.6 | <0.01 |
| Visual Obstruction 1m (cm) | 7.3 | 13.7 | <0.01 | 3.7 | 4.1 | 0.05 | 10.7 | 3.9 | <0.01 |
| Sagebrush Cover (%) | 10.3 | 10.1 | 0.75 | 6.3 | 6.3 | 0.98 | 10.2 | 6.2 | <0.01 |
| Sagebrush Hgt. (cm) | 25.8 | 29.7 | 0.04 | 23.8 | 24.0 | 0.97 | 27.9 | 23.9 | <0.01 |

Table 2. Observed mean values for habitat variables between greater sage-grouse successful and failed nests used in nest success models in northwestern South Dakota, USA, using MRPP (Mielke and Berry 2001) 2006-2007.

| | **Successful (*n* = 33)** | | **Failed (*n* = 40)** | | |
|---|---|---|---|---|---|
| **Variable** | **Mean** | **SE** | **Mean** | **SE** | **P-value** |
| Max Grass Hgt. (cm) | 30.64 | 1.6 | 23.4 | 1.0 | <0.01 |
| Litter Cover (%) | 6.4 | 0.5 | 8.1 | 0.8 | 0.07 |
| Forb Cover 0 m (%) | 5.3 | 0.8 | 3.9 | 0.6 | 0.09 |
| Visual Obstruction (cm) | 10.2 | 1.1 | 7.2 | 0.8 | 0.02 |

Table 3. Nest initiation rates of radio-marked adult and yearling greater sage-grouse in northwestern South Dakota, USA, 2006-2007.

| | Ad | | | Yearlings | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|
| **Yr** | **Estimate** | **SE** | ***n*** | **Estimate** | **SE** | ***n*** | **Estimate** | **SE** | ***n*** |
| 2006 | 90.5% | 6.6 | 21 | 94.1% | 5.9 | 17 | 92.1% | 4.4 | 38 |
| 2007 | 100.0% | 0.0 | 25 | 100.0% | 0.0 | 10 | 100.0% | 0.0 | 35 |
| Total | 95.7% | 3.0 | 46 | 96.3% | 3.7 | 27 | 95.9% | 2.3 | 73 |

Table 4. Average clutch size and average hatch dates for first nests and renests of greater sage-grouse in northwestern South Dakota, USA, 2006-2007.

| | First Nest | | | Renest | | |
|---|---|---|---|---|---|---|
| **Yr** | **Initiation Date[ab]** | **Hatch Date[a]** | **Clutch Size** | **Initiation Date[ab]** | **Hatch Date[a]** | **Clutch Size** |
| 2006 | 26 April<br>± 2.8<br>*n* = 13 | 3 June<br>± 2.6<br>*n* = 13 | 7.9<br>± 0.3<br>*n* = 26 | 10 May<br>± 1.5<br>*n* = 2 | 16 June<br>± 1.5<br>*n* = 2 | 7.3<br>± 0.5<br>*n* = 4 |
| 2007 | 21 April<br>± 1.7<br>*n* = 17 | 29 May<br>± 1.5<br>*n* = 17 | 8.5<br>± 0.2<br>*n* = 30 | 9 May<br>± 4.7<br>*n* = 3 | 12 June<br>± 3.2<br>*n* = 3 | 5.5<br>± 0.9<br>*n* = 4 |
| Avg. | 24 April<br>± 1.6<br>*n* = 30 | 31 May<br>± 1.5<br>*n* = 30 | 8.3<br>± 0.2<br>*n* = 56 | 9 May<br>± 2.6<br>*n* = 5 | 14 June<br>± 2.0<br>*n* = 5 | 6.4<br>± 0.6<br>*n* = 8 |

[a] Estimated only for successful nests.
[b] Estimated date of first egg laid.

Table 5. Results from logistic regression models predicting greater sage-grouse nest sites ($n$ = 73) versus random sites ($n$ = 74) in northwestern South Dakota, USA, 2006-2007.

| **Model**[a] | **K**[b] | **AIC*c*** | **Δ AIC*c***[c] | ***wi***[d] |
|---|---|---|---|---|
| Sagebrush Cover + Visual Obstruction 0m | 5 | 112.02 | 0.00 | 0.39 |
| Sagebrush Cover + Visual Obstruction 0m + Max Grass Hgt. 0-5m | 6 | 112.23 | 0.22 | 0.35 |
| Sagebrush Cover+ Visual Obstruction 0m + Visual Obstruction 1m | 6 | 113.96 | 1.94 | 0.15 |
| Sagebrush Cover + Visual Obstruction 0m + Visual Obstruction 1m + Max Grass Hgt. 0-5m | 7 | 114.40 | 2.39 | 0.12 |

[a] For ease of interpretation, year variable was excluded from model column. See Appendix 1 for full model results
[b] Number of habitat parameters plus intercept, SE, and year.
[c] Change in AIC*c* value
[d] Model weight

Table 6. Parameter Estimates, odds ratios, and corresponding confidence intervals for the best-approximating model of greater sage-grouse nests sites versus random sites in northwestern South Dakota, 2006-2007.

| | Parameter | | | Odds Ratio | | |
|---|---|---|---|---|---|---|
| **Variable** | **Estimate** | **Lower 95%CI** | **Upper 95%CI** | **Ratio** | **Lower 95%CI** | **Upper 95%CI** |
| Sagebrush Cover | 0.195 | 0.086 | 0.325 | 1.215 | 1.090 | 1.384 |
| Visual Obstruction 0 m | 0.220 | 0.155 | 0.300 | 1.246 | 1.168 | 1.350 |

Table 7. Summary of model selection results for nest survival between year and age of greater sage-grouse in northwestern South Dakota, USA, 2006-2007.

| **Model** [a] | **K** [b] | **AIC*c*** | **Δ AIC*c*** [c] | ***wi*** [d] |
|---|---|---|---|---|
| Max Grass Hgt. + Litter | 3 | 225.79 | 0.00 | 0.23 |
| Max Grass Hgt. + Litter + Daily Precip + Precip Lag | 5 | 226.75 | 0.96 | 0.15 |
| Max Grass Hgt. + Litter + Daily Precip | 4 | 227.39 | 1.60 | 0.11 |
| Max Grass Hgt. + Litter + Bird Age | 4 | 227.77 | 1.98 | 0.09 |

[a] See appendix 2 for full model results
[b] Number of variables
[c] Change in AIC*c* value
[d] Model weight

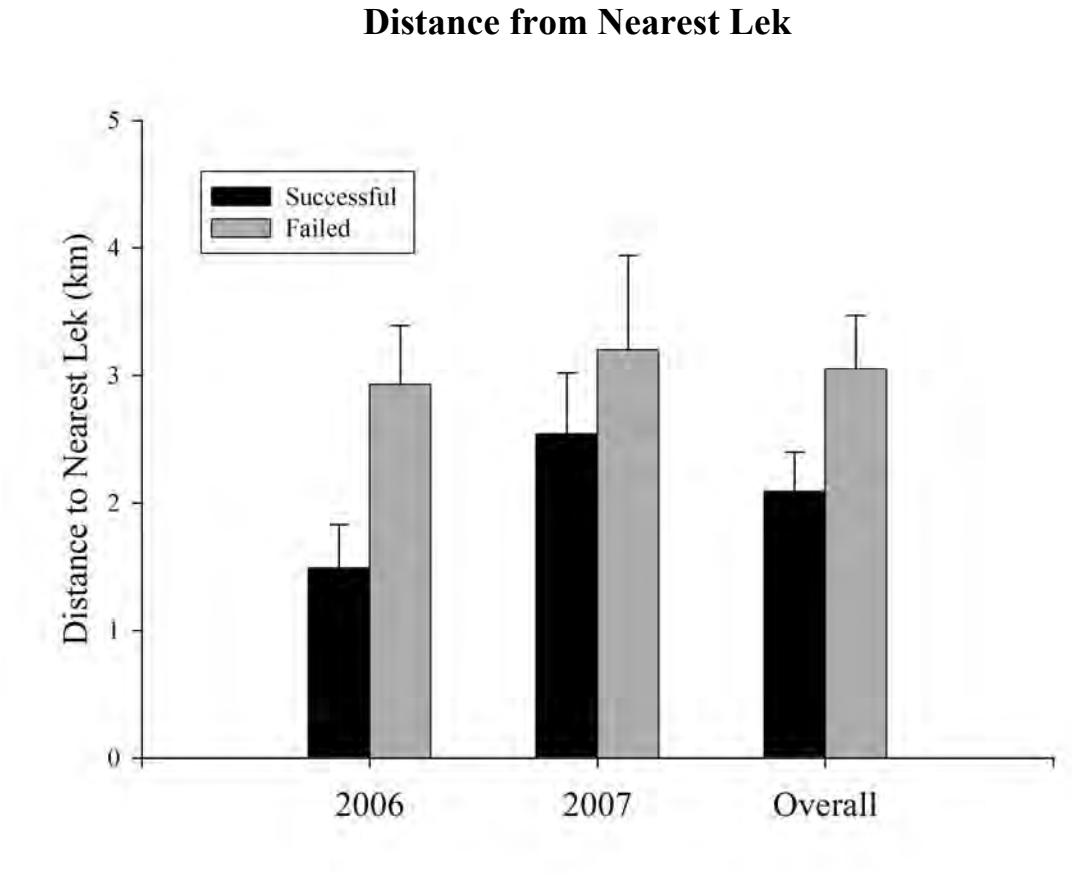



Figure 2. Mean distances plus one standard error (SE) of successful and failed greater sage-grouse nests to nearest documented active lek in northwestern South Dakota, USA, 2006-2007.

**Number of Nests Within Particular Lek Buffers**

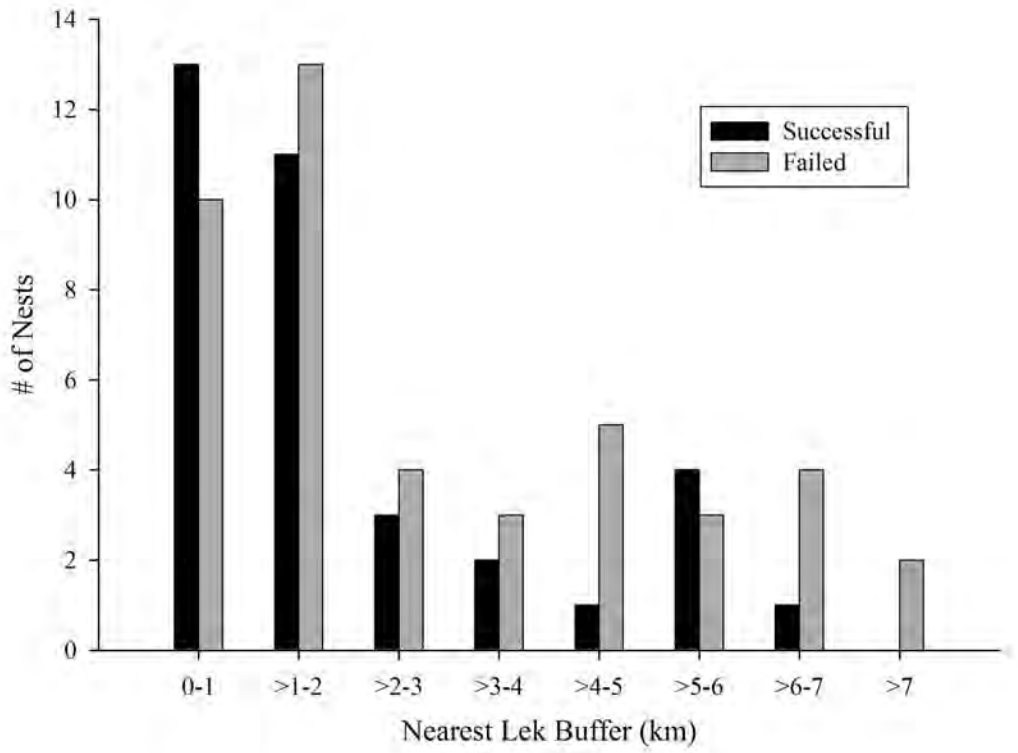



Figure 3. Distribution of successful and failed nests to nearest documented lek distances for greater sage-grouse in northwestern South Dakota, USA, 2006-2007.

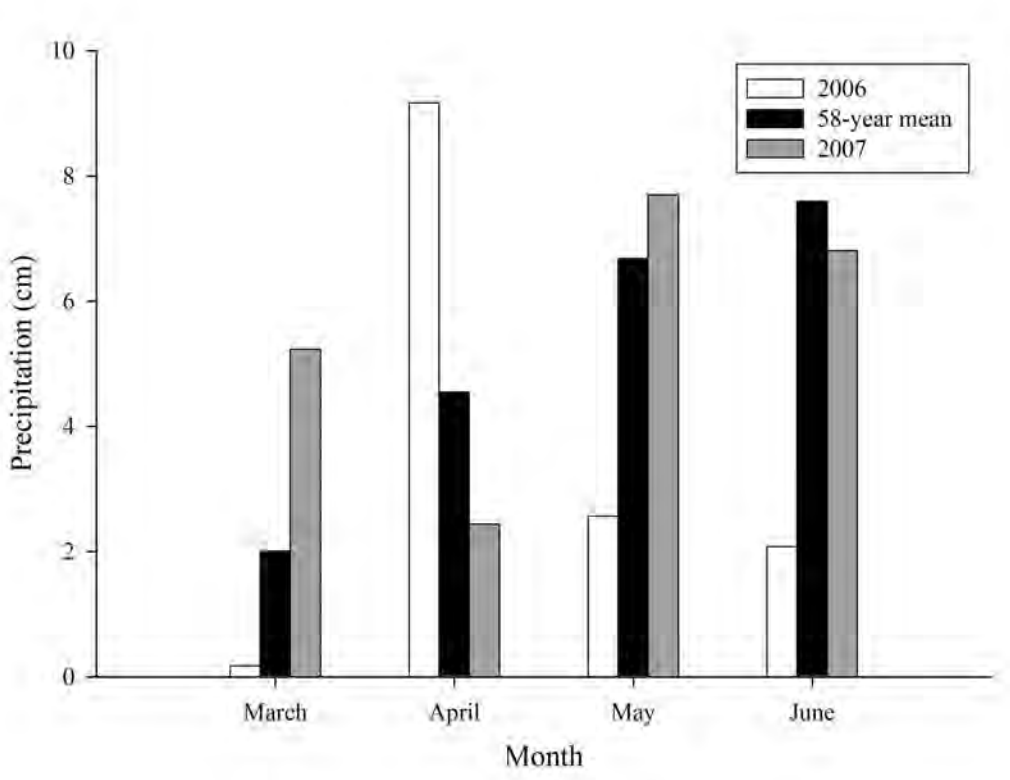



Figure 4. Monthly precipitation received during the breeding and nesting periods in 2006 – 2007 compared to the 58-year mean from the nearest daily weather station (Nisland, SD).

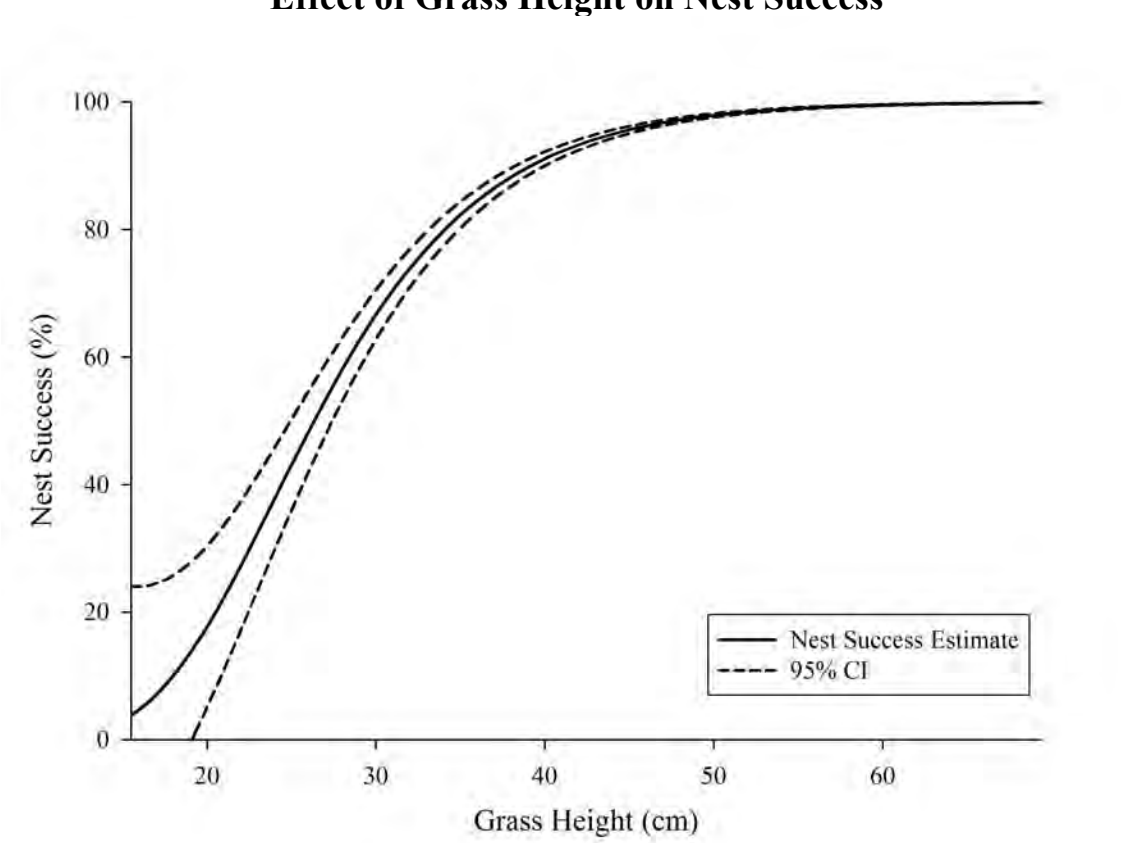



Figure 5. Effect of grass height on greater sage-grouse nest success in northwestern South Dakota, USA, 2006-2007. Nest success estimate derived from back-transformed beta estimates included in top model. Confidence intervals estimated from the delta method (Seber 1982).

## Effect of Grass Height and Litter on Nest Success

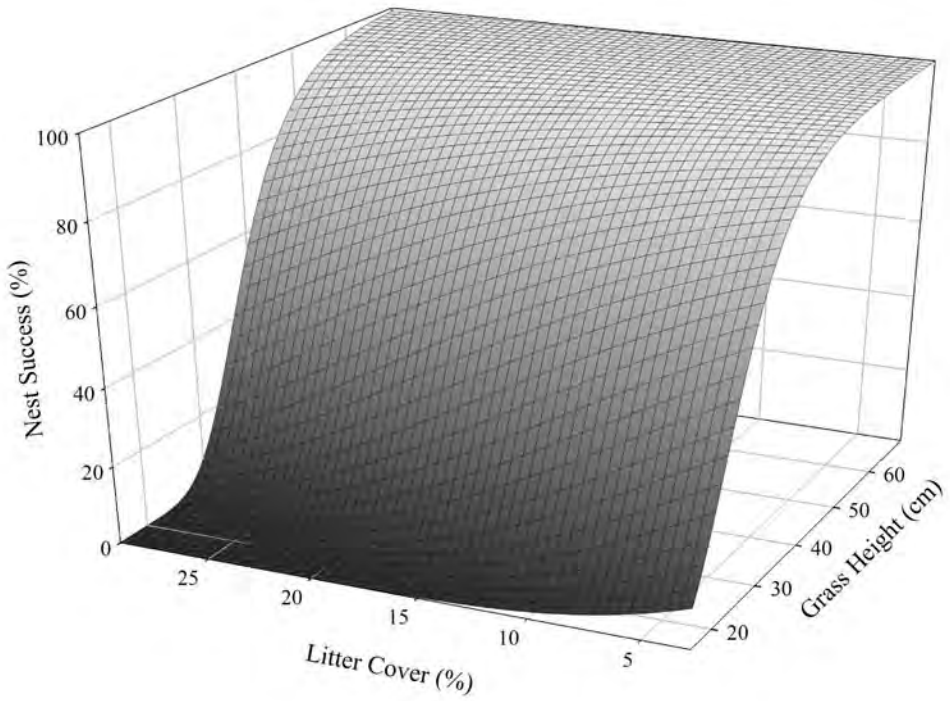



Figure 6. Effect of grass height and litter canopy coverage on greater sage-grouse nest success in northwestern South Dakota, USA, 2006-2007. Nest success estimate derived from back-transformed beta estimates included in top model.

**Effect of Litter Canopy Coverage on Nest Success**

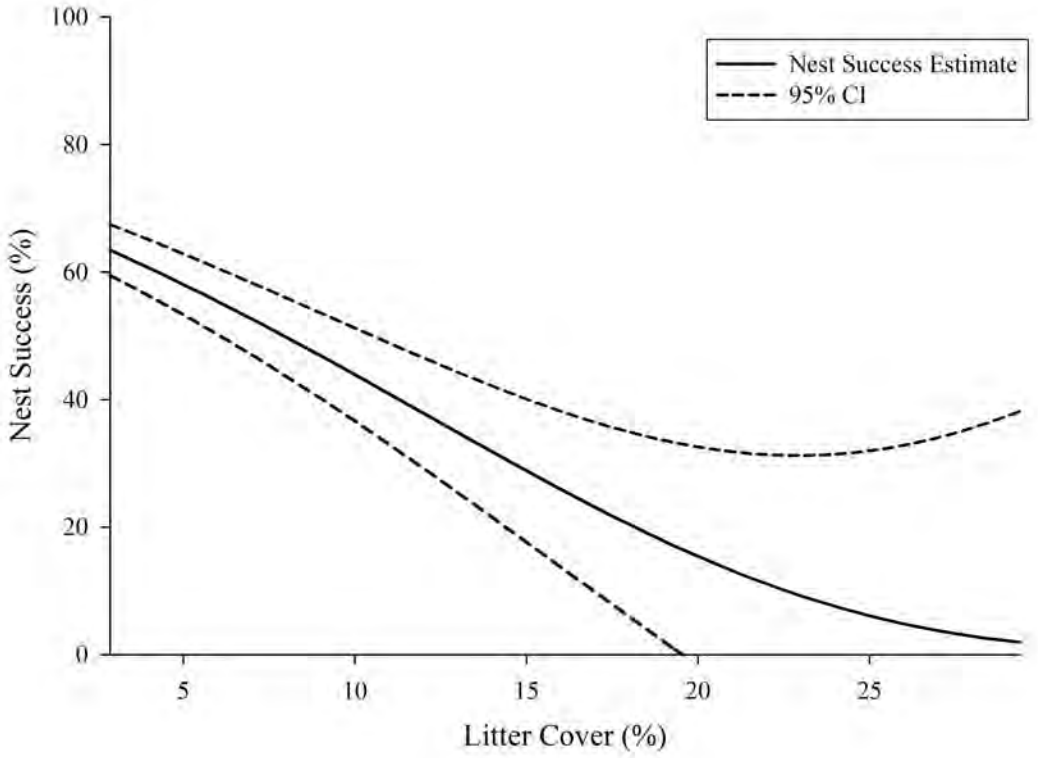



Figure 7. Effect of litter canopy coverage on greater sage-grouse nest success in northwestern South Dakota, USA, 2006-2007. Nest success estimate derived from back-transformed beta estimates included in top model. Confidence intervals estimated from the delta method (Seber 1982).

**LITERTURE CITED**

Adams, B. W., J. Carlson, D. Milner, T. Hood, B. Cairns, and P. Herzog. 2004. Beneficial grazing management practices for Sage-grouse (*Centrocercus urophasianus*) and ecology of silver sagebrush (*Artemisia cana*) in southeastern Alberta. Technical Report, Public Lands and Forests Division, Alberta Sustainable Resource Development. Pub. No. T/049. 60pp.

Aldridge, C. L. and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat based approach for endangered greater sage-grouse. Ecological Applications 17:508-526.

Aldridge, C. L. and R. M. Brigham. 2001. Nesting and reproductive activities of greater sage-grouse in a declining northern fringe population. Condor 103:537-543.

Aldridge, C. L. and R. M. Brigham. 2002. Sage-grouse nesting and brood-rearing habitat use in southern Canada. Journal of Wildlife Management 66:433-444.

Baker, M. F., R. L. Eng. J. S. Gashwiler, M. H. Schroeder, and C. E. Braun. 1976. Conservation committee report on the effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin 88:165-170.

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin 34:177-185.

Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of sage-grouse hens in Oregon. Journal of Range Management 47:114-118.

Beck, J. L., and D. L. Mitchell. 2000. Influences of livestock grazing on sage-grouse habitat. Wildlife Society Bulletin 28:993-1002.

Benkobi, L., D. W. Uresk, G. Schenbeck, and R. M. King. 2000. Protocol for monitoring standing crop in grasslands using visual obstruction. Journal of Range Management 53:627-633.

Bergerud, A. T. 1988. Population ecology of North American grouse. Pages 578-685 *in* A. T. Bergerud, and M. W. Gratson, editors. Adaptive Strategies and Population Ecology of Northern Grouse. Wildlife Management Institute, Minneapolis, Minnesota, USA.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.

Boyce, M. S., P. R. Vernier, S. E. Nielson, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modeling 157:281-300.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of Fish and Wildlife Agencies 78:139-156.

Braun, C. E. 2006. A blueprint for sage-grouse conservation and recovery [unpublished]. Grouse Inc. Tucson, AZ.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Chi, R. Y. 2004. Greater sage-grouse on Parker Mountain, Utah. Thesis, Utah State University, Logan, USA.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage-grouse use of nest sites in southeastern Idaho. Journal of Wildlife Management 55:521-524.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451-460.

Crunden, C. W. 1963. Age and sex of sage grouse from wings. Journal of Wildlife Management 27:846-849.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis, Northwest Science 33:43-64.

Dinsmore, S. J., D. H. Johnson. 2005. Population analysis in wildlife biology. Pages 154-184 *in* C. E. Braun, editor. Techniques for wildlife investigations and management. Sixth edition. The Wildlife Society, Bethesda, Maryland, USA.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476-3488.

Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal of Wildlife Management 19:267-272.

Fischer, R. A., A. D. Apa, W. L. Wakkinen, K. P. Reese, and J. W. Connelly. 1993. Nesting-area fidelity of sage-grouse in southeastern Idaho. Condor 95:1038-1041.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224-231.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13:1-21.

Gregg, M. A. 1991. Use and selection of nesting habitat by sage-grouse in Oregon. M.S. Thesis, Oregon State University, Corvallis, USA.

Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetational cover and predation of sage-grouse nests in Oregon. Journal of Wildlife Management 58:162-166.

Hagen, C. A., J. W. Connelly, and M. A. Schroeder. 2007. A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. Wildlife Biology Supplement 13:42-50.

Hart, R. H., M. J. Samuel, P. S. Test, and M. A. Smith. 1988. Cattle, vegetation, and economic responses to grazing systems and grazing pressure. Journal of Range Management 41:282-286.

Herman-Brunson, K. H. 2007. Nesting and brood-rearing habitat selection of greater sage-grouse and associated survival of hens and broods at the edge of their historic distribution. Thesis, South Dakota State University, Brookings, USA.

Herman-Brunson, K. H., N. W. Kaczor, C. C. Swanson, K. C. Jensen, M. A. Rumble, R. W. Klaver. *Submitted.* Nesting ecology of greater sage-grouse at the eastern edge of their distribution. Journal of Wildlife Management.

Hoffman, R. W., M. P. Luttrell, and W. R. Davidson. 1996. Reproductive performance of Merriam's Wild Turkeys with suspected *Mycoplasma* infection. Proceedings of National Wild Turkey Symposium. 7:145-151.

Holechek, J. L., H. Gomez, F. Molinar, and D. Galt. 1999. Grazing studies: what we've learned. Rangelands 21:12-16.

Hosmer, D. W., and S. Lemeshow. 2000. Applied Logistic Regression, 2nd Edition. John Wiley and Sons Inc. Publication, New York, NY, USA.

Hungerford, C. R. 1964. Vitamin A and productivity in Gambel's quail. Journal of Wildlife Management 28:141-147.

Johnson, J. R., and G. E. Larson. 1999. Grassland plants of South Dakota ant the northern Great Plains. South Dakota State University. Brookings, South Dakota, USA.

Lariviére, S., and Messier, F. 1998. Effect of density and nearest neighbours on simulated waterfowl nests: can predators recognize high-density nesting patches? Oikos 83:12-20.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

McCarthy, J. J., and J. D. Kobriger. 2005. Management plan and conservation strategies for greater sage-grouse in North Dakota. North Dakota Game and Fish Department. 96pp.

Mielke, P. W., and K. J. Berry. 2001. Permutation Methods: A Distance Function Approach. New York: Springer-Verlag.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of Greater sage-grouse in northcentral Montana. Journal of Wildlife Management 71:1773-1783.

Naeth, M. A., A. W. Bailey, D. J. Pluth, D. S. Chanasyk, and R. T. Hardon. 1991. Grazing impacts on litter and soil organic matter in mixed prairie and fescue grassland ecosystems in Alberta. Journal of Range Management 44:7-12.

Naylor, B. J., and J. F. Bendell. 1989. Clutch size and egg size of spruce grouse in relation to spring diet, food supply, and endogenous reserves. Canadian Journal of Zoology 67:969-980.

Peterson, B. E. 1980. Breeding and nesting ecology of female sage grouse in North Park, Colorado. Thesis, Colorado State University, Fort Collins, Colorado.

Pollard, J. H. 1971. On distance estimators of density in randomly distributed forests. Biometrics 27:991-1002.

Porter, W. F., G. C. Nelson, and K. Mattson. 1983. Effects of winter conditions on reproduction in a northern wild turkey population. Journal of Wildlife Management 47:281-290.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295-298.

Rumble, M. A., and R. A. Hodorff. 1993. Nesting ecology of Merriam's turkeys in the Black Hills, South Dakota. Journal of Wildlife Management 57:789-801.

Rumble, M. A., B. F. Wakeling, and L. D. Flake. 2003. Factors affecting survival and recruitment in female Merriam's turkeys. Intermountain Journal of Sciences 9:26-37.

Sargeant, A. B., M. A. Sovada, and R. J. Greenwood. 1998. Interpreting evidence of depredation of duck nests in the prairie pothole region. U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND and Ducks Unlimited, Inc., Memphis, TN, 72 pp.

Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99:933-941.

Schroeder, M. A., and L. A. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildlife Biology 9:291-299.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. Condor 106:363-376.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). *In* The Birds of North America, No. 425 (A. Poole. and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillan Book, New York, New York, USA.

Smith, J. 2003. Greater sage grouse on the edge of their range: leks and surrounding landscapes in the Dakotas. Thesis, South Dakota State University, Brookings, USA.

South Dakota State Climate Office. 2007. Office of the State Climatologist. http://climate.sdstate.edu Accessed on 15 December 2007.

Sveum, C. M., W. D. Edge, and J. A. Crawford. 1998. Nesting habitat selection by sage-grouse in south-central Washington. Journal of Range Management 51:265-269.

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of sage-grouse hens in central Montana. Journal of Wildlife Management 38:630-633.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120-138.

Woodward, J. K. 2006. Greater sage-grouse (*Centrocercus urophasianus*) habitat in central Montana. Thesis, Montana State University, Bozeman, USA.

Appendix 1. Complete results from logistic regression models predicting greater sage-grouse nest sites ($n$ = 73) versus random sites ($n$ = 74) in northwestern South Dakota, USA, 2006-2007.

| Model[a] | K[b] | AIC*c* | Δ AIC*c*[c] | *wi*[d] |
|---|---|---|---|---|
| Sagebrush Cover + Visual Obstruction 0m | 5 | 112.02 | 0.00 | 0.39 |
| Sagebrush Cover + Visual Obstruction 0m + Max Grass Hgt. 0-5m | 6 | 112.23 | 0.22 | 0.35 |
| Sagebrush Cover + Visual Obstruction 0m + Visual Obstruction 1m | 6 | 113.96 | 1.94 | 0.15 |
| Sagebrush Cover + Visual Obstruction 0m + Visual Obstruction 1m + Max Grass Hgt. 0-5m | 7 | 114.40 | 2.39 | 0.12 |
| Visual Obstruction 0m | 4 | 123.27 | 11.26 | 0.00 |
| Visual Obstruction 0m + Max Grass Hgt. 0-5m | 5 | 123.36 | 11.35 | 0.00 |
| Visual Obstruction 0m + Total Cover | 5 | 124.14 | 12.12 | 0.00 |
| Visual Obstruction 0m + Visual Obstruction 1m | 5 | 124.45 | 12.44 | 0.00 |
| Visual Obstruction 0m + Max Grass Hgt.+ Sagebrush Hgt. | 6 | 125.91 | 13.90 | 0.00 |
| Total Cover + Max Grass Hgt. + Visual Obstruction 0m | 6 | 125.93 | 13.91 | 0.00 |
| Total Cover + Max Grass Hgt. + Sagebrush Hgt. + Visual Obstruction 0m | 7 | 127.34 | 15.32 | 0.00 |
| Visual Obstruction 1m + Sagebrush Cover | 5 | 146.97 | 34.96 | 0.00 |
| Visual Obstruction 1m | 4 | 157.93 | 45.91 | 0.00 |
| Visual Obstruction 1m + Max Grass Hgt. 0-5m | 5 | 158.56 | 46.54 | 0.00 |
| Sagebrush Cover + Visual Obstruction | 5 | 162.19 | 50.17 | 0.00 |
| Sagebrush Cover + Max Grass Hgt. 0-5m | 5 | 166.21 | 54.20 | 0.00 |
| Sagebrush Cover + Grass Cover | 5 | 173.65 | 61.63 | 0.00 |
| Sagebrush Cover + Total Cover | 5 | 175.41 | 63.39 | 0.00 |
| Visual Obstruction | 4 | 176.55 | 64.53 | 0.00 |
| Max Grass Hgt. + Sagebrush Cover | 5 | 177.19 | 65.18 | 0.00 |
| Total Cover + Visual Obstruction | 5 | 178.69 | 66.68 | 0.00 |
| Litter + Sagebrush Cover | 5 | 180.14 | 68.12 | 0.00 |
| Litter + Max Grass Hgt. 0-5m + Sagebrush Hgt. | 6 | 181.63 | 69.62 | 0.00 |
| Max Grass Hgt. 0-5m + Sagebrush Hgt. | 5 | 182.11 | 70.10 | 0.00 |
| Sagebrush Cover | 4 | 186.55 | 74.54 | 0.00 |
| Max Grass Hgt. 0-5m + Litter | 5 | 187.00 | 74.99 | 0.00 |
| Max Grass Hgt. 0-5m | 4 | 187.20 | 75.18 | 0.00 |
| Litter + Max Grass Hgt. + Sagebrush Hgt. | 6 | 191.89 | 79.87 | 0.00 |
| Max Grass Hgt. + Sagebrush Hgt. | 5 | 193.07 | 81.06 | 0.00 |
| Max Grass Hgt. + Sagebrush Hgt. + Total Cover | 6 | 193.81 | 81.79 | 0.00 |
| Litter + Max Grass Hgt. | 5 | 199.64 | 87.63 | 0.00 |
| Litter + Sagebrush Hgt. | 5 | 199.82 | 87.80 | 0.00 |
| Max Grass Hgt. | 4 | 200.24 | 88.22 | 0.00 |
| Sagebrush Hgt. | 4 | 201.82 | 89.80 | 0.00 |
| Total Cover | 4 | 201.92 | 89.90 | 0.00 |
| Grass Cover | 4 | 206.70 | 94.68 | 0.00 |
| Litter | 4 | 208.96 | 96.94 | 0.00 |

[a] For ease of interpretation, year variable was excluded from model column.
[b] Number of habitat parameters plus intercept, SE, and year.
[c] Change in AIC*c* value
[d] Model weight

Appendix 2. Complete summary of model selection results for nest survival between year and age of greater sage-grouse in northwestern South Dakota, USA, 2006-2007.

| Model | K [a] | AIC*c* | Δ AIC*c* [c] | *wi* [d] |
|---|---|---|---|---|
| Max Grass Hgt. + Litter | 3 | 225.79 | 0.00 | 0.23 |
| Max Grass Hgt. + Litter + Daily Precip + Precip Lag | 5 | 226.75 | 0.96 | 0.15 |
| Max Grass Hgt. + Litter + Daily Precip | 4 | 227.39 | 1.60 | 0.11 |
| Max Grass Hgt. + Litter + Bird Age | 4 | 227.77 | 1.98 | 0.09 |
| Max Grass Hgt. + Litter + Forb 0m | 4 | 227.80 | 2.01 | 0.09 |
| Year*Max Grass Hgt. + Litter | 6 | 228.64 | 2.85 | 0.06 |
| Max Grass Hgt. | 2 | 228.85 | 3.06 | 0.05 |
| Max Grass Hgt. + Litter + Forb 0m + Daily Precip | 5 | 229.41 | 3.62 | 0.04 |
| Max Grass Hgt. + Litter + Forb 0m+ Bird Age | 5 | 229.79 | 3.99 | 0.03 |
| Max Grass Hgt. + DailyPrecip + Precip Lag | 4 | 229.96 | 4.17 | 0.03 |
| Year + Max Grass Hgt. | 3 | 230.15 | 4.36 | 0.03 |
| Max Grass Hgt. + DailyPrecip | 3 | 230.38 | 4.59 | 0.02 |
| Max Grass Hgt. + Forb 0m | 3 | 230.65 | 4.86 | 0.02 |
| Max Grass Hgt. + Bird Age | 3 | 230.78 | 4.99 | 0.02 |
| Year*Max Grass Hgt. | 4 | 231.18 | 5.39 | 0.02 |
| Max Grass Hgt. + Litter + Forb 0m + DailyPrecip + MinTemp | 6 | 231.35 | 5.56 | 0.01 |
| Bird Age*Max Grass Hgt. | 4 | 232.46 | 6.66 | 0.01 |
| Year*Bird Age + Max Grass Hgt. | 5 | 233.81 | 8.02 | 0.00 |
| Year*Visual Obstruction + Litter | 6 | 240.37 | 14.58 | 0.00 |
| Year*Visual Obstruction + Litter + Forb 0m | 8 | 240.82 | 15.03 | 0.00 |
| Visual Obstruction + Litter | 3 | 243.27 | 17.47 | 0.00 |
| Visual Obstruction + Litter + Forb 0m | 4 | 245.01 | 19.21 | 0.00 |
| Visual Obstruction + Litter + Bird Age | 4 | 245.11 | 19.32 | 0.00 |
| DailyPrecip + Visual Obstruction + Litter + Forb 0m | 5 | 246.05 | 20.26 | 0.00 |
| Year*Visual Obstruction | 4 | 246.35 | 20.56 | 0.00 |
| Visual Obstruction + Litter + Forb 0m+ Bird Age | 5 | 246.88 | 21.08 | 0.00 |
| Daily Precip + Min Temp + Visual Obstruction + Litter + Forb 0m | 6 | 247.27 | 21.48 | 0.00 |
| Visual Obstruction | 2 | 248.05 | 22.26 | 0.00 |
| Litter | 2 | 249.97 | 24.17 | 0.00 |
| Year + Visual Obstruction | 3 | 250.04 | 24.25 | 0.00 |
| Visual Obstruction + Forb 0m | 3 | 250.06 | 24.27 | 0.00 |
| Visual Obstruction + Bird Age | 3 | 250.06 | 24.27 | 0.00 |
| Year + Litter | 3 | 250.46 | 24.66 | 0.00 |
| Litter + Bird Age | 3 | 251.23 | 25.44 | 0.00 |
| Litter + Forb 0m | 3 | 251.49 | 25.70 | 0.00 |
| Daily Precip + Litter + Forb 0m | 4 | 251.91 | 26.12 | 0.00 |
| Visual Obstruction + Forb 0m+ Bird Age | 4 | 252.07 | 26.28 | 0.00 |
| Year*Litter | 4 | 252.47 | 26.67 | 0.00 |
| Constant | 1 | 252.71 | 26.92 | 0.00 |
| Daily Precip | 2 | 252.99 | 27.20 | 0.00 |
| Year | 2 | 253.01 | 27.22 | 0.00 |
| Min Temp | 2 | 253.04 | 27.25 | 0.00 |
| Year*Forb 0m | 4 | 253.33 | 27.54 | 0.00 |
| Daily Precip + Precip Lag | 3 | 253.70 | 27.91 | 0.00 |
| Min Temp + Temp Lag | 3 | 254.05 | 28.26 | 0.00 |
| Year*Litter + Forb 0m | 6 | 254.14 | 28.35 | 0.00 |
| Daily Precip + Precip Lag + Min Temp | 4 | 254.28 | 28.49 | 0.00 |
| Forb 0m | 2 | 254.36 | 28.57 | 0.00 |

Appendix 2. continued.

| | | | | |
|---|---|---|---|---|
| Bird Age | 2 | 254.52 | 28.73 | 0.00 |
| Daily Precip + Forb 0m | 3 | 254.73 | 28.94 | 0.00 |
| Year + Forb 0m | 3 | 255.00 | 29.21 | 0.00 |
| Daily Precip + Precip Lag + Min Temp + Temp Lag | 5 | 255.06 | 29.27 | 0.00 |
| Forb 0m + Bird Age | 3 | 256.22 | 30.42 | 0.00 |
| Year*Bird Age | 4 | 256.87 | 31.08 | 0.00 |

[a] Number of variables
[b] Change in AIC*c* value
[c] Model weight

Appendix 3. Demographic information for all greater sage-grouse captured in northwestern South Dakota, USA, 2006-2007.

| Band # | Capture Date | X[a] | Y[a] | Nearest Lek | Sex[b] | Age[c] | Weight (g) | Radio Freq. |
|---|---|---|---|---|---|---|---|---|
| 1001 | 28-Mar-06 | 583058 | 4972413 | Crago | F | A | 1654 | 150.064 |
| 1002 | 31-Mar-06 | 583874 | 4972344 | Crago | F | A | 1552 | 150.073 |
| 1003 | 1-Apr-06 | 605131 | 4983015 | Two Top | F | A | 1618 | 150.083 |
| 1004 | 1-Apr-06 | 604838 | 4982844 | Two Top | F | Y | 1612 | 150.094 |
| 1005 | 1-Apr-06 | 604840 | 4983075 | Two Top | F | A | 1602 | 150.103 |
| 1006 | 1-Apr-06 | 605197 | 4983537 | Two Top | F | A | 1732 | 150.114 |
| 1007 | 1-Apr-06 | 605399 | 4982814 | Two Top | F | A | 1648 | 151.074 |
| 1008 | 3-Apr-06 | 594044 | 4989246 | Widdoss | F | A | 1586 | 150.133 |
| 1009 | 3-Apr-06 | 595437 | 4988647 | Widdoss | F | Y | 1734 | 150.145 |
| 1010 | 3-Apr-06 | 595437 | 4988647 | Widdoss | F | Y | 1464 | 150.155 |
| 1011 | 3-Apr-06 | 595437 | 4988647 | Widdoss | F | Y | 1482 | 151.085 |
| 1012 | 3-Apr-06 | 595594 | 4988735 | Widdoss | F | A | 1594 | 150.173 |
| 1013 | 3-Apr-06 | 595758 | 4988629 | Widdoss | F | Y | 1482 | 150.183 |
| 1014 | 3-Apr-06 | 595619 | 4988954 | Widdoss | F | Y | 1520 | 150.193 |
| 1015 | 4-Apr-06 | 623696 | 4994653 | McFarland | F | A | 1758 | 150.204 |
| 1016 | 4-Apr-06 | 623922 | 4994453 | McFarland | F | Y | 1556 | 150.214 |
| 1017 | 5-Apr-06 | 583265 | 4972042 | Crago | F | A | 1650 | 150.353 |
| 1018 | 5-Apr-06 | 581965 | 4969635 | Rumph | F | Y | 1520 | 150.363 |
| 1019 | 7-Apr-06 | 606987 | 5006247 | County Line | F | Y | 1610 | 150.373 |
| 1020 | 7-Apr-06 | 606596 | 5006738 | County Line | F | A | 1704 | 150.383 |
| 1021 | 7-Apr-06 | 606596 | 5006738 | County Line | F | A | 1626 | 151.014 |
| 1022 | 7-Apr-06 | 606490 | 5006922 | County Line | F | A | 1610 | 151.022 |
| 1023 | 7-Apr-06 | 606616 | 5007299 | County Line | F | A | 1806 | 151.033 |
| 1024 | 7-Apr-06 | 606053 | 5006751 | County Line | F | A | 1590 | 150.503 |
| 1025 | 7-Apr-06 | 605932 | 5006832 | County Line | F | A | 1642 | 150.703 |
| 1026 | 7-Apr-06 | 605849 | 5006714 | County Line | F | A | 1634 | 150.714 |
| 1027 | 8-Apr-06 | 623462 | 4994283 | McFarland | F | A | 1756 | 150.732 |
| 1028 | 8-Apr-06 | 623243 | 4995268 | McFarland | F | A | 1738 | 150.973 |
| 1029 | 8-Apr-06 | 623243 | 4995268 | McFarland | F | Y | 1470 | 150.764 |
| 1030 | 8-Apr-06 | 623494 | 4994808 | McFarland | F | A | 1606 | 150.772 |
| 1031 | 9-Apr-06 | 583034 | 4972327 | Crago | F | Y | 1472 | 150.785 |
| 1032 | 9-Apr-06 | 581219 | 4969831 | Rumph | F | Y | 1628 | 150.804 |
| 1033 | 9-Apr-06 | 581315 | 4969863 | Rumph | F | Y | 1613 | 150.812 |
| 1034 | 9-Apr-06 | 581512 | 4969966 | Rumph | F | A | 1636 | 151.333 |
| 1035 | 9-Apr-06 | 581403 | 4970033 | Rumph | F | A | 1782 | 151.343 |
| 1036 | 9-Apr-06 | 583487 | 4972092 | Crago | F | Y | 1544 | 151.353 |
| 1037 | 9-Apr-06 | 594466 | 4990149 | Widdoss | F | A | 1690 | 151.362 |
| 1038 | 10-Apr-06 | 605130 | 4983164 | Two Top | F | Y | 1658 | 151.375 |
| 1039 | 10-Apr-06 | 604967 | 4983102 | Two Top | F | Y | 1594 | 151.382 |
| 1040 | 10-Apr-06 | 604946 | 4983024 | Two Top | F | Y | 1480 | 151.393 |
| 1041 | 17-Jul-06 | 626931 | 4986394 | Quad 7 | unk | C | 558 | 150.024 |
| 1042 | 17-Jul-06 | 626931 | 4986394 | Quad 7 | unk | C | 422 | 151.553 |
| 1043 | 17-Jul-06 | 626931 | 4986394 | Quad 7 | unk | C | 468 | 151.533 |
| 1044 | 17-Jul-06 | 617726 | 4993470 | McFarland | unk | C | 466 | 150.993 |
| 1045 | 17-Jul-06 | 617726 | 4993470 | McFarland | unk | C | 664 | 151.442 |
| 1046 | 17-Jul-06 | 617726 | 4993470 | McFarland | unk | C | 476 | 151.422 |
| 1047 | 18-Jul-06 | 602067 | 4986019 | Widdoss | unk | C | 490 | 150.573 |
| 1048 | 18-Jul-06 | 600432 | 4986227 | Widdoss | unk | C | 576 | 150.654 |

Appendix 3. cont.

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 1049 | 18-Jul-06 | 600432 | 4986227 | Widdoss | unk | C | 698 | 151.503 |
| 1050 | 18-Jul-06 | 600512 | 4987086 | Widdoss | unk | C | 338 | 151.151 |
| 1051 | 18-Jul-06 | 600512 | 4987086 | Widdoss | unk | C | 432 | 151.524 |
| 1052 | 18-Jul-06 | 600512 | 4987086 | Widdoss | unk | C | 600 | 151.245 |
| 1053 | 18-Jul-06 | 600512 | 4987086 | Widdoss | unk | C | 466 | 151.524 |
| 1054 | 18-Jul-06 | 596981 | 4987357 | Widdoss | unk | C | 646 | 151.562 |
| 1055 | 18-Jul-06 | 596981 | 4987357 | Widdoss | unk | C | 838 | 151.483 |
| 1056 | 17-Jul-06 | 617726 | 4993470 | McFarland | F | A | 1362 | 151.413 |
| 1057 | 18-Jul-06 | 596981 | 4987357 | Widdoss | unk | C | 812 | 151.543 |
| 1058 | 18-Jul-06 | 596981 | 4987357 | Widdoss | unk | C | 816 | 151.094 |
| 1059 | 18-Jul-06 | 596981 | 4987357 | Widdoss | unk | C | 644 | 151.533 |
| 1060 | 19-Jul-06 | 606966 | 4983857 | Two Top | unk | C | 642 | 151.713 |
| 1061 | 19-Jul-06 | 606966 | 4983857 | Two Top | unk | C | 628 | 151.453 |
| 1062 | 20-Jul-06 | 600796 | 4987123 | Widdoss | unk | C | 552 | 151.733 |
| 1063 | 31-Jul-06 | 599438 | 4991214 | Widdoss | unk | C | 430 | 150.284 |
| 1064 | 31-Jul-06 | 599438 | 4991214 | Widdoss | unk | C | 396 | 150.303 |
| 1065 | 2-Aug-06 | 606586 | 5004830 | County Line | unk | C | 566 | 151.043 |
| 1066 | 10-Aug-06 | 600069 | 5012561 | Split Lek | unk | C | 602 | 150.443 |
| 1067 | 10-Aug-06 | 600069 | 5012561 | Split Lek | unk | C | 494 | 150.524 |
| 1069 | 19-Jul-07 | 600206 | 4986435 | Two Top | M | C | 612 | 151.942 |
| 1070 | 19-Jul-07 | 600206 | 4986435 | Two Top | unk | C | 486 | 151.803 |
| 1071 | 19-Jul-07 | 600206 | 4986435 | Two Top | unk | C | 552 | 151.755 |
| 1072 | 19-Jul-07 | 600206 | 4986435 | Two Top | unk | C | 656 | 151.763 |
| 1073 | 19-Jul-07 | 600206 | 4986435 | Two Top | unk | C | 510 | 151.783 |
| 1074 | 19-Jul-07 | 600206 | 4986435 | Two Top | M | C | 552 | 151.934 |
| 1077 | 19-Jul-06 | 569728 | 4980943 | State Line | unk | C | 630 | 150.402 |
| 1078 | 19-Jul-06 | 569728 | 4980943 | State Line | unk | C | 500 | 150.127 |
| 1079 | 19-Jul-06 | 569728 | 4980943 | State Line | unk | C | 662 | 150.022 |
| 1080 | 31-Jul-06 | 570999 | 4978754 | State Line | unk | C | 420 | 150.163 |
| 1081 | 31-Jul-06 | 570999 | 4978754 | State Line | unk | C | 460 | 150.742 |
| 1082 | 20-Jul-06 | 600777 | 4987058 | Widdoss | unk | C | 632 | N/A |
| 1083 | 20-Jul-06 | 600777 | 4987058 | Widdoss | unk | C | 520 | N/A |
| 1084 | 20-Jul-06 | 600777 | 4987058 | Widdoss | unk | C | 584 | N/A |
| 1085 | 20-Jul-06 | 600234 | 4986337 | Widdoss | unk | C | 568 | N/A |
| 1086 | 20-Jul-06 | 600234 | 4986337 | Widdoss | unk | C | 626 | N/A |
| 1087 | 20-Jul-06 | 600234 | 4986337 | Widdoss | unk | C | 642 | N/A |
| 1088 | 20-Jul-06 | 600234 | 4986337 | Widdoss | unk | C | 640 | N/A |
| 1090 | 22-Aug-06 | 603221 | 4985402 | Widdoss | unk | C | N/A | N/A |
| 1092 | 22-Aug-06 | 603221 | 4985402 | Widdoss | unk | C | N/A | N/A |
| 1093 | 22-Aug-06 | 603221 | 4985402 | Widdoss | unk | C | N/A | N/A |
| 1094 | 22-Aug-06 | 603221 | 4985402 | Widdoss | F | Y | N/A | N/A |
| 1095 | 22-Aug-06 | 603221 | 4985402 | Widdoss | F | C | N/A | 151.123 |
| 1096 | 22-Aug-06 | 603221 | 4985402 | Widdoss | unk | C | N/A | N/A |
| 1097 | 20-Mar-07 | 624299 | 4994777 | McFarland | F | Y | 1566 | 150.984 |
| 1098 | 21-Mar-07 | 585688 | 4972089 | Crago | F | Y | 1474 | 150.954 |
| 1099 | 20-Mar-07 | 628371 | 4995961 | Quad 7 | F | A | N/A | N/A |
| 1100 | 21-Mar-07 | 624274 | 4994608 | McFarland | F | A | N/A | N/A |
| 1101 | 22-Mar-07 | 603438 | 5007080 | County Line | F | Y | 1492 | 151.002 |
| 1102 | 22-Mar-07 | 585462 | 4970879 | Crago | F | A | N/A | N/A |
| 1103 | 26-Mar-07 | 594427 | 4989883 | Widdoss | F | Y | 1396 | 151.053 |
| 1104 | 26-Mar-07 | 594408 | 4989863 | Widdoss | F | A | 1684 | 151.064 |
| 1105 | 1-Apr-07 | unk | unk | unk | F | unk | unk | N/A |

Appendix 3. cont.

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 1106 | 1-Apr-07 | unk | unk | unk | F | unk | unk | N/A |
| 1107 | 1-Apr-07 | unk | unk | unk | F | unk | unk | N/A |
| 1108 | 1-Apr-07 | unk | unk | unk | F | unk | unk | N/A |
| 1109 | 23-Mar-07 | 605528 | 4982812 | Two Top | F | A | N/A | N/A |
| 1110 | 26-Mar-07 | 594255 | 5990427 | Widdoss | F | Y | 1498 | 151.103 |
| 1111 | 26-Mar-07 | 593709 | 4990683 | Widdoss | F | A | 1634 | 151.115 |
| 1112 | 26-Mar-07 | 593709 | 4990683 | Widdoss | F | Y | 1552 | 151.133 |
| 1119 | 19-Jul-07 | 603730 | 4988165 | Two Top | unk | C | 560 | 151.133 |
| 1120 | 19-Jul-07 | 603730 | 4988165 | Two Top | unk | C | 380 | 150.624 |
| 1121 | 19-Jul-07 | 603730 | 4988165 | Two Top | unk | C | 422 | 150.064 |
| 1122 | 19-Jul-07 | 606678 | 4984369 | Two Top | unk | C | 798 | 150.643 |
| 1123 | 19-Jul-07 | 606678 | 4984369 | Two Top | unk | C | 774 | 150.673 |
| 1124 | 19-Jul-07 | 606678 | 4984369 | Two Top | unk | C | 772 | 150.683 |
| 1125 | 19-Jul-07 | 606678 | 4984369 | Two Top | unk | C | 812 | 151.824 |
| 1126 | 23-Jul-07 | 580091 | 4970734 | South Owl | unk | C | 590 | 150.722 |
| 1127 | 23-Jul-07 | 589059 | 4991119 | Widdoss | unk | C | 532 | 150.793 |
| 1128 | 23-Jul-07 | 589059 | 4991119 | Widdoss | unk | C | 506 | 150.824 |
| 1129 | 23-Jul-07 | 589059 | 4991119 | Widdoss | unk | C | 682 | 150.833 |
| 1130 | 23-Jul-07 | 589059 | 4991119 | Widdoss | unk | C | 562 | 150.764 |
| 1131 | 24-Jul-07 | 606022 | 5009500 | County Line | unk | C | 602 | 150.373 |
| 1132 | 24-Jul-07 | 592056 | 4990220 | Widdoss | unk | C | 914 | 151.895 |
| 1133 | 24-Jul-07 | 600496 | 4985607 | Two Top | unk | C | 874 | 150.873 |
| 1134 | 2-Aug-07 | 608346 | 5002699 | County Line | unk | C | 966 | 150.883 |
| 1135 | 2-Aug-07 | 606150 | 5009419 | County Line | unk | C | 554 | 150.914 |
| 1136 | 7-Aug-07 | 594637 | 4987901 | Widdoss | unk | C | 566 | 150.923 |
| 1151 | 24-Oct-07 | 605829 | 5006655 | County Line | M | C | 2252 | 151.583 |
| 1152 | 24-Oct-07 | 595309 | 4988513 | Widdoss | F | A | 1500 | 151.393 |
| 1153 | 24-Oct-07 | 595420 | 4988559 | Widdoss | F | A | 1544 | 150.094 |
| 1154 | 24-Oct-07 | 605921 | 5006498 | County Line | F | A | 1496 | 151.363 |
| 1155 | 24-Oct-07 | 605844 | 5006720 | County Line | F | A | 1476 | 150.973 |
| 1501 | 31-Mar-06 | 583997 | 4972302 | Crago | M | A | 3040 | 151.036 |
| 1502 | 4-Apr-06 | 623572 | 4994708 | McFarland | M | A | 2920 | 151.194 |
| 1503 | 10-Apr-06 | 604849 | 4982804 | Two Top | M | A | 3320 | 151.574 |
| 1504 | 10-Apr-06 | 604701 | 4983175 | Two Top | M | A | 3216 | 151.585 |
| 1505 | 10-Apr-06 | 604879 | 4982796 | Two Top | M | A | 3304 | 151.594 |
| 1506 | 4-May-06 | 606663 | 5006951 | County Line | M | A | 3058 | 151.604 |
| 1507 | 4-May-06 | 606476 | 5006526 | County Line | M | A | 3048 | 151.614 |
| 1508 | 4-May-06 | 606663 | 5006951 | McFarland | M | A | 3022 | 151.962 |
| 1509 | 4-May-06 | 624042 | 4994699 | McFarland | M | A | 3094 | 151.973 |
| 1510 | 4-May-06 | 606508 | 5007060 | County Line | M | A | 2962 | 151.645 |
| 1511 | 5-May-06 | 583496 | 4972516 | Crago | M | A | 3040 | 151.655 |
| 1512 | 5-May-06 | 583783 | 4972382 | Crago | M | A | 3254 | 151.664 |
| 1513 | 5-May-06 | 581257 | 4969846 | Rumph | M | A | 2954 | 151.675 |
| 1514 | 5-May-06 | 594613 | 4989913 | Widdoss | M | A | 3078 | 151.983 |
| 1515 | 5-May-06 | 594548 | 4989957 | Widdoss | M | A | 3206 | 151.994 |
| 1516 | 5-May-06 | 594573 | 4989618 | Widdoss | M | A | 3044 | 151.036 |
| 1517 | 5-May-06 | 594437 | 4989670 | Widdoss | M | A | 3066 | N/A |
| 1518 | 5-May-06 | 594393 | 4989788 | Widdoss | M | A | 3010 | N/A |
| 1519 | 5-May-06 | 594605 | 4989797 | Widdoss | M | A | 3030 | N/A |
| 1520 | 20-Mar-07 | 624060 | 4994448 | McFarland | M | A | 3344 | 151.982 |
| 1522 | 26-Mar-07 | 594402 | 4989990 | Widdoss | M | A | 3140 | 151.803 |
| 1523 | 26-Mar-07 | 593674 | 4989252 | Widdoss | M | Y | 2378 | 151.813 |

Appendix 3. cont.

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 1524 | 26-Mar-07 | 594499 | 4989909 | Widdoss | M | A | 3124 | 151.824 |
| 1525 | 26-Mar-07 | 594409 | 4989727 | Widdoss | M | A | 3206 | 151.834 |
| 1526 | 8-May-07 | 606576 | 5006401 | County Line | M | A | 2932 | 151.843 |
| 1527 | 8-May-07 | 606581 | 5006401 | County Line | M | Y | 2302 | 151.854 |
| 1528 | 8-May-07 | 606648 | 5006757 | County Line | M | A | 2762 | 151.883 |
| 1529 | 8-May-07 | 606649 | 5006756 | County Line | M | Y | 2174 | 151.903 |
| 1530 | 10-Apr-07 | 583326 | 4972901 | Crago | M | A | 3234 | 151.914 |
| 1531 | 10-Apr-07 | 583278 | 4972599 | Crago | M | Y | 2752 | 151.923 |
| 1532 | 10-Apr-07 | 583280 | 4972594 | Crago | M | Y | 2550 | 151.934 |
| 1533 | 6-Apr-07 | 623766 | 4994869 | McFarland | M | A | 3138 | 151.942 |
| 1534 | 6-Apr-07 | 623813 | 4994912 | McFarland | M | A | 3046 | 151.956 |
| 1535 | 10-Apr-07 | 583324 | 4972905 | Crago | M | A | 2958 | 151.895 |
| 1536 | 8-May-07 | 632577 | 5029924 | Squaw Creek | M | A | 3230 | N/A |
| 1537 | 8-May-07 | 632419 | 5029864 | Squaw Creek | M | A | 2804 | N/A |
| 1538 | 8-May-07 | 632427 | 5029824 | Squaw Creek | M | A | 3146 | N/A |
| 1539 | 8-May-07 | 632308 | 5029856 | Squaw Creek | M | A | 3051 | N/A |
| 1540 | 8-May-07 | 632283 | 5029860 | Squaw Creek | M | A | 3190 | N/A |
| 1541 | 8-May-07 | 632251 | 5029908 | Squaw Creek | M | A | 2962 | N/A |
| 1542 | 8-May-07 | 632296 | 5029969 | Squaw Creek | M | A | 2500 | N/A |
| 1543 | 8-May-07 | 632281 | 5029958 | Squaw Creek | M | A | 2900 | N/A |
| 1544 | 8-May-07 | 632356 | 5029936 | Squaw Creek | M | A | 3190 | N/A |
| 1545 | 8-May-07 | 632099 | 5029946 | Squaw Creek | M | A | 2806 | N/A |
| 1546 | 8-May-07 | 594446 | 4989880 | Widdoss | M | Y | 2316 | 151.175 |
| 1547 | 9-May-07 | 605043 | 4982559 | Two Top | M | A | 2926 | 151.824 |
| 1548 | 9-May-07 | 583447 | 4972548 | Crago | M | A | 2828 | 151.895 |
| 1549 | 9-May-07 | 583149 | 4972598 | Crago | M | Y | 2310 | 151.914 |
| 1550 | 9-May-07 | 583115 | 4972531 | Crago | M | A | 3134 | 151.923 |
| 1601 | 16-May-06 | 586803 | 5042787 | Valley Creek | M | Y | 2352 | N/A |
| 1604 | 16-May-06 | 586476 | 5042810 | Valley Creek | M | A | 2874 | N/A |
| 1606 | 16-May-06 | 586717 | 5042928 | Valley Creek | M | Y | 2414 | N/A |
| 1607 | 16-May-06 | 586319 | 5042651 | Valley Creek | M | A | 2868 | N/A |
| 1608 | 16-May-06 | 586522 | 5042693 | Valley Creek | M | A | 3170 | N/A |
| 1609 | 16-May-06 | 586685 | 5042726 | Valley Creek | M | A | 3002 | N/A |
| 1610 | 16-May-06 | 586528 | 5042756 | Valley Creek | M | A | 2922 | N/A |
| 1611 | 16-May-06 | 586794 | 5042842 | Valley Creek | M | Y | 2298 | N/A |
| 1612 | 16-May-06 | 586799 | 5042754 | Valley Creek | M | A | 2864 | N/A |
| 1613 | 16-May-06 | 586671 | 5042868 | Valley Creek | M | A | 2918 | N/A |
| 1614 | 16-May-06 | 586660 | 5042780 | Valley Creek | M | A | 2738 | N/A |
| 1615 | 16-May-06 | 586597 | 5042715 | Valley Creek | M | A | 2852 | N/A |
| 1616 | 16-May-06 | 586509 | 5042708 | Valley Creek | M | A | 2990 | N/A |
| 1617 | 16-May-06 | 586433 | 5042659 | Valley Creek | M | A | 2920 | N/A |
| 1618 | 16-May-06 | 586317 | 5042837 | Valley Creek | M | A | 3034 | N/A |
| 1619 | 16-May-06 | 586459 | 5042861 | Valley Creek | M | A | 2896 | N/A |

[a] UTM coordinates in NAD 27, zone 13.
[b] Sex classification are: F-female, M-male, and unk-unknown.
[c] Age classification are: A-adult, Y-yearling, and C-hatch year chick.

# CHAPTER 2 – BROOD-REARING SUCCESS AND RESOURCE SELECTION OF GREATER SAGE-GROUSE IN NORTHWESTERN SOUTH DAKOTA

## INTRODUCTION

Knowledge of seasonal habitat selection and associated survival is important in developing management strategies for sensitive wildlife species. Concerns that greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) populations may be declining, date back > 90 years (Hornaday 1916). In the past decade, at least seven petitions have been filed to list sage-grouse under the Endangered Species Act (ESA) of 1973 (Connelly et al. 2004). More recently, data suggest that sage-grouse populations have declined range-wide at a rate of 2.0% per year since 1965 (Connelly et al. 2004). Sage-grouse population estimates in South Dakota declined steadily from 1973 to 1997, but appeared to recover some from 1997 to 2002 (Smith 2003, Connelly et al. 2004). However, the data in South Dakota were inconsistent and firm conclusions could not be made (Connelly et al. 2004). In addition, information is lacking on the ecological requirements of sage-grouse in western South Dakota.

Initial sage-grouse brood-rearing sites are typically in close proximity of nest sites and must provide high invertebrate abundance and diversity. Invertebrates are necessary for growth, development and survival of sage-grouse chicks (Johnson and Boyce 1990). Invertebrates continue to be important in the development and survival of sage-grouse chicks >3 weeks of age (Johnson and Boyce 1990), as chicks include greater amounts of forbs in their diet after 3 weeks (Klebenow and Gray 1968). Chicks that fed in forb-rich habitats gained more weight than when they fed in forb-poor habitats (Huwer 2004) and

areas with greater forb cover may attract higher numbers of invertebrates (Jamison et al. 2002). Greater invertebrate abundance may explain why sage-grouse tend to select areas with higher forb cover (Drut et al. 1994*a*, Apa 1998, Sveum et al. 1998, Holloran 1999).

Estimates of sage-grouse chick survival are limited, and have not been based on standardized time periods, thus making comparisons among studies difficult (Beck et al. 2006). Chick survival during the first 50 days post-hatch is generally low ranging from 18 – 33% (Schroeder 1997, Aldridge and Brigham 2001). Juvenile sage-grouse survival is greater ranging from 64% to 86% for chicks 10 weeks old to about 40 weeks (Beck et al. 2006). Combined, survival from hatch to first breeding season is estimated to be about 10% (Crawford et al. 2004). To our knowledge, no study has attempted, or been able to follow sage-grouse chicks from hatch to recruitment of 1 March.

Sage-grouse in northwestern South Dakota occupy transitional habitats between the northern wheatgrass-needlegrass prairie that dominates most of the Dakotas and the big sagebrush plains of Wyoming (Johnson and Larson 1999). In South Dakota, sage-grouse are imperiled because of rarity or some factor(s) making them very vulnerable to extinction within the state (South Dakota Department of Game, Fish, and Parks 2006). The objectives of this study were to develop an understanding of brood-rearing survival, home range, and resource selection of sage-grouse in northwestern South Dakota. This information will be useful in developing conservation and management plans for sage-grouse in South Dakota and other eastern fringe populations.

## METHODS

### Data Collection

*Female Capture* – We identified six active sage-grouse leks for which we had landowner cooperation for trapping. We captured female sage-grouse with large nets by spotlighting from all-terrain vehicles between March 2006-2007 and mid-April 2006-2007 (Giesen et al. 1982). Females were weighed and equipped with a 22-g necklace-style transmitter, which were ~1.4% of mean female sage-grouse body mass and a life-expectancy of 434 days. Transmitters could be detected from approximately 2.0 to 5.0 km from the ground and were equipped with an 8-hour mortality switch. Females were classified as adults (≥2 yr old) or yearlings (≤1 yr old) based upon primary wing feather characteristics (Eng 1955, Crunden 1963). The South Dakota State University Institutional Animal Care and Use Committee approved trapping and handling techniques, and study design (Approval #07-A032).

*Monitoring and Chick Capture* – We located radio-marked female sage-grouse twice each week throughout the nesting season. For hens that successfully nested, we located these hens and broods twice each week. Broods were approached cautiously to minimize the possibility of flushing or scattering the brood, with most locations being acquired within 20 m of actual locations. When chicks reached approximately 3 and 5 weeks of age we flushed the brood and searched the area to obtain estimates of brood size. We recorded the site as brood failure if no chicks were present with a hen, and subsequent locations of the hen for 2 weeks showed no evidence of chicks.

At 7 weeks of age, we attempted to capture and radio-mark as many chicks in each remaining brood as possible. Aided by radio-telemetry of the female, chicks were captured at night by a 3-5 person crew using a spotlight. We counted chicks that flew off during chick capture to estimate survival to 7 weeks of age. Chicks were weighed and equipped with a 10.7 g necklace style transmitter with mortality indicator which weighed <3% of mean chick body mass at the time of capture. These transmitters had a guaranteed life-expectancy of 150 days. The South Dakota State University Institutional Animal Care and Use Committee approved all trapping and handling techniques and study design (Approval #07-A032).

We located radio-marked chicks twice each week to obtain survival estimates. Field necropsies were conducted to identify primary predators. Dead birds that yielded testable carcasses (i.e., brain, wing or leg bones, internal organs, or spinal column present) were tested for West Nile virus (WNv) infections using real-time polymerase chain reaction (Shi 2001) and immunohistochemistry (Kiupel et al. 2003).

*Habitat Measurements* - We characterized vegetation at sites used by females with broods about 12.6 ± 0.6 days after the location. Two 50 m transects were established in the north-south cardinal directions. A modified Robel pole (Robel et al. 1970, Benkobi et al. 2000) was used to quantify visual obstruction readings (VOR) and maximum grass height at 10 m intervals ($n$ = 11). We estimated sagebrush (*Artemisia. tridentata spp.* and *A. cana spp.*) density and height at 10 m intervals ($n$ = 11) using the point-centered-quarter method (Cottam and Curtis 1956). Canopy coverage was estimated using a 0.10 $m^2$ quadrat (Daubenmire 1959) at each 10 m interval. Four

Daubenmire frames were placed at the interval in an H-shape with each leg 1 m long, resulting in 44 quadrats per site. We recorded total cover, grass cover, forb cover, shrub cover, litter cover, bare ground, shrub species, grass species, and forb species cover. In addition, we measured an equal number of random sites during the same period. Random points were generated within a 10 km buffer of capture leks in a Geographic Information System (GIS) (ESRI, Inc. ArcMap 9.1, Redlands, CA.). Random points were not sampled if they were on a road, in a road ditch, or on private land we did not have access.

**Data Analyses**

*Survival* – We estimated apparent survival for chicks at 3, 5, and 7 weeks of age. Mean hatch date of first nests (31 May) was used as the starting point for chick survival. Broods <7 weeks old were censored from the analysis if we witnessed brood-mixing (>1 female present), or chick-adoption (more chicks present than hatched). If the female died before chicks reached 7 weeks of age, we assumed complete brood loss. For chicks that were radio-marked at 7 weeks, we used a Kaplan-Meier product-limit method (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989) starting at the 7-week apparent survival rate. We monitored chicks at least once each week until they were recruited into the population (1 March). We used Program CONTRAST (Hines and Sauer 1989) to test for differences between years, with a critical value of $\alpha \leq 0.05$.

Because some carcasses of chicks were not suitable for testing for WNv infections, we estimated a minimum and maximum WNv mortality rate during the peak WNv transmission period of 12 July through 31 September for chicks (Walker et al. 2007). Minimum mortality rates were based on confirmed WNv mortalities, while maximum

mortality rates were based on total mortalities minus negative cases and included mortalities where the carcass was not testable, no carcass was recovered and inconclusive tests (Walker et al. 2007).

*Brood Home Range* – We used the home range extension (Rodgers et al. 2007) in a Geographic Information System (GIS) (ESRI, Inc. ArcMap 9.1, Redlands, CA.) to calculate 50% and 95% adaptive kernel brood-rearing home ranges. Home ranges were estimated for broods with at least 18 locations between hatch and 31 August. If a female was monitored both years, only the home range with the most points was used to reduce dependency in our data set.

*Resource Selection* – All measurements were summarized to a value for the site. Sagebrush density and height was estimated from a maximum likelihood estimate (Pollard 1971). Canopy coverage values were to mid-point values of categories and summarized to an average value for the site. To reduce biologically insignificant variables, we screened canopy coverage variables and excluded any variables with canopy coverage less than 2% on sites which they were present. We then conducted a principal components analysis to distinguish important variables that captured the variation among sites. We could not discriminate between early (<5 weeks of age) and late brood sites (5 to 11 weeks of age), thus we combined early and late brood-rearing sites to test for overall habitat selection.

We identified 8 variables (Table 8) with a year effect to investigate sage-grouse brood habitat resource selection. These included: sagebrush density, visual obstruction, maximum grass height, total cover, grass cover, sagebrush cover, bluegrass (*Poa spp.*)

cover, and Japanese brome (*Bromus japanicus*) cover. Year was considered a design variable in all candidate models. We used an information theoretic approach (Burnham and Anderson 2002) with nominal logistic regression to estimate the importance of various *a priori* and *post-hoc* exploratory models in SAS JMP (2005 SAS Institute Inc.). Due to a small sample size with respect to the number of parameters estimated, AIC*c* (Akaike's Information Criterion) was used. Model predictive strength was estimated using a receiver operation characteristic curve (ROC) with values between 0.7 and 0.8 considered as acceptable discrimination and values higher than 0.8 were considered excellent discrimination (Hosmer and Lemeshow 2000).

**RESULTS**

**Chick Survival**

We monitored 10 and 14 broods in 2006 and 2007, respectively. Survival at 3 weeks post hatch was similar between years at 52%. Apparent chick survival to 7 weeks post-hatch, ranged between years from 31% in 2007 to 43% in 2006 (Table 9). Recruitment was estimated to be 9.5% (95% CI: 2.8 to 16.1%, $n$ =31) in 2006 (Figure 8) and 5.1% (95% CI: 0 to 10.1%, $n$ =24) in 2007 (Figure 9). There was no statistical difference between years ($x^2$ = 1.09, df = 1, $P$ = 0.30), and combined recruitment for both years was 6.3% (95% CI: 2.7 – 9.9%, $n$ = 55). Mortalities were attributed to WNv infections and predation by red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), long-tailed weasels (*Mustela frenata*), and red-tailed hawks (*Buteo jamaicensis*).

Between 12 July and 31 September, WNv infection was attributed ≥ 6.5% (95% CI: 0 – 15.1%, *n* =31) of chick mortalities in 2006, but may have caused up to 71.0% (95% CI: 55.0 – 86.9%, *n* =31) of mortalities (Table 10). In 2007 the minimum WNv mortality rate was 20.8% (95% CI: 4.6 – 37.1%, *n* =24) which did not differ from 2006 ($x^2 = 2.32$, df = 1, $P = 0.13$). Maximum WNv mortality rate for 2007 was 62.5% (95% CI: 43.1 – 8.19%, *n* =21), which also did not differ from 2006 ($x^2 = 0.42$, df = 1, $P = 0.52$).

**Brood-rearing Home Range**

We estimated home ranges for 15 broods. Mean 50% adaptive kernel home range was 7.59 ± 2.35 km$^2$ and did not vary between years ($x^2 = 1.498$, df = 1, $P = 0.221$). Mean 95% adaptive kernel home range was 51.81 ± 16.31 km$^2$ and did not vary between years ($x^2 = 1.279$, df = 1, $P = 0.258$). The largest estimated 50 and 95% adaptive kernel home ranges were 31.39 km$^2$ and 201.76 km$^2$ ($n = 21$), respectively, while the smallest home ranges were 0.22 km$^2$ ($n = 22$) and 1.48 km$^2$, respectively.

**Resource Selection**

We sampled 59 and 60 brood sites and 56 and 60 random sites in mid June through August 2006 and 2007, respectively. All variables were significantly different between years for either brood or random sites, thus we applied a design variable, year, to all logistic models (Table 11). Brood-rearing sites had higher visual obstruction, taller grass heights, greater total cover, grass cover, sagebrush cover, Japanese brome cover, and bluegrass cover than random sites (Table 8). In contrast, sagebrush density was higher at random sites. The best approximating model (AIC*c* weight = 0.23) indicated

visual obstruction and bluegrass cover to be the best habitat predictors for brood-rearing sites (Table 11). The addition of other non-correlated habitat variables to the top model (sagebrush cover, sagebrush density, or Japanese brome), did not increase model fit. Model discrimination was acceptable with a ROC value of 0.73.

Both visual obstruction and bluegrass cover positively influenced brood-rearing site selection as parameter estimates were positive (Table 12), with visual obstruction having a slightly larger impact (Figure 10). Broods were 3.06 times (95% CI: 2.84– 3.34) more likely to select an area if visual obstruction increased by 2.54 cm, and 5.61 times (95% CI: 5.15 – 6.13) more likely to select an area if bluegrass cover increased by 5% canopy cover.

## DISCUSSION

### Survival

Survival of sage-grouse chicks to 3 to 4 weeks of age is generally low, ranging from 22 to 50% (Burkepile et al. 2002, Aldridge 2005, Gregg et al. 2007, Herman-Brunson 2007). We did not attach transmitters to sage-grouse chicks <1 week, but our estimated survival rate to 3 weeks (52%) was among the highest reported. Sage-grouse chick survival to 7 weeks (34%) in our study was higher than reported for a declining population in Alberta (Aldridge and Brigham 2001, Aldridge 2005), but similar to a stable population in Washington (Schroeder 1997). Our estimate to 7 weeks is conservative, as flush counts may underestimate chick survival (Aldridge and Brigham 2001). We feel that our 7 week survival estimate is fairly accurate as it was conducted at night when broods tend to group together, and the count was always conducted by at least

3 people. Furthermore, survival rates between flush counts and telemetry estimates for sage-grouse chicks at approximately 8 weeks of age have been documented to be similar (Aldridge 2005). Aldridge (2005) suggested that accuracy of flush counts increase as chicks become larger in size, making them easier to locate and flush.

Survival of sage-grouse chicks from 10 weeks through the following March, ranges from 64 to 86% (Beck et al. 2006). Sage-grouse chick survival to 1 January in North Dakota was 13 to 17% (Herman-Brunson 2007). However, our data suggest that chick survival to recruitment would be half that. Although seemingly low, our recruitment rate of 6% suggests that the index of recruitment by Crawford et al. (2004) was realistic. However, West Nile virus infections in 2006 decreased chick recruitment the next spring by about 2%. In 2007, WNv decreased chick recruitment by approximately 4%.

Using our estimates of nest initiation (95.9%), breeding success (47.9%), clutch size (8.0), egg hatchability (78.3%), 1:1 sex ratio, and recruitment rates of 5.1 and 9.5%, annual survival of adult hens would need to be 93 to 86% to maintain a stable population, respectively. If recruitment increased to 15 or 20%, hen survival necessary for a stable population would be lower at 78 and 71%, respectively. The latter estimate may be more reasonable for sage-grouse populations as annual female survival varies from 37 to 78% (Connelly et al. 2004). However, fluctuations of nesting parameters and recruitment could substantially alter these estimates, but chick recruitment of >10% should help maintain stable populations even in years with poor nesting success or extreme WNv infections.

**Brood-rearing Home Range**

Few studies have attempted to quantify brood-rearing home ranges for sage-grouse (Wallestad 1971, Connelly and Markham 1983, Drut et al. 1994*a*). However, home range estimates have ranged widely from 0.51 $km^2$ (Wallestad 1971) to 51.00 $km^2$, Drut et al. 1994*a*). Differences in home range size have been suggested to be related to forb availability with home ranges being both smaller and larger in areas with increased forb abundance (Drut et al. 1994*a*, Connelly and Markham 1983). However, forbs did not appear to be an important predictor variable in our analyses, suggesting other variables (e.g., visual obstruction, sagebrush distribution) may better explain why home range estimates in South Dakota were rather large.

**Resource Selection**

Visual obstruction and bluegrass cover were identified to be the best variables at predicting brood-rearing sites for sage-grouse in South Dakota. Increased visual obstruction provides protection from predators, and perhaps more importantly, greater herbaceous biomass which is correlated with greater invertebrate abundance (Healy 1985, Rumble and Anderson 1996). Invertebrates are an important component of sage-grouse chicks' diets (Johnson and Boyce 1990, Drut et al. 1994*b*). Female sage-grouse tend to move their broods from upland, nesting-type areas, to more mesic, greener areas later in the summer (Peterson 1970, Dunn and Braun 1986, Sveum et al. 1998). Adapted to a broad range of soils, bluegrass is common on sites with abundant soil moisture in South Dakota (Stubbendieck et al. 1997). Although we were not able to differentiate between early and late brood-rearing habitats, broods may be selecting areas with greater

bluegrass cover for the increased invertebrate abundance that greener areas tend to provide.

Sage-grouse brood-rearing habitats are generally linked to forb abundance (Drut et al. 1994a, Apa 1998, Sveum et al. 1998, Holloran 1999). Forbs not only provide direct food resources (Drut et al. 1994*b*), but increased invertebrate abundance (Jamison et al. 2002). We did not note a difference in forb cover between brood (7.6%) and random sites (7.1%), and it was not an important predictor in our analysis, while other studies have shown sage-grouse broods to use areas with forb cover up to 41.3% (Schoenberg 1982). In contrast, females with broods in South Dakota selected areas with higher grass cover that was greater than typically reported in the literature (Klott and Lindzey 1990, Drut et al. 1994*b*, Sveum et al. 1998, Thompson et al. 2006). Western South Dakota forms a transition zone between the northern wheatgrass-needlegrass prairie that dominates most of the Dakotas and the big sagebrush plains of Wyoming (Johnson and Larson 1999), and possesses a greater grass component compared to the shrub-steppe region (Lewis 2004). Grass structure is highly correlated with visual obstruction, which, provides increased protection from predators and invertebrate abundance. Therefore, forbs may be more important to sage-grouse brood-rearing habitat in core sagebrush areas (e.g., Columbia Basin) where there is more bareground, while grass structure may be more important for broods on the eastern edge of their range (e.g., South Dakota). In Alberta, another edge-type habitat, key brood habitat in moist areas and drainages was suggested to be limiting sage-grouse productivity (Aldridge and Brigham 2002).

## MANAGEMENT IMPLICATIONS

With possible listing under the Endangered Species Act, sage-grouse conservation and preservation will be a priority for many western land management agencies. For sage-grouse brood-rearing habitat in western South Dakota and other eastern edge populations, management strategies should focus on maintaining or increasing grass structure (cover and height) which provides high visual obstruction for sage-grouse broods. In addition, managers should promote and protect greener areas during mid to late summer. These areas typically have higher production and invertebrate abundance. This may include government programs that defer or eliminate grazing and haying operations in these areas.

Domestic livestock grazing by cattle (*Bos taurus*) and sheep (*Ovis aries*) has been shown to have both positive and negative impacts on rangeland condition and health in the sagebrush ecosystem (Holechek et al. 2001) and sage-grouse habitats (Beck and Mitchell 2000). Grazing by sheep can be an effective way of reducing sagebrush (Baker et al. 1976) which could negatively affect sage-grouse productivity in South Dakota, particularly during the nesting period. High intensity cattle grazing of the herbaceous understory (grasses and forbs), may allow for greater forb and sagebrush growth (Paige and Ritter 1999) but that may also negatively influence sage-grouse productivity by decreasing plant biomass and protective cover and consequently, reduce insect abundance. However, light or moderate grazing in dense, grassy meadows increased sage-grouse use (Klebenow 1982) but overgrazing of these areas reduced sage-grouse habitat (Klebenow 1985, Oakleaf 1971) and were avoided by sage-grouse (Klebenow 1982).

WNv was an important factor for sage-grouse chick survival. Management practices to mitigate its affect on sage-grouse chick survival appear to be minimal and tied to anthropogenic water sources, particularly coal-bed natural gas ponds (Walker et al. 2007). Unless sage-grouse develop stronger immunity to this disease, their future looks uncertain. However, small increases in chick recruitment, either through increased nesting success or increased chick survival should have positive effects on sage-grouse populations.

With 75% of the study area in private ownership and the patchy network of public land; sage-grouse conservation and persistence lies in hands of private landowners. To increase sage-grouse habitats, long-term (>20 yrs) partnerships and incentives with ranchers will be imperative. This will require cooperation from state wildlife agencies, federal land management agencies, local natural resource conservation districts, and committed landowners. Forming a South Dakota sage-grouse working group may be in order to accomplish this goal, as many landowners were interested in sage-grouse conservation.

Table 8. Observed mean values for habitat variables between greater sage-grouse brood-rearing and random sites, and between years used in logistic regression in northwestern South Dakota, USA, using MRPP (Mielke and Berry 2001) 2006-2007.

| | Brood | | | Random | | | Both Years | | |
|---|---|---|---|---|---|---|---|---|---|
| **Variable** | **2006 (*n*=59)** | **2007 (*n*=60)** | **P-value** | **2006 (*n*=56)** | **2007 (*n*=60)** | **P-value** | **Brood (*n*=119)** | **Random (*n*=116)** | **P-value** |
| Sagebrush Density (plants/$m^2$) | 0.3 | 0.5 | <0.01 | 0.7 | 0.4 | <0.01 | 0.4 | 0.5 | 0.08 |
| Sagebrush Cover (%) | 4.6 | 4.7 | 0.94 | 4.5 | 2.8 | 0.03 | 4.6 | 3.6 | 0.04 |
| Visual Obstruction (cm) | 5.4 | 7.1 | 0.12 | 2.3 | 4.7 | <0.01 | 6.2 | 3.5 | <0.01 |
| Grass Height (cm) | 23.3 | 37.5 | <0.01 | 19.2 | 31.9 | <0.01 | 30.5 | 25.7 | <0.01 |
| Total Cover (%) | 61.3 | 55.6 | <0.01 | 51.0 | 51.0 | 1.00 | 58.4 | 51.0 | <0.01 |
| Grass Cover (%) | 34.4 | 28.3 | <0.01 | 28.6 | 24.8 | 0.26 | 31.3 | 26.6 | <0.01 |
| Japanese Brome Cover (%) | 10.4 | 9.9 | 0.66 | 4.9 | 11.4 | <0.01 | 10.1 | 8.3 | 0.04 |
| Bluegrass Cover (%) | 5.9 | 2.3 | <0.01 | 3.8 | 2.2 | <0.01 | 4.0 | 3.0 | 0.08 |

Table 9. Apparent greater sage-grouse chick survival to 7 weeks post hatch, and recruitment as of 1 March using a Kaplan-Meier product-limit method (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989) in northwestern South Dakota, USA, 2006-2008. Estimated survival rates given as mean (95% CI).

| Year | 3 Week Survival (Apparent) | 5 Week Survival (Apparent) | 7 Week Survival (Apparent) | Recruitment (Apparent + Kaplan-Meier) |
|---|---|---|---|---|
| 2006 | 52.4% ($n$ = 42) | 45.2% ($n$ = 42) | 42.9% ($n$ = 42) | 9.5% (2.8 – 16.1%, $n$ = 31) |
| 2007 | 52.2% ($n$ = 115) | 41.7% ($n$ = 115) | 31.3% ($n$ = 115) | 5.1% (0 – 10.1%, $n$ = 24) |
| Combined | 52.2% ($n$ = 157) | 42.7% ($n$ = 157) | 34.3% ($n$ = 157) | 6.3% (2.7 – 9.9%, $n$ = 55) |

Table 10. West Nile virus (WNv) mortality rates and testing for greater sage-grouse chicks during the peak WNv transmission period (12 July – 31 September) in northwestern South Dakota, USA, 2006-2007. Estimated minimum and maximum mortality given as mean (95% CI) after Walker et al. (2007).

| Year | No. Monitored | No. Mortalities | No. Tested | No. Positive | No. Negative | No. Inconclusive | Minimum WNv mortality rate | Maximum WNv mortality rate |
|---|---|---|---|---|---|---|---|---|
| 2006 | 31 | 22 | 10 | 2 (23 July - 22 Aug.) | 0 | 8 | 6.5% (0 – 15.1%) | 71.0% (55.0 – 86.9%) |
| 2007 | 24 | 18 | 10 | 5 (8 Aug. – 14 Sept.) | 3 | 2 | 20.8% (4.6 – 37.1%) | 62.5% (43.1 – 81.9%) |

Table 11. Results from logistic regression models predicting greater sage-grouse brood-rearing sites ($n$ = 119) versus random sites ($n$ = 116) in northwestern South Dakota, USA, 2006-2007.

| **Model**[a] | **K**[b] | **AIC*c*** | **Δ AIC*c***[c] | ***wi***[d] |
|---|---|---|---|---|
| Visual Obstruction + Bluegrass Cover | 5 | 303.547 | 0.000 | 0.231 |
| Visual Obstruction + Bluegrass Cover + Sagebrush Cover | 6 | 304.275 | 0.728 | 0.160 |
| Visual Obstruction + Bluegrass Cover + Sage Density | 6 | 304.455 | 0.908 | 0.146 |
| Visual Obstruction + Bluegrass Cover + Japanese Brome Cover | 6 | 304.798 | 1.251 | 0.123 |
| Visual Obstruction + Bluegrass Cover + Japanese Brome Cover + Sage Density | 7 | 305.459 | 1.911 | 0.089 |
| Herbaceous Cover + Bluegrass Cover + Grass Height. | 6 | 305.503 | 1.956 | 0.087 |

[a] For ease of interpretation, year variable was excluded from model column. See Appendix 3 for full model results
[b] Number of habitat parameters plus intercept, SE, and year.
[c] Change in AIC*c* value
[d] Model weight

Table 12. Parameter Estimates, odds ratios, and corresponding confidence intervals for the best-approximating model of greater sage-grouse brood-rearing sites versus random sites in northwestern South Dakota, 2006-2007.

| | Parameter | | | Odds | | |
|---|---|---|---|---|---|---|
| **Variable** | **Estimate** | **Lower 95%CI** | **Upper 95%CI** | **Ratio** | **Lower 95%CI** | **Upper 95%CI** |
| Visual Obstruction | 0.186 | 0.110 | 0.272 | 1.204 | 1.116 | 1.313 |
| Bluegrass | 0.114 | 0.029 | 0.204 | 1.121 | 1.029 | 1.226 |

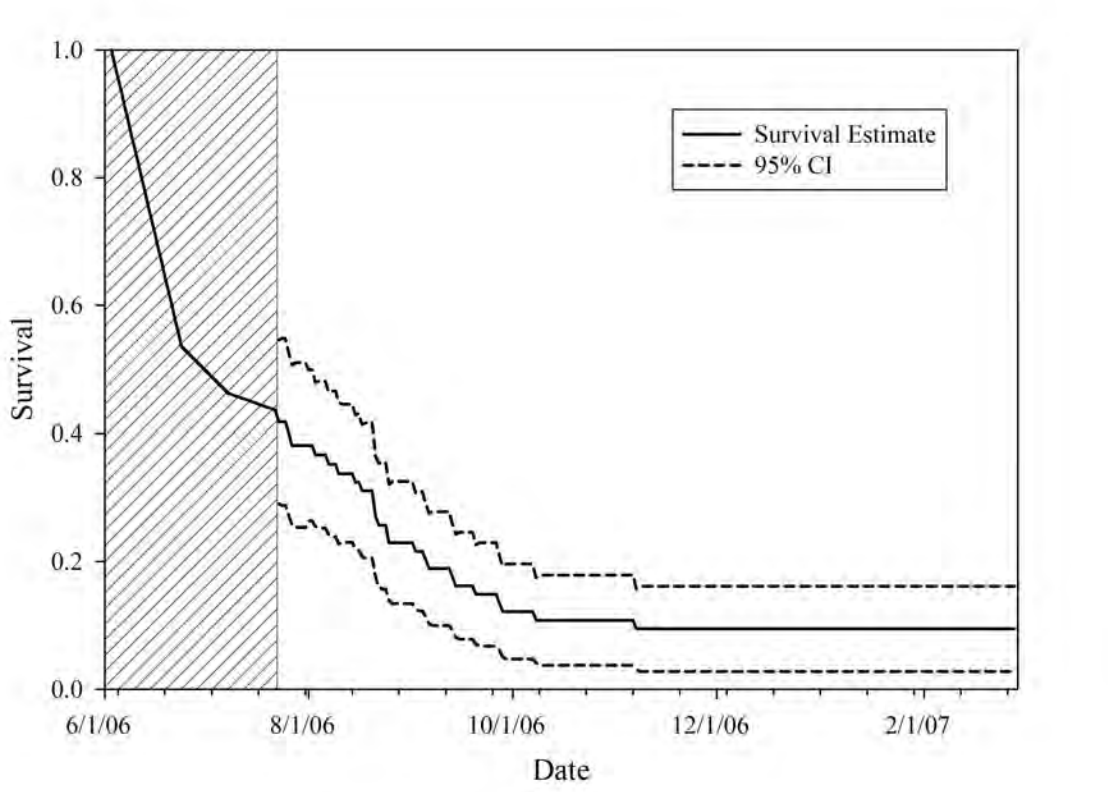



Figure 8. Greater sage-grouse apparent chick survival to 7 weeks post hatch (dashed area), and recruitment as of 1 March 2007 using a Kaplan-Meier product-limit method (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989) in northwestern South Dakota, USA, 2006-2007. A sample size of $n = 31$, was used in the Kaplan-Meier analysis.

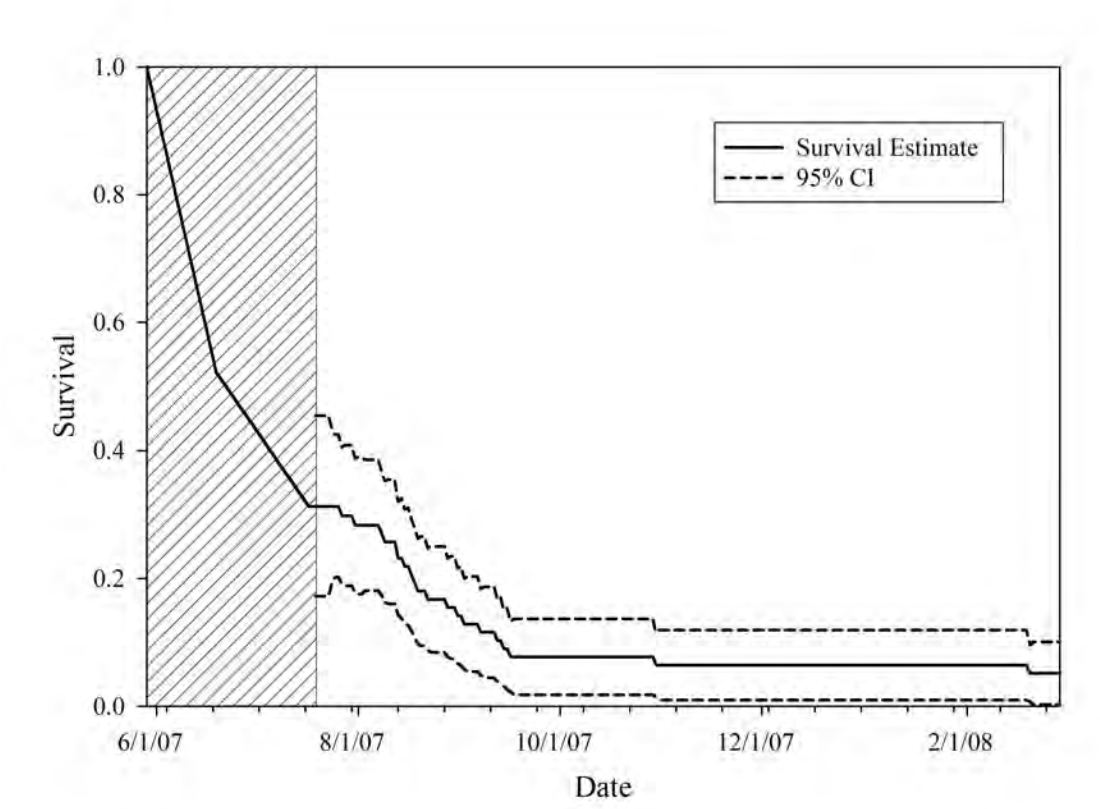



Figure 9. Greater sage-grouse apparent chick survival to 7 weeks post hatch (dashed area), and recruitment as of 1 March 2008 using a Kaplan-Meier product-limit method (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989) in northwestern South Dakota, USA, 2007-2008. A sample size of $n = 24$, was used in the Kaplan-Meier analysis.

**Effect of Visual Obstruction and Bluegrass Cover On Brood-rearing Habitat Selection**

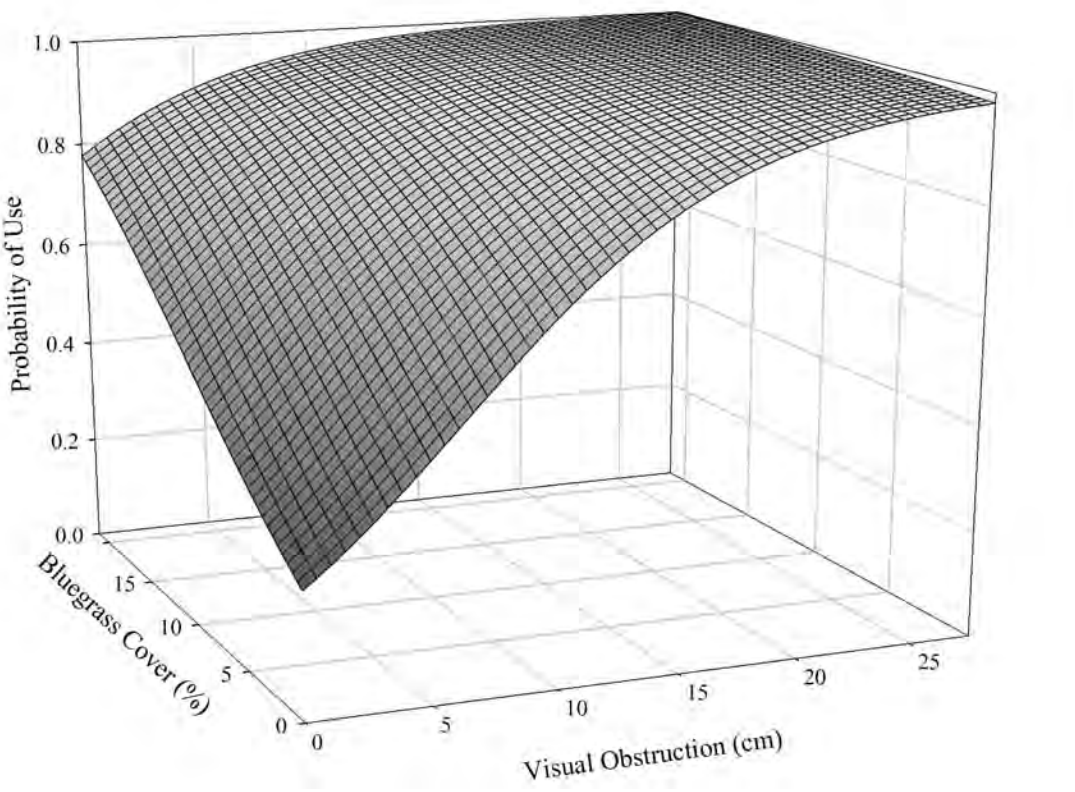



Figure 10. Effect of visual obstruction and bluegrass cover on greater sage-grouse brood-rearing habitat selection in northwestern South Dakota, USA, 2006-2007. Probability of use derived from parameter estimates in best approximated model (visual obstruction + bluegrass cover).

**LITERATURE CITED**

Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation, University of Alberta, Edmonton, Canada.

Aldridge, C. L. and R. M. Brigham. 2001. Nesting and reproductive activities of greater sage-grouse in a declining northern fringe population. Condor 103:537-543.

Aldridge, C. L. and R. M. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Canada. Journal of Wildlife Management 66:433-444.

Apa, A. D. 1998. Habitat use and movements of sympatric sage and Columbian sharp-tailed grouse in southeastern Idaho. Dissertation, University of Idaho, Moscow, USA.

Baker, M. F., R. L. Eng. J. S. Gashwiler, M. H. Schroeder, and C. E. Braun. 1976. Conservation committee report on the effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin 88:165-170.

Beck, J. L., and D. L. Mitchell. 2000. Influences of livestock grazing on sage-grouse habitat. Wildlife Society Bulletin 28:993-1002.

Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070-1078.

Benkobi, L., D. W. Uresk, G. Schenbeck, and R. M. King. 2000. Protocol for monitoring standing crop in grasslands using visual obstruction. Journal of Range Management 53:627-633.

Burkepile, N. A., J. W. Connelly, D. W. Stanley, and K. P. Reese. 2002. Attachment of radiotransmitters to one-day-old sage-grouse chicks. Wildlife Society Bulletin 30:93-96.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Connelly, J. W., and O. D. Markham. 1983. Movements and radionuclide concentrations of sage-grouse in southeastern Idaho. Journal of Wildlife Management 47:169-177.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451-460.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2-19.

Crunden, C. W. 1963. Age and sex of sage grouse from wings. Journal of Wildlife Management 27:846-849.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis, Northwest Science 33:43-64.

Drut, M. S., J. A. Crawford, and M. A. Gregg. 1994*a*. Brood habitat use by sage-grouse in Oregon. Great Basin Naturalist 54:170-176.

Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994*b*. Diets and food selection of sage-grouse chicks in Oregon. Journal of Range Management 47:90-93.

Dunn, P. O., and C. E. Bruan. 1986. Summer habitat use by adult female and juvenile sage-grouse. Journal of Wildlife Management 50:228-235.

Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal of Wildlife Management 19:267-272.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224-231.

Gregg, M. A., M. R. Dunbar, and J. A. Crawford. 2007. Use of implanted radiotransmitters to estimate survival of greater sage-grouse chicks. Journal of Wildlife Management 71:646-651.

Healy, W. M., 1985. Turkey poult feeding activity, invertebrate abundance and vegetation structure. Journal of Wildlife Management 49:466-472.

Herman-Brunson, K. H. 2007. Nesting and brood-rearing habitat selection of Greater sage-grouse and associated survival of hens and broods at the edge of their historic distribution. Thesis, South Dakota State University, Brookings, USA.

Hines, J. E., and J. R. Sauer. 1989. Program CONTRAST - a general program for the analysis of several survival or recovery rate estimates. Fish and Wildlife Technical Report 24:1-7.

Holechek, J. L., R. D. Pieper, and C. H. Herbel. 2001. Range management principles and practices. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Holloran, M. J. 1999. Sage-grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. M.S. Thesis, University of Wyoming, Laramie, USA.

Hornaday, W. T. 1916. Save the sage-grouse from extinction, a demand from civilization to the western states. New York Zoological Park Bulletin 5:179-219.

Hosmer, D. W., and S. Lemeshow. 2000. Applied Logistic Regression, Second Edition. John Wiley and Sons Inc. Publication, New York, NY, USA.

Huwer, S. L. 2004. Evaluating greater sage-grouse brood habitat use using human-imprinted chicks. M.S. Thesis, Colorado State University, Fort Collins, USA.

Jamison, B. E., R. J. Robel, J. S. Pontius, and R. D. Applegate. 2002. Invertebrate biomass: associations with Lesser Prairie Chicken habitat use and sand sagebrush density in southwestern Kansas. Wildlife Society Bulletin. 30:517-526.

Johnson, G. D., and M. S. Boyce. 1990. Feeding trials with insects in the diet of sage-grouse chicks. Journal of Wildlife Management 54:89-91.

Johnson, J. R., and G. E. Larson. 1999. Grassland plants of South Dakota ant the northern Great Plains. South Dakota State University. Brookings, South Dakota, USA.

Kaplan, E., and P. Meier. 1958. Non parametric estimation from incomplete observation. Journal of the American Statistical Association 53:457-481.

Kiupel, M. H., H. A. Simmons, S. D. Fitzgerald, A. Wise, J. G. Sikarskie, T. M. Cooley, S. R. Hollamby, and R. Maes. 2003. West Nile virus infection in eastern fox squirrels (*Sciurus niger*). Veterinary Pathology 40:703-707.

Klebenow, D. A. 1982. Livestock grazing interactions with sage-grouse. Pages 113-123 *in* J. M. Peek and P. D. Dalke, editors. Proceedings of the Wildlife-Livestock Relationships Symposium, 20-22 April 1981, Coeur d'Alene, Idaho. Proceeding 10, University of Idaho Forestry, Wildlife, and Range Experiment Station, Moscow, USA.

Klebenow, D. A. 1985. Habitat management of sage-grouse in Nevada. World Pheasant Association Journal 10:34-46.

Klebenow, D. A., and G. M. Gray. 1968. Food habits of juvenile sage-grouse. Journal of Range Management 12:80-83.

Klott, J. H., and F. G. Lindzey. 1990. Brood habitats of sympatric sage-grouse and Columbian sharp-tailed grouse in Wyoming. Journal of Wildlife Management 54:84-88.

Lewis, A. R. 2004. Sagebrush steppe habitats and their associated bird species in South Dakota, North Dakota, and Wyoming: Life on the edge of the sagebrush ecosystem. Dissertation, South Dakota State University, Brookings, South Dakota, USA.

Oakleaf, R. J. 1971. The relationship of sage-grouse to upland meadows in Nevada. Thesis, University of Nevada, Reno, USA.

Paige, C. and S. A. Ritter. 1999. Birds in a sagebrush sea: managing sagebrush habitats for bird communities. Partners in Flight Western Working Group, Boise, ID.

Peterson, J. G., 1970. The food habits and summer distribution of juvenile sage-grouse in central Montana. Journal of Wildlife Management 34:147-155.

Pollard, J. H. 1971. On distance estimators of density in randomly distributed forests. Biometrics 27:991-1002.

Pollock, K., S. Winterstein, C. Bunck, and P. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7-15.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295-298.

Rodgers, A.R., A.P. Carr, H.L. Beyer, L. Smith, and J.G. Kie. 2007. HRT: Home Range Tools for ArcGIS. Version 1.1. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Rumble, M. A., and S. H. Anderson. 1996. Habitat selection of Merriam's turkey (*Meleagris gallopavo merriami*) in the Black Hills, South Dakota, American Midland Naturalist 136:157-171.

Schoenberg, T. J., 1982. Sage-grouse movements and habitat selection in North Park, Colorado. Thesis, Colorado State University, Fort Collins, USA.

Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99:933-941.

Shi. P. 2001. High-throughput detection of West Nile virus RNA. Journal of Clinical Microbiology 39:1264-1271.

Smith, J. 2003. Greater sage grouse on the edge of their range: leks and surrounding landscapes in the Dakotas. M.S. Thesis, South Dakota State University, Brookings, USA.

South Dakota Department of Game, Fish, and Parks. 2006. South Dakota comprehensive wildlife conservation plan. South Dakota Dept. of Game, Fish, and Parks, Pierre, Wildlife Division Report 2006-08.

Stubbendieck, J., S. L. Hatch, and C. H. Butterfield. 1997. North American Range Plants. Fifth edition. University of Nebraska Press, Lincoln, Nebraska, USA.

Sveum, C. M., J. A. Crawford, and W. D. Edge. 1998. Use and selection of brood-rearing habitat by sage-grouse in south-central Washinton. Great Basin Naturalist 58:344-351.

Thompson, K. M., M. J. Holloran, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2006. Early brood-rearing habitat use and productivity of greater sage-grouse in Wyoming. Western North American Naturalist 66:332-342.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2007. West Nile virus and greater sage-grouse: Estimating infection rate in a wild bird population. Avian Diseases 51:691-696.

Wallestad, R. O. 1971. Summer movement and habitat use by sage-grouse broods in Montana. Journal of Wildlife Management 35:129-136.

Appendix 4. Complete results from logistic regression models predicting greater sage-grouse brood-rearing sites ($n$ = 119) versus random sites ($n$ = 116) in northwestern South Dakota, USA, 2006-2007.

| Model[a] | K[b] | AIC*c* | Δ AIC*c*[c] | *wi*[d] |
|---|---|---|---|---|
| Visual Obstruction + Bluegrass | 5 | 303.547 | 0.000 | 0.231 |
| Visual Obstruction + Bluegrass + Sagebrush Cover | 6 | 304.275 | 0.728 | 0.160 |
| Visual Obstruction + Bluegrass + Sage Density | 6 | 304.455 | 0.908 | 0.146 |
| Visual Obstruction + Bluegrass + Jap. Brome | 6 | 304.798 | 1.251 | 0.123 |
| Visual Obstruction + Bluegrass + Jap. Brome + Sage Density | 7 | 305.459 | 1.911 | 0.089 |
| Total Cover + Bluegrass + Grass Hgt. | 6 | 305.503 | 1.956 | 0.087 |
| Grass Hgt. + Total Cover | 5 | 307.403 | 3.856 | 0.034 |
| Visual Obstruction + Sagebrush Cover | 5 | 307.961 | 4.414 | 0.025 |
| Visual Obstruction | 4 | 308.259 | 4.712 | 0.022 |
| Grass Hgt. + Sage Density + Bluegrass | 6 | 308.829 | 5.281 | 0.016 |
| Grass Hgt. + Total Cover + Sage Density | 6 | 309.376 | 5.829 | 0.013 |
| Visual Obstruction + Jap. Brome | 5 | 309.416 | 5.869 | 0.012 |
| Grass Hgt. + Bluegrass | 5 | 309.893 | 6.346 | 0.010 |
| Grass Hgt. + Bluegrass + Sagebrush Cover | 6 | 310.219 | 6.671 | 0.008 |
| Visual Obstruction + Sage Density | 5 | 310.330 | 6.783 | 0.008 |
| Bluegrass + Sage Density + Grass Hgt. + Jap. Brome | 7 | 310.395 | 6.848 | 0.008 |
| Grass Hgt. + Sagebrush Cover | 5 | 312.905 | 9.358 | 0.002 |
| Grass Hgt. + Grass Cover | 5 | 313.128 | 9.581 | 0.002 |
| Grass Hgt. | 4 | 313.669 | 10.122 | 0.001 |
| Sagebrush + Grass Hgt. + Jap. Brome | 6 | 314.112 | 10.565 | 0.001 |
| Grass Hgt. + Sagebrush Density | 5 | 314.348 | 10.800 | 0.001 |
| Grass Hgt. + Jap. Brome | 5 | 315.110 | 11.563 | 0.001 |
| Sagebrush + Total Cover | 5 | 318.870 | 15.323 | 0.000 |
| Total Cover + Bluegrass | 5 | 320.013 | 16.465 | 0.000 |
| Total Cover | 4 | 320.699 | 17.152 | 0.000 |
| Grass Cover + Sagebrush Cover | 5 | 321.890 | 18.343 | 0.000 |
| Sage Density + Total Cover | 5 | 322.539 | 18.992 | 0.000 |
| Grass Cover + Bluegrass | 5 | 324.656 | 21.109 | 0.000 |
| Grass Cover | 4 | 326.626 | 23.078 | 0.000 |
| Bluegrass + Sage Density | 5 | 326.866 | 23.319 | 0.000 |
| Bluegrass + Jap. Brome + Sage Density | 6 | 327.142 | 23.595 | 0.000 |
| Bluegrass + Jap. Brome | 5 | 328.135 | 24.588 | 0.000 |
| Sage Density + Grass Cover | 5 | 328.447 | 24.900 | 0.000 |
| Bluegrass | 4 | 328.972 | 25.425 | 0.000 |
| Sagebrush Cover + Bluegrass | 5 | 329.056 | 25.509 | 0.000 |
| Sagebrush Cover + Jap. Brome | 5 | 330.167 | 26.620 | 0.000 |
| Sagebrush Cover | 4 | 330.739 | 27.191 | 0.000 |
| Sage Density | 4 | 331.620 | 28.073 | 0.000 |
| Jap. Brome | 4 | 331.657 | 28.110 | 0.000 |
| Sage Density + Jap. Brome | 5 | 332.235 | 28.688 | 0.000 |

[a] For ease of interpretation, year variable was excluded from model column.
[b] Number of habitat parameters plus intercept, SE, and year.
[c] Change in AIC*c* value
[d] Model weight

Ecology and Evolution

Open Access

# Modeling ecological minimum requirements for distribution of greater sage-grouse leks: implications for population connectivity across their western range, U.S.A.

Steven T. Knick[1], Steven E. Hanser[1] & Kristine L. Preston[2]

[1]U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 970 Lusk Street, Boise, Idaho 83706
[2]Center for Conservation Biology, University of California, 1303 Webber Hall, Riverside, California 92521

**Keywords**
Ecological minimums, greater sage-grouse, landscape modeling, partitioned Mahalanobis $D^2$, population connectivity, sagebrush, species distribution models.

**Correspondence**
Steven T. Knick, U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 970 Lusk Street, Boise, ID 83706.
Tel: 1-208-426-5208; Fax: 1-208-426-5210;
E-mail: steve_knick@usgs.gov

**Funding Information**
Funding for this project was provided by the United States Fish and Wildlife Service, Great Northern Landscape Conservation Cooperative. Ancillary support was provided by the United States Geological Survey and the University of California, Riverside.

Received: 12 December 2012; Revised: 12 March 2013; Accepted: 13 March 2013

***Ecology and Evolution*** **2013; 3(6): 1539–1551**

doi: 10.1002/ece3.557

## Abstract

Greater sage-grouse *Centrocercus urophasianus* (Bonaparte) currently occupy approximately half of their historical distribution across western North America. Sage-grouse are a candidate for endangered species listing due to habitat and population fragmentation coupled with inadequate regulation to control development in critical areas. Conservation planning would benefit from accurate maps delineating required habitats and movement corridors. However, developing a species distribution model that incorporates the diversity of habitats used by sage-grouse across their widespread distribution has statistical and logistical challenges. We first identified the ecological minimums limiting sage-grouse, mapped similarity to the multivariate set of minimums, and delineated connectivity across a 920,000 km$^2$ region. We partitioned a Mahalanobis $D^2$ model of habitat use into $k$ separate additive components each representing independent combinations of species–habitat relationships to identify the ecological minimums required by sage-grouse. We constructed the model from abiotic, land cover, and anthropogenic variables measured at leks (breeding) and surrounding areas within 5 km. We evaluated model partitions using a random subset of leks and historic locations and selected $D^2$ ($k$ = 10) for mapping a habitat similarity index (HSI). Finally, we delineated connectivity by converting the mapped HSI to a resistance surface. Sage-grouse required sagebrush-dominated landscapes containing minimal levels of human land use. Sage-grouse used relatively arid regions characterized by shallow slopes, even terrain, and low amounts of forest, grassland, and agriculture in the surrounding landscape. Most populations were interconnected although several outlying populations were isolated because of distance or lack of habitat corridors for exchange. Land management agencies currently are revising land-use plans and designating critical habitat to conserve sage-grouse and avoid endangered species listing. Our results identifying attributes important for delineating habitats or modeling connectivity will facilitate conservation and management of landscapes important for supporting current and future sage-grouse populations.

## Introduction

The greater sage-grouse *Centrocercus urophasianus* (Bonaparte) is an obligate resident of semiarid sagebrush *Artemisia* (L.) shrublands in western North America (Fig. 1). Although sage-grouse are still widely distributed across 11 states and 2 provinces, their current range is only 56% of their historical distribution prior to Euro-American settlement (Schroeder et al. 2004). Greater sage-grouse was recently designated as a candidate species for listing under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2010). Although biological data coupled with lack of regulatory mechanisms warranted listing, endangered status was precluded because other species were considered to be higher priorities.

Sage-grouse are managed as an umbrella species for over 350 species of plants and animals that depend on sagebrush (Suring et al. 2005). The long-term future for

© 2013 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.



**Figure 1.** A male greater sage-grouse displays on a lek (traditional breeding ground). Photo credit: Matt T. Lee.

this ecosystem is uncertain (Davies et al. 2011). Extensive regions of sagebrush have been burned by wildfire or lost to agriculture, energy and infrastructure development, and other resource demands by increasing human populations within the sage-grouse range (Knick et al. 2011). Remaining sagebrush landscapes are threatened further by exotic plant invasions leading to altered fire regimes and conversions to unsuitable expanses of exotic annual grasslands (Chambers et al. 2007; Miller et al. 2011; Balch et al. 2013). Long-term effects of changing climate could result in further loss of sagebrush by the end of this century: as much as 80% of the current sagebrush distribution could disappear under extreme projections (Neilson et al. 2005). Thus, current trajectories and future loss of sagebrush are likely to further imperil sage-grouse and other dependent species (U.S. Fish and Wildlife Service 2005, 2010).

Sage-grouse differ from many threatened species whose populations often are at risk because of localized ranges, restrictive habitat requirements, or are jeopardized by a dominant stressor. In contrast, sage-grouse are broadly distributed, occupy a diversity of environments containing sagebrush, and face multiple but cumulative threats throughout their range (Knick and Connelly 2011). Because conservation resources and time are limiting, delineating important areas and connecting corridors among populations could help focus actions in critical regions. Spatially explicit models delineating habitat for a species are important tools for directing land use or planning long-term conservation (Guisan and Zimmerman 2000; Elith et al. 2006). Numerous species distribution models have been developed for sage-grouse and have been important for understanding site-specific habitat relationships (Aldridge and Boyce 2007; Doherty et al. 2008; Shepherd et al. 2011). However, translating these habitat relationships into broad-scale maps has been hindered due to limited availability of accurate and consistent data spanning regional or range-wide distributions. Standard statistical approaches also present challenges because models based on ecological means, optimums, or correlational relationships often fail when applied to novel environments outside the inference space of the original data and do not accurately track either spatial or temporal change (Knick and Rotenberry 1998). Therefore, we used a partitioned Mahalanobis $D^2$ model of resource selection to identify environmental characteristics that varied least at locations where a species occurs (Dunn and Duncan 2000; Browning et al. 2005). These consistent environmental characteristics, which correspond to an ecological niche, represent the most essential set of requirements limiting a species distribution (Rotenberry et al. 2002, 2006).

Identifying minimum requirements underlying sage-grouse distributions is particularly relevant because agencies responsible for managing sagebrush-dominated lands are considering sage-grouse needs while currently revising land-use plans and delineating priority regions (U.S. Bureau of Land Management 2011). Our second objective was to map a habitat similarity index (HSI) relative to the multivariate model of ecological minimums for the western portion of the sage-grouse range. We then converted the HSI to a resistance surface to model connectivity among delineated populations. These results are necessary to identify populations vulnerable to extirpation because of habitat loss or isolation, delineate potential corridors for movement among populations, and to provide a foundation from which to assess the implications of current or future habitat change.

## Study Area

Our study area encompassed approximately 920,000 km$^2$ of the western portion of the historic range occupied by sage-grouse, including areas outside of mapped population boundaries (Fig. 2) (Schroeder et al. 2004). A small part of our study area also included populations in the eastern range, which is generally delineated by the Rocky Mountains. The area is dominated by big sagebrush *A. tridentata* (Nutt.), little sagebrush *A. arbuscula* (Nutt.), and black sagebrush *A. nova* (A. Nelson) communities and is topographically and climatically diverse (Miller et al. 2011). Sage-grouse breed each spring (March–June) at traditional locations (leks) throughout this region. Thirty-six population units were delineated (Connelly et al. 2004), including six that may be extirpated based on absence of male sage-grouse at leks from 1998 to 2007.


© 2013 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

## Materials and Methods

### Sage-grouse locations and environmental variables

We modeled species presence from locations of 3184 sage-grouse leks known to be active between 1998 and 2007. State wildlife biologists count displaying males each year to estimate population status; active leks were defined on an annual basis as those with $\geq 1$ male sage-grouse attending (Garton et al. 2011).

We characterized the environment from land cover, anthropogenic, edaphic, topographic, and climatic variables represented in a 1-km grid within a Geographical Information System. We used an existing database of environmental variables that had been developed previously for broad-scale studies of sage-grouse population trend and habitat selection (Johnson et al. 2011; Wisdom et al. 2011). When possible, we matched time-specific predictor variables with the temporal period for lek data.

Most variables were measured for the 1-km grid cell within which the lek was located and also at larger scales represented by 5- and 18-km radii surrounding the lek location. We used these distances because a large proportion of females in nonmigratory and migratory populations nest within 5 and 18 km of the lek location (Connelly et al. 2000). Variables measured at 18-km radii did not perform as well in initial models as those at 5 km and were dropped in subsequent analyses.

The percentage of land cover class was measured from a 90-m resolution vegetation map (Landfire 2007). Land cover included agriculture, big sagebrush shrubland, big sagebrush steppe, conifer forest, developed, grassland, low sagebrush, mountain sagebrush, pinyon *Pinus* (L.) – juniper *Juniperus* (L.), riparian and all sagebrush types combined. Our environmental variables did not include understory components because these were not mapped explicitly (Landfire 2007). However, land cover communities described in the classification included associations for subdominant components.

We used fire perimeter data to characterize fire history by measuring total area burned between 1980 and 2007 (U.S. Geological Survey 2011a). Densities of anthropogenic features were developed from road, power line, pipeline, and communication tower distributions (U.S. Geological Survey 2011b). Soil variables were measured only at the lek location and included soil depth, available water capacity, salinity, and percent silt, clay, and sand (U.S. Department of Agriculture 2011). Topographic variables (slope and topographic heterogeneity) were calculated from a 90-m resolution raster-based digital elevation model (U.S. Geological Survey 2011c). We quantified local topographic heterogeneity using a vector ruggedness model (Sappington et al. 2007). Climate variables included mean annual, winter (November–February) and summer (May–August) precipitation, and mean annual minimum and maximum temperatures (Daly et al. 2004). Temperature and precipitation were averaged for 1998 through 2007 using 800-m resolution monthly climate data obtained from the PRISM Climate Group (Oregon State University 2011).

### Partitioned Mahalanobis $D^2$

Mahalanobis $D^2$ measures the standardized difference between the multivariate mean for $p$ environmental variables calculated at $n$ species occurrence locations and the values of those environmental variables at different points in the landscape being modeled (Clark et al. 1993). Smaller $D^2$ values represent more similar conditions relative to the vector of multivariate means describing a species environment. An HSI can be created by rescaling $D^2$ to range continuously from 0 to 1; an HSI of 1 indicates environmental conditions identical to the mean habitat vector whereas a value near 0 indicates very dissimilar conditions. Although these models identify areas most similar to characteristics of occupied habitat, other factors may determine actual occupancy (Pulliam 2000).

Mahalanobis $D^2$ can be partitioned into $k$ separate components, each reflecting independent relationships between a species occurrence and the set of selected environmental variables (Dunn and Duncan 2000; Rotenberry et al. 2002). Total number of partitions equals the number of variables in the model. Partitions are orthogonal and additive; summing all partitions equals the full rank model and provides the original $D^2$ value. Independent partitions are derived in a principal components analysis (PCA) of the $n \times p$ matrix. An eigenvalue provides the variance accounted for by each partition and an eigenvector describes the linear contribution of each variable. Because partitions that have eigenvalues $\leq 1.0$ explain little variance, they represent invariant environmental relationships in a species distribution. As such, these partitions define a multivariate model of limiting factors or environmental minimums (Dunn and Duncan 2000; Browning et al. 2005). Model precision can be increased by adding partitions, but at the cost of decreasing predictive capability.

### Model construction and evaluation

We randomly selected 70% of the leks ($n = 2070$) to calibrate models (Fig. 3A) and withheld the remaining 30% ($n = 1114$) to evaluate performance (Fig. 3B). We estimated distributions of variables from 1000 iterative

© 2013 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd. 

samples created by bootstrapping the calibration data. To better incorporate conditions in both large and small populations, we restricted the contribution from each population in a sample to a random selection of a maximum of 25 leks. We then performed a PCA on each of the 1000 iterative samples. The final model was created by subsequently averaging the PCA output after correcting for sign ambiguity (Bro et al. 2008) across all iterations.

We evaluated the ability of each $D^2(k)$ partition to predict habitat by calculating median HSI scores for calibration and evaluation data (Rotenberry et al. 2006). We also used 99 locations where sage-grouse historically occurred but are no longer extant to evaluate how well models distinguished current from unoccupied habitat (Wisdom et al. 2011). To further evaluate model performance, we calculated the area under the curve (AUC) for a receiver operating characteristic (ROC) to assess sensitivity (fraction of occurrences correctly classified) and specificity (fraction of unoccupied points predicted as occupied) (Fielding and Bell 1997). To calculate the AUC, we used the HSI values for 3184 randomly selected locations in the study area and for the 3184 lek to construct the ROC and calculate AUC (Phillips et al. 2006).

We used multiple criteria to select the final partition (Dunn and Duncan 2000). First, we examined each $k$ partition having an eigenvalue $\leq 1.0$ for relative differences in the spacing of eigenvalues among adjacent partitions. We also considered performance against evaluation data and our subjective knowledge of use areas predicted by each partition. Finally, we assessed the interpretability of eigenvector coefficients from the broader context of known sage-grouse biology (Connelly et al. 2011).

## Ecological minimums

We assumed first that all variables directly measured and included in the model contributed to the $p$-dimensional $D^2(k)$ space describing sage-grouse environmental requirements. We also assumed that variables not measured directly nonetheless were captured within that statistical characterization. We then identified variables that were highly correlated with partitions maintaining a consistent value where sage-grouse occurred (small eigenvalues <1).

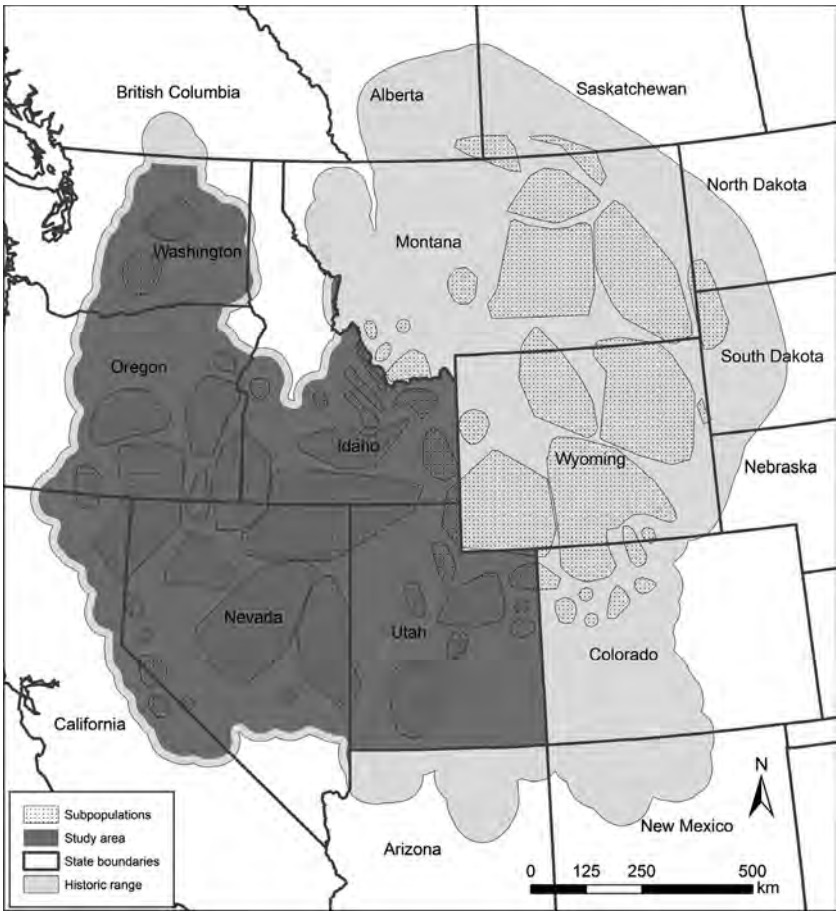



**Figure 2.** Study area and greater sage-grouse population boundaries within the historic sage-grouse range in western North America.


© 2013 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

These variables were most likely to be associated with limiting factors compared to those correlated with partitions explaining large amounts of variation (larger eigenvalues) (Rotenberry et al. 2006). Finally, we considered a variable as an important contributor to the ecological minimum vector if it was correlated with the selected partition (eigenvectors > |0. 3| and to HSI scores (Halama et al. 2008).

We used dose-response curves (Hanser et al. 2011) to examine relationships between predicted HSI values and estimates for environmental variables measured at locations of sage-grouse leks active between 1998 and 2007 and for the study area grid. Relationships potentially identified include values for predictor variables relative to HSI scores at a threshold level estimated for 90% of the lek occurrences, strong linear relationships, or optimum of HSI scores. We also evaluated whether proportion of lek locations with high HSI scores differed from the proportion of points in the study area falling within that range of values. We calculated means and 95% confidence intervals for each variable to compare environmental characteristics among active leks, historic locations, and the study area.

### Population connectivity

We used mapped HSI scores to model pathways of potential sage-grouse movement among leks and populations (Circuitscape 3.5; McRae 2006). Models based on circuit theory treat landscapes as conductive surfaces to predict movement and connectivity patterns. Current flowing across the landscape can then be used to identify areas important for connectivity. Number, width, and permeability of available pathways determine the robustness of connections between two locations of interest (McRae et al. 2008). Important model attributes include strength of the current source, landscape resistance, and juxtaposition of current source to grounds. We set the strength of each current source equal to the mean annual count of individuals (1998–2007) at leks within 1-km cells to incorporate size variation. We assumed that individuals would move more easily through areas meeting their habitat requirements and estimated resistance for each 1-km cell in the study area by scaling the inverse of the HSI from 1 (low resistance/high HSI) to 100,000 (high resistance/low HSI). Areas outside the historic range of sage-grouse were given a value of 100,000 to reduce influence from map boundaries (Koen et al. 2010). Each lek cell was iteratively activated as a source with all others as ground that simulated an increased likelihood of individuals to move to adjacent leks. We combined all current (movement potential) map outputs to produce a cumulative map of connectivity.

**Table 1.** Model partition ($k$) and eigenvalues for a Mahalanobis $D^2$ model of 27 environmental variables describing sage-grouse environments.

| Model partition ($k$) | Eigenvalue |
|---|---|
| 1 | 3.85 |
| 2 | 2.98 |
| 3 | 2.36 |
| 4 | 1.85 |
| 5 | 1.70 |
| 6 | 1.48 |
| 7 | 1.29 |
| 8 | 1.18 |
| 9 | 1.11 |
| 10 | 1.01 |
| 11 | 0.94 |
| 12 | 0.86 |
| 13 | 0.81 |
| 14 | 0.75 |
| 15 | 0.67 |
| 16 | 0.56 |
| 17 | 0.53 |
| 18 | 0.49 |
| 19 | 0.46 |
| 20 | 0.43 |
| 21 | 0.40 |
| 22 | 0.32 |
| 23 | 0.29 |
| 24 | 0.23 |
| 25 | 0.21 |
| 26 | 0.13 |
| 27 | 0.11 |

Partition eigenvalues were averaged from 1000 models using iterative subsamples randomly drawn from 2070 active sage-grouse lek locations.

## Results

Eighteen of 27 $D^2(k)$ partitions met our criteria of having an eigenvalue $\leq 1$ (Table 1). We selected $D^2(k = 10)$ because of its relative difference among adjacent partitions ($\Delta\text{eigenvalue}_{D^2(k\ =\ 9\text{–}10)} = 0.10$), performance against evaluation data (median HSI: evaluation leks = 0.85; historic locations = 0.0, AUC = 0.85), our subjective assessment of accuracy in map delineations (Fig. 4), and our ability to interpret $D^2(k = 10)$ based on relative importance of variables (Table 2).

### Ecological minimums

Land cover of sagebrush and anthropogenic features were the primary variables defining the multivariate vector of ecological minimums (Table 2). Sagebrush in the surrounding landscape was highly important, particularly the big sagebrush shrub steppe type (Table 2). When all four sagebrush types were summed, 79% of the area within

© 2013 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd. 

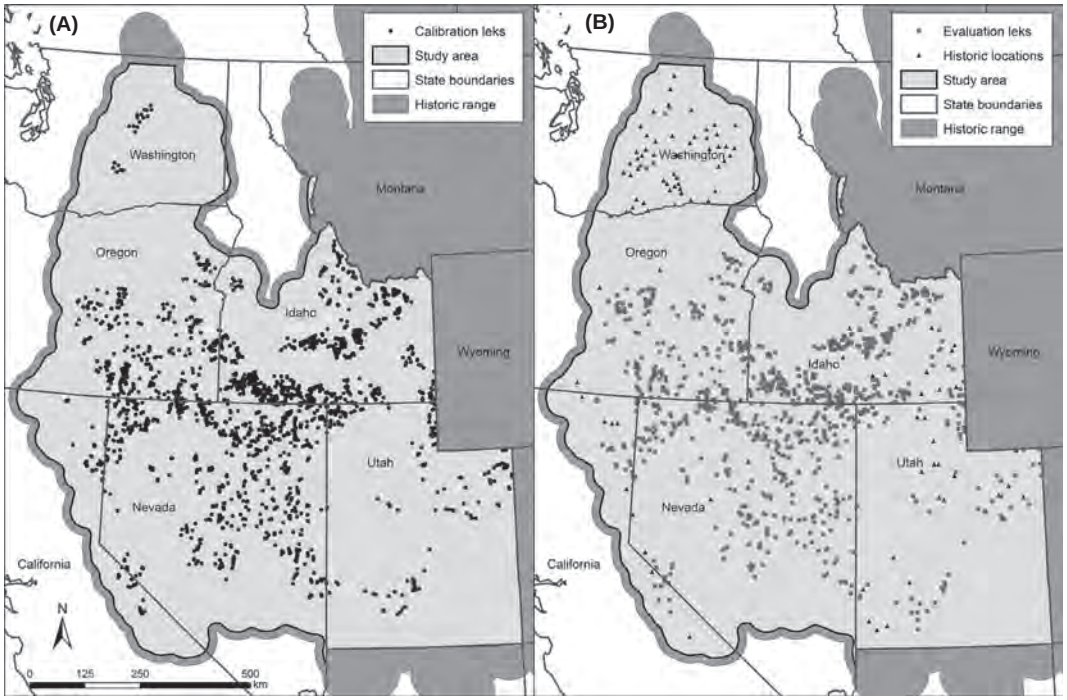



**Figure 3.** Distribution of greater sage-grouse lek locations active between 1998 and 2007 in the western range used to calibrate and evaluate models. Leks were randomly selected into calibration (A, black circles) and evaluation subsets (B, gray squares). Historic, but currently unoccupied sage-grouse locations (B, black triangles) were also used to test model performance.

5 km of the lek was in sagebrush land cover compared to 28% at 99 historic but no longer occupied locations and 35% for the study area. Lek locations had approximately twice the average large-scale sagebrush cover for the study area and nearly three times that of historic locations. Using the distribution of HSI scores for 90% of the leks as a threshold, active leks were surrounded by >40% landscape cover of sagebrush on average (Fig. 5A). Of the other dominant land cover types in our analysis, leks were absent from regions with $\geq$40% conifer and averaged <1% conifer forest within 5 km compared to an average of 13% for the study area and 3.4% for historic grouse locations (Table 2). Historic locations also had nearly five times more grassland and the study area nearly twice that of active leks (Table 2).

The HSI declined with increasing levels of human land use. Percent agriculture varied widely across individual lek locations, but <2% of the leks were in areas surrounded by >25% agriculture within a 5-km radius, and 93% by <10% agriculture (Fig. 5B). Ninety-nine percent of active leks were in landscapes with <3% developed; all lands surrounding leks were <14% developed (Fig. 5C). Historic locations where sage-grouse no longer occur were associated with landscapes dominated by >10 times the agriculture and >25 times the developed land as currently active leks (Table 2). Because large fires seldom occur in agriculture or developed landscapes, active leks had larger burned areas on average than historic locations and for the study area (Table 2).

Active leks also had lower densities of individual anthropogenic features than the study area or historic sage-grouse locations (Table 2). High lek HSI scores ($\geq$0.60) were associated with large-scale densities of <1.0 km/km$^2$ of secondary roads, 0.05 km/km$^2$ of highways, and 0.01 km/km$^2$ of interstate highways. Ninety-three percent of active leks fell below this threshold for interstate highways (Fig. 5D). Habitat suitability was highest at power line densities <0.06 km/km$^2$ and pipeline and communication tower densities <0.01 km/km$^2$. Leks were absent from areas where power line densities exceeded 0.20 km/km$^2$, pipeline densities exceeded 0.47 km/km$^2$, or communication towers exceeded 0.08 km/km$^2$.

Active leks were situated on shallow slopes with less rugged terrain compared to the study area or historic locations (Table 2). No leks were characterized by slopes $\geq$27° or terrain ruggedness $\geq$0.05, although the study area included slopes to 70° and terrain ruggedness to 0.35. Mean annual precipitation for active leks and historic locations was on average 88% of that for the study area (Table 2) and varied from 169 to 835 mm. Minimum annual temperatures were lower at active leks and the study area compared with historic sage-grouse locations, whereas maximum annual temperatures were similar across datasets (Table 2). Maximum temperature varied between 11 and


© 2013 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

**Table 2.** Mean (SE), range, and absolute values of $D^2$ ($k$ = 10) eigenvectors for environmental variables measured at 3184 sage-grouse leks, 99 historic but currently extant locations, and for the study area.

| | Active leks | | Historic | | Study area | | |
|---|---|---|---|---|---|---|---|
| Environmental variables | Mean (SE) | Range | Mean (SE) | Range | Mean (SE) | Range | Eigenvector $D^2$ ($k$ = 10) |
| Land cover (%) | | | | | | | |
| Big sagebrush shrubland | 29.8 (0.4) | 0–97.6 | 11.8 (1.3) | 0–66.1 | 15.3 (0.02) | 0–99.5 | 0.09 |
| Big sagebrush shrub steppe | 19.5 (0.4) | 0–94.5 | 8.0 (1.1) | 0–51.3 | 6.9 (0.01) | 0–100 | 0.33 |
| Low sagebrush | 20.1 (0.4) | 0–95.4 | 4.1 (0.9) | 0–59.1 | 8.0 (0.01) | 0–97.1 | 0.12 |
| Mountain sagebrush | 9.4 (0.3) | 0–89.1 | 3.7 (1.1) | 0–77.8 | 4.7 (0.01) | 0–98.8 | 0.10 |
| All sagebrush | 78.84 (0.33) | 1.93–99.98 | 34.87 (0.03) | 0–100 | 27.7 (2.01) | 0.43–80.22 | |
| Agriculture | 2.1 (0.1) | 0–83.1 | 26.6 (2.4) | 0–93.5 | 8.1 (0.02) | 0–97.8 | 0.36 |
| Conifer forest | 0.8 (0.1) | 0–44.4 | 3.4 (0.7) | 0–40.6 | 12.5 (0.03) | 0–99.1 | 0.21 |
| Developed land | 0.3 (0.01) | 0–14.1 | 8.7 (1.5) | 0–83.9 | 1.4 (0.004) | 0–99.5 | 0.04 |
| Grassland | 2.2 (0.1) | 0–71.0 | 9.8 (1.3) | 0–61.2 | 3.8 (0.01) | 0–84.1 | 0.09 |
| Riparian | 1.9 (0.1) | 0–33.5 | 2.2 (0.5) | 0–50.7 | 2.1 (0.003) | 0–87.1 | 0.10 |
| Burn | | | | | | | |
| Burned area 1980–2007 (ha) | 1421 (40) | 0–7974 | 587 (121) | 0–6145 | 770 (2) | 0–7974 | 0.18 |
| Anthropogenic | | | | | | | |
| Secondary roads (km/km$^2$)[1] | 66.6 (0.6) | 0–288.8 | 164.7 (16.5) | 26.3–1242.6 | 75.7 (0.1) | 0–1332.4 | 0.11 |
| Highways (km/km$^2$)[1] | 2.0 (0.1) | 0–32.3 | 11.0 (1.3) | 0–58.7 | 3.4 (0.01) | 0–77.1 | 0.12 |
| Interstate highways (km/km$^2$)[1] | 0.1 (0.02) | 0–19.8 | 3.8 (0.8) | 0–46.6 | 0.6 (0.003) | 0–52.0 | 0.33 |
| Power lines (km/km$^2$)[1] | 2.5 (0.1) | 0–34.6 | 14.4 (1.4) | 0–52.1 | 4.3 (0.01) | 0–79.5 | 0.11 |
| Pipelines (km/km$^2$)[1] | 1.4 (0.1) | 0–78.1 | 8.6 (1.5) | 0–64.3 | 2.7 (0.01) | 0–208.2 | 0.08 |
| Communication towers (towers/km$^2$)[1] | 0.1 (0.01) | 0–8.9 | 18.3 (5.5) | 0–286.5 | 0.6 (0.01) | 0–2005.3 | 0.22 |
| Soil | | | | | | | |
| Soil depth (cm) | 102.6 (0.7) | 0–152.0 | 110.4 (4.1) | 0–152.0 | 104.0 (0.1) | 0–152.0 | 0.06 |
| Sand (% soil volume) | 28.8 (0.2) | 0–85.5 | 32.0 (1.7) | 0–90.2 | 30.5 (0.02) | 0–92.0 | 0.14 |
| Silt (% soil volume) | 28.3 (0.2) | 0–70.0 | 37.9 (1.7) | 0–70.0 | 30.0 (0.02) | 0–81.5 | 0.08 |
| Clay (% soil volume) | 21.5 (0.2) | 0–50.1 | 14.8 (0.7) | 0–34.5 | 15.8 (0.01) | 0–57.4 | 0.34 |
| Salinity (mmhos/cm) | 1.1 (0.02) | 0–10.7 | 0.9 (0.1) | 0–11.0 | 1.6 (0.003) | 0–21.1 | 0.16 |
| Available water capacity (cm/cm) | 4.2 (0.03) | 0–12.3 | 5.6 (0.3) | 0–12.3 | 4.7 (0.003) | 0–25.0 | 0.04 |
| Topography | | | | | | | |
| Slope (degrees) | 3.1 (0.1) | 0–26.0 | 5.7 (0.7) | 0–36.0 | 7.3 (0.01) | 0–69.3 | 0.15 |
| Terrain ruggedness index | 1.0 (0.1) | 0–46.4 | 2.6 (0.7) | 0–55.1 | 4.1 (0.01) | 0–354.6 | 0.13 |
| Climate | | | | | | | |
| Precipitation (mm) | 333.3 (1.6) | 169.0–835.8 | 329.3 (11.7) | 140.4–782.0 | 376.3 (0.2) | 76.4–3810.4 | 0.06 |
| Minimum temperature (°C) | −9.5 (0.04) | −17.0 to −3.9 | −6.6 (0.3) | −15.3 to −1.3 | −8.3 (0.003) | −19.6 to 3.9 | 0.09 |
| Maximum temperature (°C) | 30.5 (0.03) | 23.5–35.7 | 31.8 (0.2) | 21.7–37.6 | 30.9 (0.004) | 11.0–46.1 | 0.07 |

Land cover, burn area, and anthropogenic variables were measured within a 5-km radius of the lek. Soil, topography, and climate were measured at the lek location. Source data are available at http://sagemap.wr.usgs.gov.
[1]Multiplied by $10^2$.

46°C across the study area but was 27 to 32°C at leks having the highest HSI values.

## Population connectivity

The majority of populations were connected through landscapes characterized by moderate-to-high potential for animal movement ($\geq$0.16, Fig. 6). Notable exceptions included both the Columbia Basin (Washington) and Bi-State (California–Nevada) Distinct Population Segments. Movement potential was higher among leks within individual populations than between populations. Large core populations in Nevada, Oregon, and Idaho were especially well connected. Small populations (mean annual count of males summed across all leks <250) were smaller in spatial area and had lower connectedness compared to large populations. Five populations with no active leks observed between 1998 and 2007 had limited connectivity to only one or two neighboring populations; four of these also were among the smallest designated populations by area (Fig. 6).

© 2013 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd. 

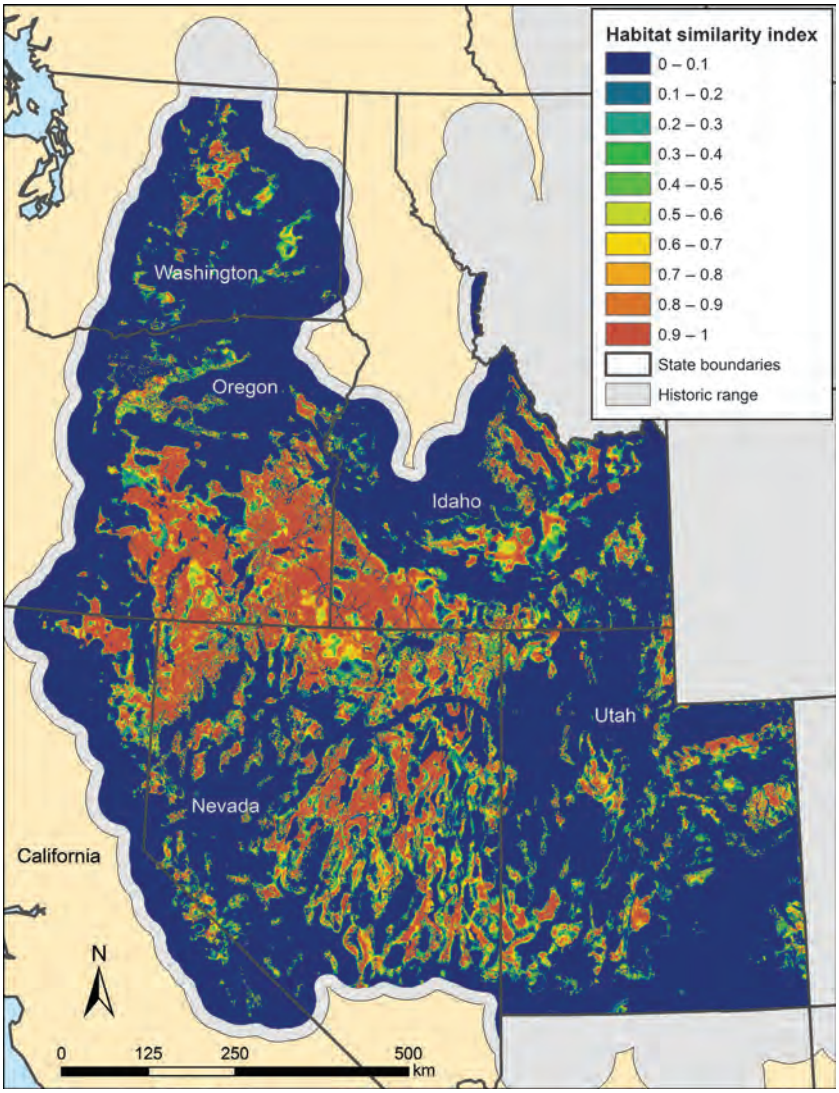



**Figure 4.** Habitat similarity index (HSI) values for greater sage-grouse across their western range. HSI values represent the relationship of environmental values at map locations to the multivariate model of minimum requirements for sage-grouse defined by land cover, anthropogenic variables, soil, topography, and climate.

## Discussion

Sage-grouse are broadly distributed across western North America and occupy landscape matrices that vary widely in cover and configuration of sagebrush and other environmental characteristics (Johnson et al. 2011). Given this variability, it is difficult to accurately model habitat at fine spatial and thematic resolutions across the species range. Trade-offs are inherent because statistical relationships developed from small study extents can have high accuracy and use specific environmental variables, but have little predictive power elsewhere. Conversely, models developed from a general set of broad-scale, range-wide variables often fail to capture critical environmental factors specific to local areas (Scott et al. 2002). Therefore, developing a habitat model for sage-grouse required an approach that not only captured the spatial variability in their local environments but also maximized accuracy when applied across broad spatial extents. We developed and mapped an HSI representing a multivariate vector of ecological minimums that accurately discriminated the majority of lek locations including those in small, outlying populations from the study area and also from historic, but unoccupied locations.

### Ecological minimums

Species distribution models provide insights into how a species is linked to its environment. Alternative forms of statistical functions and models each address different questions relative to species-habitat relationships (Scott et al. 2002; Elith et al. 2006). Among these statistical options, partitioned $D^2$ models that identify ecological minimums may not only be useful for modeling species


© 2013 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

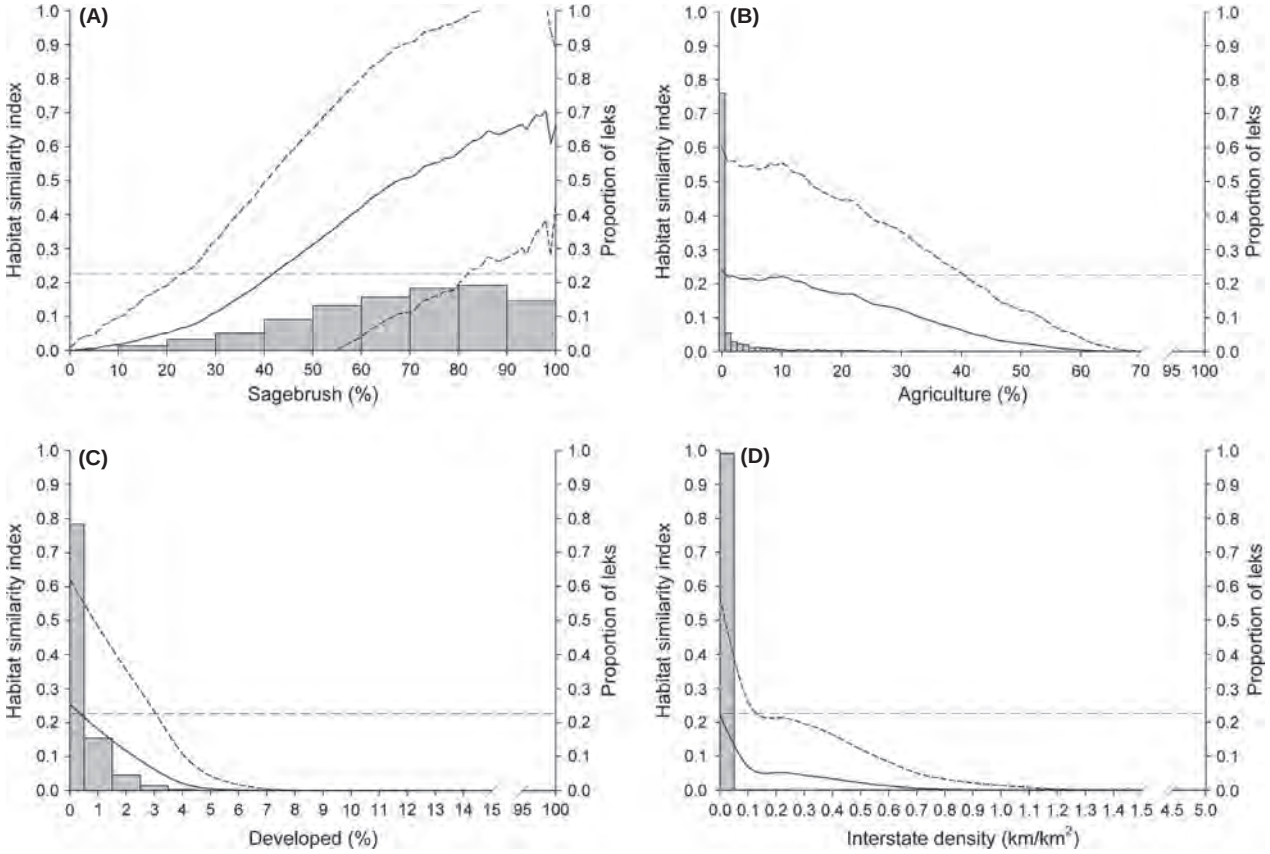



**Figure 5.** Changes in the habitat similarity index (HSI) relative to (A) sagebrush, (B) agriculture, (C) developed lands, and (D) density of interstate highways in the landscape within 5 km. Mean HSI values for study area (black line, ±1 SD [stippled lines]) and proportion of total leks (gray bars) were calculated for each increment of the environmental variables. Range of environmental variable values relates to the values within the study area. The dashed horizontal line indicates the HSI value (0.22) above which characterizes 90% of active leks.

distributions across large or changing environments but also provide important insights into that basic combination of factors necessary to support a species (Rotenberry et al. 2002; Browning et al. 2005). We used variables for land cover and human activities variables that affected sage-grouse directly but also included soil and abiotic characteristics because of their influence on distribution of sagebrush. We could not model fine-grained features, such as grass and forb understory composition, despite their seasonal importance to sage-grouse (Connelly et al. 2011) but suggest that these unmeasured components were captured within the environmental space of the ecological minimum.

Each partition of a $D^2$ model delineates a relationship between a species and a multivariate configuration of the selected variables. We selected the partition that defined ecological minimums based on multiple but somewhat subjective criteria (Dunn and Duncan 2000). Of the partitions having eigenvalues <1.0, $D^2(k = 10)$ provided the best combination of ability to identify lek locations in independent evaluation data, accurately map current sage-grouse regions based on known distributions, and was readily interpreted relative to sage-grouse habitat requirements.

The multivariate vector defined by $D^2(k = 10)$ not only clearly reflected dependence on sagebrush by sage-grouse but also revealed other factors associated with core environmental conditions in landscapes used by sage-grouse. Minimum thresholds for sagebrush land cover required by sage-grouse in the landscape are emerging from this and other range-wide studies. In this study, 90% of the active leks had at least 40% of the large-scale landscape dominated by sagebrush, which compares to 25% to 30% sagebrush within 18- and 30-km scales previously identified as necessary to support sage-grouse persistence (Aldridge et al. 2008; Wisdom et al. 2011). Our estimate that 98% of the active leks were in regions containing <25% agriculture in the landscape also concurs with other range-wide analyses on effects of cultivated croplands (Aldridge et al. 2008; Wisdom et al. 2011). Leks were absent from areas with relatively low levels of anthropogenic development and infrastructure. Historic sage-grouse locations that cur-

© 2013 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd. 

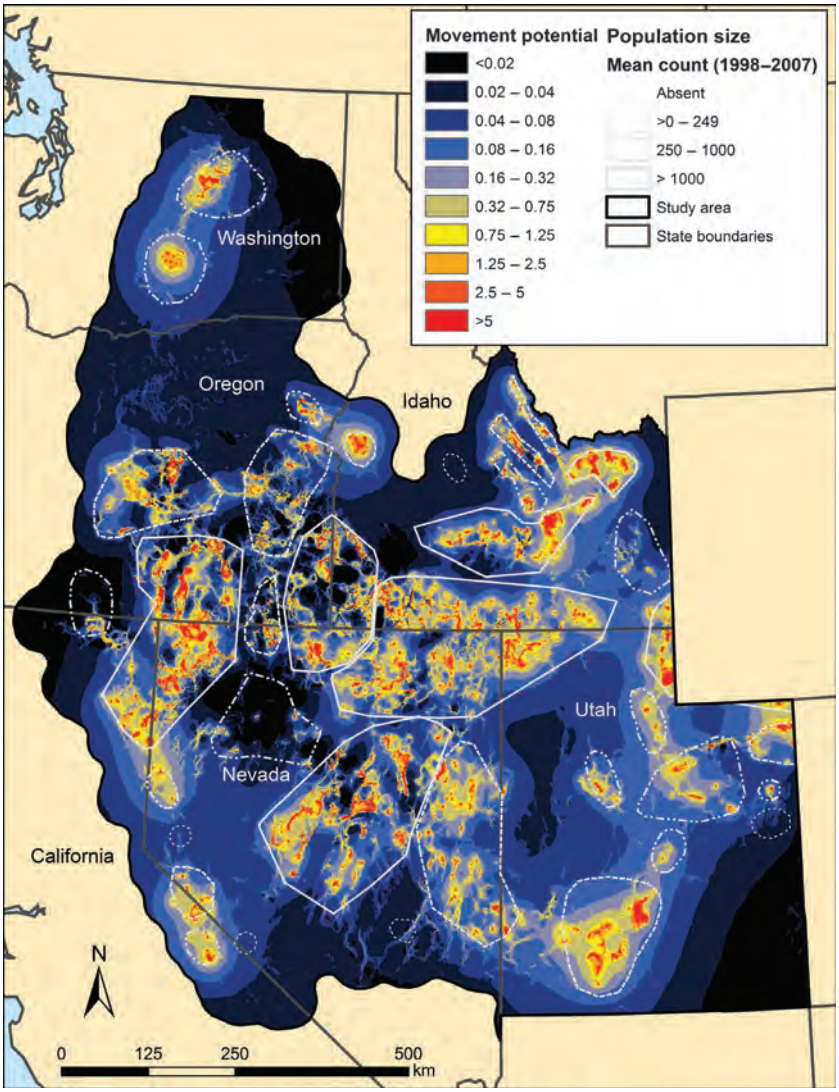



**Figure 6.** Estimated potential for sage-grouse movement among sage-grouse leks (Circuitscape; McRae 2006). Rescaled HSI values were used as a measure of landscape resistance.

rently are unoccupied were located in areas that now have high levels of development, indicating that human activity in addition to habitat loss may have contributed to extirpation from these areas (Aldridge et al. 2008; Wisdom et al. 2011). The ability of some leks to persist in landscapes containing lower amounts of sagebrush or greater levels of development likely was due to ameliorating presence of other ecological requirements.

Large-scale expansion and increasing dominance of invasive grasses in sagebrush shrublands at lower elevations is adversely affecting sage-grouse habitats (Knick et al. 2003). Synergistic feedbacks between invasive grasses and increased fire frequency and size has reduced sagebrush shrub cover and plant diversity and resulted in type conversions from sagebrush shrublands to non-native grassland landscapes (Davies 2011; Davies et al. 2011). The risk of further invasion by exotic grasses and ecosystem disruption over 100,000s of kilometers is moderate-to-high (Miller et al. 2011). At higher elevations, conifer and juniper woodlands are encroaching into sagebrush shrublands (Tausch et al. 1981; Miller et al. 2011), again resulting in lower habitat suitability for sage-grouse. Almost all leks were in areas containing little conifer or grassland cover in the surrounding landscape. Thus, two widespread trajectories of vegetation change are likely to further reduce habitat suitability across large areas of the sage-grouse range.

Active leks occurred only within a subset of the precipitation and temperature ranges even though climate varied widely across the study area. Sage-grouse currently occur in drier regions dominated by sagebrush. Thus, sage-grouse may have the ability to redistribute to areas that presently are cooler and wetter assuming that environmental conditions in new regions will be suitable and


© 2013 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

available for sagebrush expansion. The southwestern United States is projected to become more arid and is likely to experience more extensive and intensive droughts (Intergovernmental Panel on Climate Change 2007; Seager et al. 2007). Sage-grouse population extirpations have been linked to severe droughts (Aldridge et al. 2008), suggesting that populations in southern and more arid portions of the range may be most vulnerable.

### Population connectivity

Accurate maps of a species distribution are a primary goal of ecological niche-modeling (Elith et al. 2006). These maps can have an important role in conservation planning by delineating metapopulations and connecting corridors. Land and wildlife agencies currently are developing conservation actions for sage-grouse based on core or priority areas containing highest densities of breeding birds (Doherty et al. 2011). Less clear are land-use plans for regions outside of core areas that might be important for dispersal and gene flow. Species that have multiple interconnected populations are more likely to persist because risk of extirpation caused by regional events is confined to local populations; connectivity among populations ensures that recolonization can occur following local extirpation assuming that sufficient habitat remains (Thomas 1994; Hanski 1998). Populations within the interior portion of the sage-grouse range were highly interconnected. However, peripheral populations often were connected by habitat corridors only to one adjacent population. Human development or habitat loss that eliminates habitat in these corridors would further isolate those populations.

## Synthesis and Applications

Sagebrush shrublands are likely to be lost and fragmented in the future from a broad array of stressors (Miller et al. 2011). Extensive wildfires, expansion of agriculture, and development of utility and transportation infrastructures within the western range of the sage-grouse may continue to reduce habitat for sage-grouse across their western range. In addition, sagebrush distribution is predicted to decrease under future climate and land cover changes in the southern portion of the range may be most affected (Neilson et al. 2005; Bradley 2010). Leks persisting in landscapes already below the basic minimum ecological requirements might be most at risk and could be targeted for conservation actions. Minimum thresholds defining lek presence provide a basis from which to determine effects of projected or proposed levels of land use and anthropogenic development in areas that currently support active leks or to identify areas suitable for restoration of future sage-grouse habitat. We also caution that our results were based solely on lek locations. Although leks are important focal points for breeding and subsequent nesting in the surrounding region, other seasonal use areas and habitat requirements may be equally limiting to sage-grouse populations.

Population size and isolation can have serious negative impacts on genetic variability and population persistence (Frankham 2006; Höglund et al. 2007). Our mapped corridors of habitat among populations provide an important step in designing conservation actions that facilitate dispersal and gene flow and reduce isolation and risk of extirpation.

## Acknowledgments

Funding for this project was provided by the Great Northern Landscape Conservation Cooperative. State agency biologists, climate change ecologists, and modeling experts reviewed our approach at a workshop conducted in Reno, Nevada in November 2010. Lek data were used by permission. We appreciate assistance from V. Rorive and R. Johnson, University of California, Riverside. The reviews by J. W. Connelly and Q. S. Latif improved the manuscript. The authors declare that there is no conflict of interest related to this publication.

## Conflict of Interest

None declared.

### References

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecol. Appl. 17:508–526.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, et al. 2008. Range-wide patterns of greater sage-grouse persistence. Divers. Distrib. 14:983–994.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Glob. Change Biol. 19:173–183.

Bradley, B. A. 2010. Assessing ecosystem threats from global and regional change: hierarchical modeling of risk to sagebrush ecosystems from climate change, land use and invasive species in Nevada, USA. Ecography 33:198–208.

Bro, R., E. Acar, and T. G. Kolda. 2008. Resolving the sign ambiguity in the singular value decomposition. J. Chemom. 22:135–140.

Browning, D. M., S. J. Beaupré, and L. Duncan. 2005. Using partitioned Mahalanobis $D^2(k)$ to formulate a GIS-based model of timber rattlesnake hibernacula. J. Wildl. Manag. 69:33–44.

© 2013 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd. 

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecol. Monogr. 77:117–145.

Clark, J. D., J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. J. Wildl. Manag. 57:519–526.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildl. Soc. Bull. 28:967–985.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Unpublished Report. Western Association of Fish and Wildlife Agencies, Cheyenne, WY.

Connelly, J. W., E. T. Rinkes, and C. E. Braun. 2011. Characteristics of sage-grouse habitats. Pp. 69–83 *in* S. T. Knick and J. W. Connelly, eds. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biol. Vol. 38. Univ. California Press, Berkeley, CA.

Daly, C., P. Gibson, M. Doggett, J. Smith, and G. Taylor. 2004. Up to date climate maps for the conterminous United States. Proceedings 14th AMS Conference on Applied Climatology, 84th AMS Annual Meeting, Combined Preprints to American Meteorological Society Meeting, Seattle, WA, 13–16 January, 2004, Paper P5.1, CD Rom.

Davies, K. W. 2011. Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. Oecologia 167:481–491.

Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biol. Conserv. 144:2573–2584.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. J. Wildl. Manag. 72:187–195.

Doherty, K. E., D. E. Naugle, H. E. Copeland, A. Pocewicz, and J. M. Kiesecker. 2011. Energy development and conservation trade-offs: systematic planning for greater sage-grouse in their eastern range. Pp. 505–516 *in* S. T. Knick and J. W. Connelly, eds. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biol. Vol. 38. Univ. California Press, Berkeley, CA.

Dunn, J. E., and L. Duncan. 2000. Partitioning Mahalanobis $D^2$ to sharpen GIS classification. Pp. 195–204 *in* C. A. Brebbia and P. Pascolo, eds. Management information systems 2000: GIS and remote sensing. WIT Press, Southampton, U.K.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24:38–49.

Frankham, R. 2006. Genetics and landscape connectivity. Pp. 72–96 *in* K. R. Crooks and M. Sanjayan, eds. Connectivity conservation. Cambridge Univ. Press, Cambridge, U.K.

Garton, E. O., J. W. Connelly, J. S. Horne, C. A. Hagen, A. Moser, and M. A. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Pp. 293–381 *in* S. T. Knick and J. W. Connelly, eds. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biol. Vol. 38. Univ. California Press, Berkeley, CA.

Guisan, A., and N. E. Zimmerman. 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135:147–186.

Halama, K. J., A. J. Malisch, M. Aspell, J. T. Rotenberry, and M. F. Allen. 2008. Modeling the landscape niche characteristics of red diamondback rattlesnakes (*Crotalus ruber*): implications for biology and conservation. Pp. 463–472 *in* W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush, eds. The biology of rattlesnakes. Loma Linda Univ. Press, Loma Linda, CA.

Hanser, S. E., C. L. Aldridge, M. Leu, and S. E. Nielsen. 2011. Dose-response calculator for ArcGIS. U.S. Geological Survey Data Series 631. U.S. Geological Survey, Reston, VA.

Hanski, I. 1998. Metapopulation dynamics. Nature 396:41–49.

Höglund, J., J. Larsson, H. Jansman, and G. Segelbacher. 2007. Genetic variability in European black grouse (*Tetrao tetrix*). Conserv. Genet. 8:239–243.

Intergovernmental Panel on Climate Change. 2007. Climate change 2007: synthesis report. Available at http://www.ipcc.ch/publications_and_data/ar4/syr/en/main.html (accessed 28 June 2012).

Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. L. Amundson, and S. T. Knick. 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations, 1997-2007. Pp. 407–450 *in* S. T. Knick and J. W. Connelly, eds. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biol. Vol. 38. Univ. of California Press, Berkeley, CA.

Knick, S. T., and J. W. Connelly, eds. 2011. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biol. Vol. 38. Univ. of California Press, Berkeley, CA.

Knick, S. T., and J. T. Rotenberry. 1998. Limitations to mapping habitat use areas in changing landscapes using the Mahalanobis distance statistic. J. Agric. Biol. Environ. Stat. 3:311–322.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. van Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611–634.

Knick, S. T., S. E. Hanser, R. F. Miller, D. A. Pyke, M. J. Wisdom, S. P. Finn, et al. 2011. Ecological influence and pathways of land use in sagebrush. Pp. 203–251 *in* S. T. Knick and J. W. Connelly, eds. Greater sage-grouse: ecology and conservation of a landscape species and its habitats.

 © 2013 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

Studies in Avian Biol. Vol. 38. Univ. of California Press, Berkeley, CA.

Koen, E. L., C. J. Garroway, P. J. Wilson, and J. Bowman. 2010. The effect of map boundary on estimates of landscape resistance to animal movement. PLoS ONE 5:e11785.

Landfire. 2007. LANDFIRE 1.0.0 existing vegetation type layer, U.S.I Geological Survey. Available at http://landfire.cr.usgs.gov/viewer/ (accessed December 2011).

McRae, B. H. 2006. Isolation by resistance. Evolution 60: 1551–1561.

McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology and conservation. Ecology 10:2712–2724.

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, et al. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pp. 145–184 *in* S. T. Knick and J. W. Connelly, eds. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biol. Vol. 38. Univ. of California Press, Berkeley, CA.

Neilson, R. P., J. M. Lenihan, D. Bachelet, and R. J. Drapek. 2005. Climate change implications for sagebrush ecosystems. Trans. North Am. Wildl. Nat. Resour. Conf. 70:145–159.

Oregon State University. 2011. PRISM digital temperature and precipitation data. Available at http://www.prism.oregonstate.edu (accessed 28 December 2011).

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190:231–259.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecol. Lett. 3:349–361.

Rotenberry, J. T., S. T. Knick, and J. E. Dunn. 2002. A minimalist approach to mapping species' habitat: Pearson's planes of closest fit. Pp. 281–289 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, DC.

Rotenberry, J. T., K. L. Preston, and S. T. Knick. 2006. GIS-based niche modeling for mapping species' habitat. Ecology 87:1458–1464.

Sappington, J. M., K. M. Longshore, and D. B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mohave Desert. J. Wildl. Manag. 71:1419–1426.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, et al. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

Scott, J. M., P. J. Heglund, M. L. Morrison, J. B. Hauffler, M. G. Raphael, W. A. Wall, et al., eds. 2002. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, DC.

Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, et al. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316:1181–1184.

Shepherd, J. F., K. P. Reese, and J. W. Connelly. 2011. Landscape fragmentation and nonbreeding greater sage-grouse. Pp. 77–88 *in* B. K. Sandercock, K. Martin, and G. Segelbacher, eds. Ecology, conservation, and management of grouse. Studies in Avian Biol. Vol. 39. Univ. of California Press, Berkeley, CA.

Suring, L. H., M. M. Rowland, and M. J. Wisdom. 2005. Identifying species of conservation concern. Pp. 150–162 *in* M. J. Wisdom, M. M. Rowland, and L. L. Suring, eds. Habitat threats in the sagebrush ecosystem: methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, KS.

Tausch, R. J., N. E. West, and A. A. Nabi. 1981. Tree age and dominance patterns in Great Basin pinyon-juniper woodlands. J. Range Manag. 34:259–264.

Thomas, C. D. 1994. Extinction, colonization, and metapopulations: environmental tracking by rare species. Conserv. Biol. 8:373–378.

U.S. Bureau of Land Management. 2011. Notice of intent to prepare environmental impact statements and supplemental environmental Impact statements to incorporate greater sage-grouse conservation measures into land-use plans and land management plans. Fed. Reg. 76:7708–77011.

U.S. Department of Agriculture. 2011. Soil survey staff natural resources conservation service, US Department of Agriculture General Soils Map (STATSGO). Available at http://soildatamart.nrcs.usda.gov (accessed 28 December 2011).

U.S. Fish and Wildlife Service. 2005. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Fed. Reg. 70:2244–2282.

U.S. Fish and Wildlife Service. 2010. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Fed. Reg. 75:13910–14014.

U.S. Geological Survey. 2011a. Western fire map (1870–2007). Available at http://sagemap.wr.usgs.gov (accessed December 2011).

U.S. Geological Survey. 2011b. Road, pipeline, power line, and communication tower digital layers compiled from various sources. Available at http://sagemap.wr.usgs.gov (accessed December 2011).

U.S. Geological Survey. 2011c. Digital elevation model. Available at: http://seamless.usgs.gov/ (accessed December 2011).

Wisdom, M. J., C. W. Meinke, S. T. Knick, and M. A. Schroeder. 2011. Factors associated with extirpation of sage-grouse. Pp. 451–472 *in* S. T. Knick and J. W. Connelly, eds. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biol. Vol. 38. Univ. of California Press, Berkeley, CA.

© 2013 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd. 

To the University of Wyoming:

The members of the Committee approve the thesis of Chad W. LeBeau presented on 4/18/2012.

Jeffrey L. Beck, Ph.D., Chairperson

Kenneth Gerow, Ph.D., External Department Member

Matthew J. Holloran, Ph.D.

Gregory D. Johnson

Scott N. Miller, Ph.D.

APPROVED:

John A. Tanaka, Head, Department of Ecosystem Science and Management

Francis D. Galey, Dean, College of Agriculture and Natural Resources

LeBeau, Chad, W, Evaluation of Greater Sage-Grouse Reproductive Habitat and Response to Wind Energy Development in South-Central, Wyoming, MS, Department of Ecosystem Science and Management, August 2012.

The demand for clean renewable energies and tax incentives has prompted a nationwide increase in wind energy development. Renewable energy development is occurring in a wide variety of habitats potentially impacting many species including greater sage-grouse (*Centrocercus urophasianus*). Greater sage-grouse require contiguous intact sagebrush (*Artemisia* spp.) habitats. The addition of wind energy infrastructure to these landscapes may negatively impact population viability. Greater sage-grouse are experiencing range-wide population declines and are currently listed as a candidate species under the Endangered Species Act of 1973. The purpose of my study was to investigate the response of greater sage-grouse to wind energy development. Mine is the first study to document the short-term effects of wind energy infrastructure on greater sage-grouse habitat selection, nest, brood, and female survival, and male lek attendance. I hypothesized that greater sage-grouse would select for habitats farther from wind energy infrastructure, particularly wind turbines, during the nesting, brood-rearing, and summer periods. In addition, I hypothesized that greater sage-grouse nest, brood, and female survival would decline in habitats with close proximity to wind turbines. Lastly, I hypothesized that greater sage-grouse male lek attendance would experience greater declines from pre wind energy development to 4 years post development at leks with close proximity to wind turbines compared to leks farther from turbines.

My study area was located in south-central Wyoming between the towns of Medicine Bow and Hanna and consisted of one study area influenced by wind energy development (Seven

Mile Hill) and a second study area that was not impacted by wind energy development (Simpson Ridge). I identified 14 leks within both study areas and conducted lek counts at each of these leks from 2008 to 2012. I captured 116 female greater sage-grouse from both study areas from 2009 to 2010. I equipped each female grouse with a VHF necklace-mounted transmitter and monitored them via telemetry during the nesting, brood-rearing, and summer periods within both study areas from 2009 to 2010. I documented greater sage-grouse habitat selection as well as nest and brood-rearing success and female survival. I used binary logistic regression in a use versus availability study design to estimate the odds of habitat selection within both study areas during the nesting, brood-rearing, and summer periods. I used Cox proportional hazards and Andersen-Gill survival models to estimate nest, brood, and female survival relative to wind energy infrastructure. Lastly, I used ratio of means tests and linear mixed effects models to estimate the degree of decline in male lek attendance at leks influenced by wind energy development versus leks with no influence 1 year prior to development to 4 years post development.

Greater sage-grouse did not avoid wind turbines during the nesting and brood-rearing periods, but did select for habitats closer to turbines during the summer season. Greater sage-grouse nest and brood survival decreased in habitats in close proximity to wind turbines, whereas female survival appeared not to be affected by wind turbines. Peak male lek attendance within both study areas experienced significant declines from 1 year pre development to 4 years post development; however, this decline was not attributed to the presence of the wind energy facility.

The results from my study are the first examining the short-term impacts to greater sage-grouse populations from wind energy development. Greater sage-grouse were not avoiding the wind energy development two years following construction and operation of the wind energy facility. This is likely related to high site fidelity inherent in sage-grouse. In addition, more

suitable habitat may exist closer to turbines at Seven Mile Hill, which may also be driving selection. Fitness parameters including nest and brood survival were reduced in habitats of close proximity to wind turbines and may be the result of increased predation and edge effects associated with the wind energy facility. Lastly, wind energy infrastructure appears not to be affecting male lek attendance 4 years post development; however, time lags are characteristic in greater sage-grouse populations, which may result in impacts not being quantified until 2–10 years following development. Future wind energy developments should identify greater sage-grouse nest and brood-rearing habitats prior to project development to account for the decreased survival in habitats of close proximity to wind turbines. More than 2 years of occurrence data and more than 4 years of male lek attendance data may be necessary to account for the strong site fidelity and time lags present in greater sage-grouse populations.

# EVALUATION OF GREATER SAGE-GROUSE REPRODUCTIVE HABITAT AND RESPONSE TO WIND ENERGY DEVELOPMENT IN SOUTH-CENTRAL, WYOMING

By

Chad W. LeBeau

A thesis submitted to the Department of Ecosystem Science and Management

and the University of Wyoming

in partial fulfillment of the requirements

for the degree of

MASTER OF SCIENCE

in

RANGELAND ECOLOGY AND WATERSHED MANAGEMENT

Laramie, Wyoming

August 2012

COPYRIGHT PAGE

Copyright 2012, Chad W. LeBeau

## ACKNOWLEDGMENTS

The initial portion of my study was primarily funded by the wind energy industry, with EDP Renewable (formerly Horizon Wind Energy) being the principal source of funding. Iberdrola Renewables contributed funding for radio-telemetry collars, and the Shirley Basin/Bates Hole Local Sage-Grouse Working Group provided funding for relocation flights. I thank the United States Department of Energy for providing a substantial grant that assisted in funding my study. The University of Wyoming School of Energy Resources and EDP Renewables provided tuition and fees for my graduate studies at the University of Wyoming. I thank Greg Johnson of Western EcoSystems Technology, Inc. and Matt Holloran of Wyoming Wildlife Consultants, LLC for providing access to the data for this study. I thank Ryan Nielson of Western EcoSystems Technology, Inc. for providing valuable input to statistical procedures used in my thesis. I thank PacifiCorp for allowing access to the Seven Mile Hill Wind Energy Facility for study purposes. I especially thank Burt and Kay Lynn Palm for providing access to their private land. I thank Christopher Kirol for his valuable input on study design used in my study. I thank my advisor Dr. Jeff Beck, for providing me with this opportunity, obtaining funding for my graduate support, and guiding me through my study. In addition, I thank my committee members, Dr. Jeff Beck, Dr. Scott Miller, and Dr. Ken Gerow with the University of Wyoming, Greg Johnson of Western EcoSystems Technology, Inc., and Dr. Matt Holloran of Wyoming Wildlife Consultants, LLC. I appreciate the assistance of Troy Rintz, Jason Herreman, and Victoria Poulton who helped capture sage-grouse. Jamey Eddy, Greg Leighty, Jason Herreman, Ariana Malone, and Brandon Smith assisted with relocating radio-marked sage-grouse and conducting lek counts; all of whom were valuable contributors to my study. Lastly, I would like to thank my wife Rachel for all her support.

TABLE OF CONTENTS

ACKNOWLEDGMENTS ..... iii

LIST OF TABLES ..... vii

LIST OF FIGURES ..... x

CHAPTER 1 Introduction ..... 1

**WIND ENERGY DEVELOPMENT ..... 1**

**GREATER SAGE-GROUSE POPULATION TRENDS ..... 3**

**STUDY PURPOSE ..... 4**

**STUDY AREA ..... 5**

**LITERATURE CITED ..... 7**

CHAPTER 2 Greater Sage-Grouse Habitat Selection Relative to Wind Energy Infrastructure in South-Central, Wyoming ..... 13

**ABSTRACT ..... 13**

**INTRODUCTION ..... 14**

**STUDY AREA ..... 15**

**METHODS ..... 16**

*Field Methods ..... 17*

*GIS Covariates ..... 19*

*Model development ..... 20*

**RESULTS ..... 24**

*Nest Site Selection ..... 25*

*Brood-rearing Habitat Selection ..... 26*

*Summer Habitat Selection ..... 28*

**DISCUSSION** ..... **29**

*Nest Site Selection* ..... *31*

*Brood-rearing Habitat selection* ..... *32*

*Summer Habitat Selection* ..... *33*

**MANAGEMENT IMPLICATIONS** ..... **35**

**LITERATURE CITED** ..... **36**

CHAPTER 3 Greater Sage-grouse Fitness Parameters Associated with Wind Energy Development ..... 61

**ABSTRACT** ..... **61**

**INTRODUCTION** ..... **62**

**STUDY AREA** ..... **65**

**METHODS** ..... **65**

*Field Methods* ..... *65*

*GIS Covariates* ..... *67*

*Survival Parameters* ..... *68*

*Model Development* ..... *70*

**RESULTS** ..... **73**

*Nest Survival* ..... *73*

*Brood Survival* ..... *75*

*Female Survival* ..... *77*

**DISCUSSION** ..... **79**

**MANAGEMENT IMPLICATIONS** ..... **82**

**LITERATURE CITED** ..... **83**

CHAPTER 4 Greater Sage-Grouse Male Lek Attendance Relative to Wind Energy Development ..... 101

**ABSTRACT ..... 101**

**INTRODUCTION ..... 102**

**STUDY AREA ..... 103**

**METHODS ..... 103**

*Field Methods ..... 103*

*Analytical Methods ..... 105*

**RESULTS ..... 108**

*Model Development ..... 109*

**DISCUSSION ..... 110**

**LITERATURE CITED ..... 112**

## LIST OF TABLES

Table 2-1. Explanatory anthropogenic and environmental covariates used in model selection for sage-grouse nest site, brood-rearing, and summer habitat selection at the Seven Mile Hill and Simpson Ridge study areas, Carbon County Wyoming, USA, 2009 and 2010 (Homer et al. 2012). ..... 42

Table 2-2. Model fit statistics for greater sage-grouse nest site selection at the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010. Models are listed according to the model best fitting the data and ranked by (ΔAIC*c*), the difference between the model with the lowest Akaike's Information Criterion for small samples (AIC*c*) and the AIC*c* for the current model. The value of the maximized log-likelihood function (log[L]), the number of estimated parameters (K), and Akaike's weights ($w_i$) for each model are also presented. ..... 43

Table 2-3. Odds ratios, slope coefficients, and 90% confidence intervals (CI) in the sage-grouse top nest site selection model for the Seven Mile Hill and Simpson Ridge study areas in Carbon County, Wyoming, USA, 2009 and 2010. Odds ratios measure the multiplicative change in odds of selection when a covariate changes by 1 unit, assuming all other covariates remain constant. ..... 44

Table 2-4. Model fit statistics for greater sage-grouse brood selection at the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010. Models are listed according to the model best fitting the data and ranked by (ΔAIC*c*), the difference between the model with the lowest Akaike's Information Criterion for small samples (AIC*c*) and the AICc for the current model. The value of the maximized log-likelihood

function (log[L]), the number of estimated parameters (K), and Akaike's weights ($w_i$) for each model are also presented..... 45

Table 2-5. Odds ratios, slope coefficients, and 90% confidence intervals (CI) for covariates in the sage-grouse top brood-rearing selection model for the Seven Mile Hill and Simpson Ridge study areas in Carbon County, Wyoming, USA, 2009 and 2010. Odds ratios measure the multiplicative change in odds of selection when a covariate changes by 1 unit, assuming all other covariates remain constant. Odds ratios were not calculated for covariates involved with a quadratic effect because they were dependent on values of other covariates. ..... 46

Table 2-6. Model fit statistics for greater sage-grouse summer selection at the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010. Models are listed according to the model best fitting the data and ranked by ($\Delta$AIC*c*), the difference between the model with the lowest Akaike's Information Criterion for small samples (AIC*c*) and the AIC*c* for the current model. The value of the maximized log-likelihood function (log[L]), the number of estimated parameters (K), and Akaike's weights ($w_i$) for each model are also presented. ..... 47

Table 2-7. Odds ratios, slope coefficients, and 90% confidence intervals (CI) for covariates in the sage-grouse top summer selection model for the Seven Mile Hill and Simpson Ridge study areas in Carbon County, Wyoming, USA, 2009 and 2010. Odds ratios measure the multiplicative change in odds of selection when a covariate changes by 1 unit, assuming all other covariates remain constant. Odds ratios were not calculated for covariates involved with a quadratic effect because they were dependent on values of other covariates. ..... 48

Table 3-1. Explanatory anthropogenic and environmental covariates used in modeling of sage-grouse nest, brood, and female survival at the Seven Mile Hill and Simpson Ridge study areas, Carbon County Wyoming, USA, 2009 and 2010. ..... 91

Table 3-2. Model fit statistics for greater sage-grouse nest, brood, and survival at the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010. Models are listed according to the model best fitting the data and ranked by (Δ AIC*c*), the difference between the model with the lowest Akaike's Information Criterion for small samples (AIC*c*) and the AIC*c* for the current model. The value of the maximized log-likelihood function (log[L]), the number of estimated parameters (K), and Akaike's weights ($w_i$) for each model are also presented. ..... 92

Table 3-3. Relative risks of sage-grouse for each covariate or risk factor included in the top model for the Seven Mile Hill and Simpson Ridge study areas in Carbon County, Wyoming, USA, 2009 and 2010. ..... 93

Table 4-1. Disturbance metrics included in the mixed modeling procedure to determine potential extents of impact from turbines to male lek attendance at leks located within the Seven Mile Hill and Simpson Ridge study areas in Carbon County Wyoming, USA, 2008–2012. Metrics were derived from male breeding use areas (0.60 km), identified management areas (3.2 km), or disturbance distances previously determined from oil and gas development. ..... 116

Table 4-2. Maximum counts, yearly averages, and totals of male sage-grouse on occupied leks located within the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2008–2012. Entries of "NA" indicate no count was conducted. ..... 117

## LIST OF FIGURES

Figure 1-1. Seven Mile Hill and Simpson Ridge study areas located in Carbon County, Wyoming, USA. The Seven Mile Hill Wind Energy facility consisted of 79, 1.5-MW wind turbines. The Simpson Ridge study area comprised of the area within and surrounding the Simpson Ridge Wind Resource Area (SRWRA). ..... 12

Figure 2-1. Odds ratios or relative probability of sage-grouse nest site selection and 90% confidence intervals (dashed lines) within the Seven Mile Hill study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value. Overlapping confidence limits indicate a non-significant estimate. ..... 49

Figure 2-2. Odds ratios or relative probability of sage-grouse nest site occurrence and 90% confidence intervals (dashed lines) within the Simpson Ridge study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value. ..... 50

Figure 2-3. Predicted nesting habitat used within a 129 $km^2$ minimum convex polygon by sage-grouse within the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010..... 51

Figure 2-4. Predicted nesting habitat used within a 217 $km^2$ minimum convex polygon by sage-grouse within the Simpson Ridge Study area, Carbon County, Wyoming, USA, 2009 and 2010..... 52

Figure 2-5. Odds ratios or relative probability of sage-grouse brood-rearing selection and 90% confidence intervals (dashed lines) within the Seven Mile Hill study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. Confidence

intervals were not calculated for distance to transmission line because confidence intervals for quadratic effects depend on values of other covariates. ..... 53

Figure 2-6. Odds ratios or relative probability of sage-grouse brood-rearing occurrence and 90% confidence intervals (dashed lines) within the Simpson Ridge study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value. Overlapping confidence limits indicate a non-significant estimate. ..... 54

Figure 2-7. Predicted brood-rearing habitat used within a 126 $km^2$ minimum convex polygon by sage-grouse within the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010. ..... 55

Figure 2-8. Predicted brood-rearing habitat used within a 650 $km^2$ minimum convex polygon by sage-grouse within the Simpson Ridge study area, Carbon County, Wyoming, USA, 2009 and 2010. ..... 56

Figure 2-9. Odds ratios or relative probability of female sage-grouse summer occurrence and 90% confidence intervals (dashed lines) within the Seven Mile Hill study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value. ..... 57

Figure 2-10. Odds ratios or relative probability of female sage-grouse summer occurrence and 90% confidence intervals (dashed lines) within the Simpson Ridge study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value.

Confidence intervals were not calculated for distance to major road because confidence intervals for quadratic effects depend on values of other covariates. ..... 58

Figure 2-11. Predicted summer habitat used within a 243 $km^2$ minimum convex polygon by sage-grouse within the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010. ..... 59

Figure 2-12. Predicted summer habitat used within a 751 $km^2$ minimum convex polygon by sage-grouse within the Simpson Ridge study area, Carbon County, Wyoming, USA, 2009 and 2010. ..... 60

Figure 3-1. Relative hazard rate of nest survival adjusted for the SD of shrub height within 0.30 km, and the distance to nearest turbine and transmission line at the Simpson Ridge and Seven Mile Hill study areas, Carbon County, Wyoming, USA, 2009 and 2010. Dashed lines indicate the lower and upper 90% confidence limits. ..... 94

Figure 3-2. Expected nest survival and 90% confidence intervals for nests located in higher risk habitats (closer to turbines, further from transmission lines, and higher SD of shrub height within 0.30 km; poor nest survival) and for nests located in lower risk habitats (good nest survival) within the Simpson Ridge and Seven Mile Hill study areas Carbon County, Wyoming, USA, 2009 and 2010. ..... 95

Figure 3-3. Spatial variation in the predicted relative risk of sage-grouse nest failure (low – high) within the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010. ..... 96

Figure 3-4. Relative hazard rate of brood survival adjusted for distance to nearest turbine, terrain ruggedness, and percent shrub cover at the Simpson Ridge and Seven Mile Hill study

areas, Carbon County, Wyoming, USA, 2009 and 2010. Dashed lines indicate the lower and upper 90% confidence limits..... 97
Figure 3-5. Spatial variation in the predicted relative risk of sage-grouse brood failure (low – high) within the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010..... 98
Figure 3-6. Relative hazard rate of female survival adjusted for the distance to nearest major road and distance to nearest overhead transmission line at the Simpson Ridge and Seven Mile Hill study areas, Carbon County, Wyoming, USA, 2009 and 2010. Dashed lines indicate the lower and upper 90% confidence limits..... 99
Figure 3-7. Spatial variation in the predicted relative risk of sage-grouse summer mortality (low – high) within the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010..... 100
Figure 4-1. Lek locations within the Seven Mile Hill and Simpson Ridge study areas located in Carbon County, Wyoming, USA, 2008–2011..... 118
Figure 4-2. Ratio of means (± 90% CI) of peak male lek attendance observed at Simpson Ridge (SR), Seven Mile Hill (SMH), and regional (REG) leks from 2008–2012, Carbon County Wyoming, USA. Pre-development (2008) counts were used as the baseline to detect changes in peak male lek attendance to 4 years post development. The 2012 lek data was not available for the regional lek population at time of publication..... 119
Figure 4-3. The distribution of standardized residuals from the linear regression model comparing male lek attendance to year and study area in Carbon County, Wyoming, USA, 2008–2012. The standardized residuals were plotted against individual leks within both study areas. Leks located above and below the zero residual line indicate within lek

correlation. Boxes include the interquartile range (25th–75$^{th}$ percentile) in standardized residuals; horizontal lines inside boxes are median standardized residuals; lower and upper whiskers are standardized residuals extending to 1.5 times the interquartile range. ..... 120

# CHAPTER 1

# Introduction

## WIND ENERGY DEVELOPMENT

Increasing concern for environmental sustainability and the demand for domestic energy have led to investment in renewable energies including biofuels, geothermal, hydropower, solar, and wind in the United States. The United States has adopted a nationwide energy policy focused on renewable energies that states that 20% of all electricity will be provided by wind energy by 2030 (DOE 2008). This initiative has triggered a nationwide increase in wind energy development. In addition, energy demand and tax incentives are encouraging prolific development of wind energy resources, making wind energy the fastest growing renewable energy source.

Wind energy development is occurring across many different landscapes, potentially resulting in habitat fragmentation for numerous wildlife species, ultimately leading to indirect and direct impacts (Kuvlesky et al. 2007). Direct impacts to wildlife species include bird and bat collisions with wind turbine blades or other infrastructure associated with wind energy development (e.g., guy wires, meteorological towers, and power lines). Such impacts to birds and bats are well documented (e.g., Erickson et al. 2001, Johnson et al. 2003). While direct impacts of wind energy development to birds and bats have been well documented, knowledge of indirect impacts is lacking. Indirect impacts potentially resulting from size, noise, and placement of turbines and associated wind energy infrastructure, including roads, transmission lines, and power transfer stations, pose the greatest threat to wildlife (Kuvlesky et al. 2007). The cumulative direct and indirect impacts from wind energy development to wildlife and their

habitats may contribute to overall declines in productivity and population persistence (WGFD 2009).

Wind energy development is increasing in prairie habitats with high wind capacity (AWEA 2010). This has raised concerns over impacts to prairie grouse species including greater sage-grouse (*Centrocercus urophasianus*), sharp-tailed grouse (*Tympanuchus phasianellus*), and lesser (*T. pallidicinctus*), and greater (T. *cupido*) prairie-chickens (Kuvlesky et al. 2007). Although direct impacts to prairie grouse are likely to be low, indirect impacts from anthropogenic features are likely to occur (Kuvlesky et al. 2007). Pruett et al. (2009*a*) suggest that indirect impacts of wind turbines and associated power transmission lines are likely to impact prairie grouse movement because the species avoid tall structures and areas with human activities. Pruett et al. (2009*b*) determined that lesser and greater prairie-chickens avoided transmission lines and some major roads by at least 100 m in Oklahoma. There few publicly available studies examining the response of prairie grouse species to wind energy development (Johnson and Stephens 2010). Near an operating wind energy facility in Nebraska, prairie-chicken and sharp-tailed grouse lek attendance appeared to be within the range of other non-impacted leks during a 4-yr period (NGPC 2009). In Minnesota, nesting female prairie chickens did not avoid wind turbines when selecting of adequate nesting habitat (Toepfer and Vodehnal 2009). Lastly, black grouse (*Lyrurus tetrix*) lek attendance was negatively impacted by wind turbines 4-yrs after development of a facility in Austria (Zeiler and Grunschachner-Berger 2009).

Little information exists on the impacts of wind energy development on greater sage-grouse (hereafter sage-grouse). However, numerous studies indicate that sage-grouse are influenced by anthropogenic features including energy development (Lyon and Anderson 2003, Holloran 2005, Doherty et al. 2008, Holloran et al. 2010). In addition, the degree of influence

varies by proximity to these features (Holloran 2005, Aldridge and Boyce 2007, Holloran et al. 2010). Holloran (2005) reported that adult female sage-grouse remained in traditional nesting areas regardless of increasing development levels, though yearling females avoided energy infrastructure by nesting farther away from development. Furthermore, Holloran et al. (2010) determined the number of yearling female nests within 950 m of infrastructure was less than expected and the number of nests outside of 950 m was more than expected. Holloran (2005) found that sage-grouse nests were more successful in areas of lower natural gas well densities, compared to that of higher density areas. In addition, nest initiation rates were reduced in areas of greater vehicle traffic from gas development (Lyon and Anderson 2003).

Similar to nesting parameters, impacts from anthropogenic features also influence brood-rearing parameters. Aldridge and Boyce (2007) reported that chick mortality was 1.5-times higher in habitats where oil and gas wells were visible 1 km from brood-rearing sites. Lastly, male sage-grouse lek attendance rates have been negatively impacted by oil and gas development (Holloran 2005, Walker et al. 2007, Doherty 2008, Harju et al. 2010).

These examples describe some degree of influence by anthropogenic features on sage-grouse distribution and productivity (Holloran 2005, Aldridge and Boyce 2007, Holloran et al. 2010). However, studies addressing the potential impacts of wind energy development to prairie grouse, especially sage-grouse, are lacking.

**GREATER SAGE-GROUSE POPULATION TRENDS**

Sage-grouse occur in Alberta, California, Colorado, Idaho, Montana, Nevada, North Dakota, Oregon, Saskatchewan, South Dakota, Utah, Washington, and Wyoming, where they occupy about 56% of their historical pre-settlement range (Schroeder et al. 2004). Sage-grouse have been experiencing range-wide population declines, and many monitored populations have been

declining 2% per year since 1965 (Connelly et al. 2004). Garton et al. (2011) predicted that at least 13% of sage-grouse populations may decline below effective population sizes of 500 within the next 30 years. Also, Garton et al. (2011) projected that 75% of populations and 29% of the 7 management zones in the United States are likely to decline below effective population sizes of 500 within 100 yrs if current conditions and trends persist.

The decline in sage-grouse populations has been attributed to degradation of sagebrush habitats (Knick et al. 2003, Connelly et al. 2004, and Aldridge et al. 2008) from disturbance factors including agricultural conversion (Swenson et al. 1987, Connelly et al. 2004), invasions of exotic plants leading to increased fire frequencies (Knick et al. 2003, Connelly et al. 2004), and more recently energy exploitation and extraction (Lyon and Anderson 2003, Holloran 2005, Holloran et al. 2010, Doherty et al. 2011, Naugle et al. 2011). Sage-grouse are a sagebrush obligate species (Braun et al. 1977), entirely dependent on healthy continuous sagebrush habitats for successful reproduction and survival (Schroeder et al. 1999, Connelly et al. 2004). Fragmentation and degradation of these sagebrush habitats inhibit sage-grouse productivity and survival, which have long-term impacts on affected sage-grouse populations. Understanding the current threats and potential new threats to the viability of sage-grouse populations is imperative to the conservation of this species.

**STUDY PURPOSE**

The conservation efforts of sage-grouse populations must consider all potential threats that inhibit population viability. Energy exploitation that includes oil and gas development is considered a threat to sage-grouse population viability (Lyon and Anderson 2003, Holloran 2005, Holloran et al. 2010, Doherty et al. 2011, Naugle et al. 2011). Energy exploitation in the form of wind energy may pose similar threats to sage-grouse populations; however, the extent of

these impacts on population viability is unknown. My study was the first study examining the potential short-term impacts to sage-grouse populations from wind energy development. The purpose of my study was to estimate the effects of wind energy infrastructure, particularly wind turbines, on sage-grouse habitat selection patterns, population demographics, and male lek attendance.

**STUDY AREA**

My study area was located in Carbon County, Wyoming between the towns of Medicine Bow and Hanna (Fig. 1-1). The area was positioned north of Elk Mountain and Interstate-80 and south of the Shirley Basin. Land ownership included Bureau of Land Management (BLM), private, and State of Wyoming lands. Seven Mile Hill (SMH) was situated in the northern portion of my study area, and had an operating wind energy facility. The Seven Mile Hill Wind Energy Facility (SWEF) located within SMH consisting of 79-General Electric 1.5-MW turbines capable of producing 118.5 MW of electricity on an annual basis (Fig. 1-1). Construction of this facility began in late summer of 2008 and the facility became operational by December 2008. The facility was situated north of U.S. Highway 30/287 and south of the Medicine Bow River (Fig. 1-1). Elevations in the northern portion of the study area range from 1,737 to 2,118 m above sea level with the highest point being Seven Mile Hill. Mean annual precipitation averaged 26.7 cm and the area was classified as semiarid, cold desert with average temperatures ranging from -2.33°C to 13.61°C (WRCC 2012). Scrub and shrub, dominated primarily by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), was the most common cover type in the SMH study area (USGS 2001). There were 5 occupied sage-grouse leks located within the SMH study area (Fig. 1-1).

Simpson Ridge (SR), an area absent of wind turbines, lies adjacent to the SMH wind energy facility, south of U.S. Highway 30/287 (Fig. 1-1). The Simpson Ridge Wind Resource Area (SRWRA) is a proposed wind energy facility and is located within SR (Fig. 1-1). Due to high densities of breeding sage-grouse, most of the SRWRA was within an area mapped by the State of Wyoming as a sage-grouse "Core Population Area" (version 3, (EO) 2010-4, which was updated on June 2, 2011 by Governor Mead's EO 2011-5). Currently, development of this site has been terminated. The SR study area comprised the SRWRA and the surrounding area south of U.S. Highway 30/287. The SR contained numerous ridges interspersed with rolling to hilly plains. Elevations ranged from 2,040–2,390 m above sea level. Simpson Ridge was situated near the base of the Snowy Range Mountains to the south, and south of the Shirley Basin. Climate was classified as a semiarid, cold desert with a mean annual precipitation average of 26.7 cm and the area was classified as semiarid, cold desert with average temperatures ranging from -2.33°C to 13.61°C (WRCC 2012). Land cover classifications indicate that SR was almost entirely comprised of scrub-shrub dominated by Wyoming big sagebrush (USGS 2001). There were 9 occupied sage-grouse leks located within the SR study area (Fig. 1-1).

The SWEF included 79 turbines and approximately 29 km of access roads; however, other anthropogenic features associated with wind energy development occur throughout the entire study area including SR. There were approximately 8 km of paved roads (US HWY 30) and 26 km of overhead transmission lines within the SMH study area. In addition, there were approximately 50 km of paved roads (I-80, US HWY 30, and state HWY 72) and 17 km of overhead transmission lines within the SR study area. The overhead transmission lines and paved roads have existed on the landscape for more than 10 years. The only anthropogenic features

added to the landscape were the SWEF wind turbines and the associated access roads located within SMH (Fig. 1-1).

**LITERATURE CITED**

Aldridge C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. Diversity and Distributions 14: 983–994.

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

American Wind Energy Association (AWEA). 2010. U.S. Projects Database. <http://www.awea.org/la_usprojects.cfm>. Accessed 1 Feb 2011.

Braun, C. E., T. Britt, and R. O. Wallestad. 1977. Guidelines for maintenance of sage-grouse habitats. Wildlife Society Bulletin 5:99–106.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Cheyenne, Wyoming, USA.

Doherty, K. 2008. Sage-grouse and energy development: Integrating science with conservation planning to reduce impacts. Dissertation, The University of Montana, Missoula, Montana, USA.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187−195.

Doherty, K. E., D. E. Naugle, H. Copeland, A. Pocewiz, and J. Kiesecker. 2011. Energy development and conservation tradeoffs: systematic planning for sage-grouse in their eastern range. Pages 505-517 in S. T. Knick and J. W. Connelly, editors. Greater sage-

grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38. University of California Press, Berkeley, California, USA.

Erickson, W.P., G.D. Johnson, M.D. Strickland, D.P. Young, Jr., K.J. Sernka, and R.E. Good. 2001. Avian collisions with wind turbines: A summary of existing studies and comparisons to other sources of bird collision mortality in the United States. National Wind Coordinating Committee Publication and Resource Document. <http://www.nationalwind.org/assets/archive/Avian_Collisions_with_Wind_Turbines_-_A_Summary_of_Existing_Studies_and_Comparisons_to_Other_Sources_of_Avian_Collision_Mortality_in_the_United_States__2001_.pdf>. Accessed 10 Nov 2011.

Garton, E. O., J. W. Connelly, J. S. Horne, C. A. Hagen, A. Moser, and M. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Pages 293-383 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38. University of California Press, Berkeley, California, USA.

Harju, S. M., M. R. Dzialak, R. C. Taylor, L. D. Hayden-Wing, J. B. Winstead. 2010. Thresholds and time lags in effects of energy development on greater sage-grouse populations. Journal of Wildlife Management 74:437–448.

Holloran, M. J. 2005. Greater sage-grouse (Centrocercus urophasianus) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Johnson, G. D., M. K. Perlik, W. P. Erickson, M. D. Strickland, D. A. Shepherd, and P. Sutherland, Jr. 2003. Bat interactions with wind turbines at the Buffalo Ridge, Minnesota Wind Resource Area: an assessment of bat activity, species composition, and collision mortality. Electric Power Research Institute, Palo Alto, California and Xcel Energy, Minneapolis, Minnesota, USA.

Johnson, D. H. and S. E. Stephens. 2011. Windpower and biofuels: A geen dilemma for wildlife conservation. Pages 131-157 in D. E. Naugle, editor. Wildlife Conservation in Western North America. Island Press, Washington, DC, USA.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. S. Schroeder, W. M. Vander Hagen, and C. V. Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611−634.

Kuvlesky, W. P., L. A. Brennan, M. L. Morrison, K. K. Boydston, B. M. Ballard, F. C. Bryant. 2007. Wind energy development and wildlife challenges and opportunities. Journal of Wildlife Management 71:2487–2498.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486–491.

Naugle, D. E., K. E. Doherty, B. L. Walker, M. J. Holloran, and H. E. Copeland. 2011. Energy development and greater sage-grouse. Pages 489-505 in S. T. Knick and J. W. Connelly, editors. Greater Sage-Grouse: Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38. University of California Press, Berkeley, California, USA.

Nebraska Game and Parks Commission (NGPC). 2009. Locations of sharp-tailed grouse and greater prairie-chicken display grounds in relation to NPPD Ainsworth Wind Energy Facility: 2006-2009. Nebraska Game and Parks Commission, Lincoln, Nebraska, USA.

Pruett, C. L., M. A. Patten, D. H. Wolfe. 2009a. It's not easy being green: Wind energy and a declining grassland bird. Bioscience 59: 257–262.

Pruett, C. L., M. A. Patten, D. H. Wolfe. 2009b. Avoidance behavior by prairie grouse: Implications for development of wind energy. Conservation Biology 23:1253–1259.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. Condor 106:363–373.

Schroeder, M.A., J.R. Young, and C.E. Braun. 1999. Sage grouse (Centrocercus urophasianus). Pages 1-28 in A. Pool and F. Gill, editors. The Birds of North America. The Birds of North America, Inc, Philadelphia, Pennsylvania, USA.

Swenson, J. E., C. A. Simmons, and C. D. Eustace. 1987. Decrease in sage grouse *Centrocercus urophasianus* after ploughing of sagebrush steppe. Biological Conservation 41:125-132.

Toepfer, J. E. and W. L. Vodehnal. 2009. Greater prairie chickens: Grassland and vertical structures. Presentation at the 28th meeting of the Prairie Grouse Technical Council, Portales, New Mexico, USA.

United States Department of Energy (DOE). 2008. 20% Wind energy by 2030, increasing wind energy's contribution to U.S. electricity supply. United States Department of Energy, Washington, D. C., USA.

US Geological Survey National Land Cover Database (USGS). 2001. Land Use/Land Cover NLCD Data. USGS Headquarters, USGS National Center, Reston, Virginia, USA.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

Western Regional Climate Center (WRCC). 2012. Medicine Bow, Wyoming (486120). <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wy6120>. Accessed 01 Feburary 2012.

Zeiler, H.P. and V. Grünschachner-Berger. 2009. Impact of wind power plants on black grouse, *Lyrurus tetrix* in Alpine regions. Folia Zoologica 58:173-182.

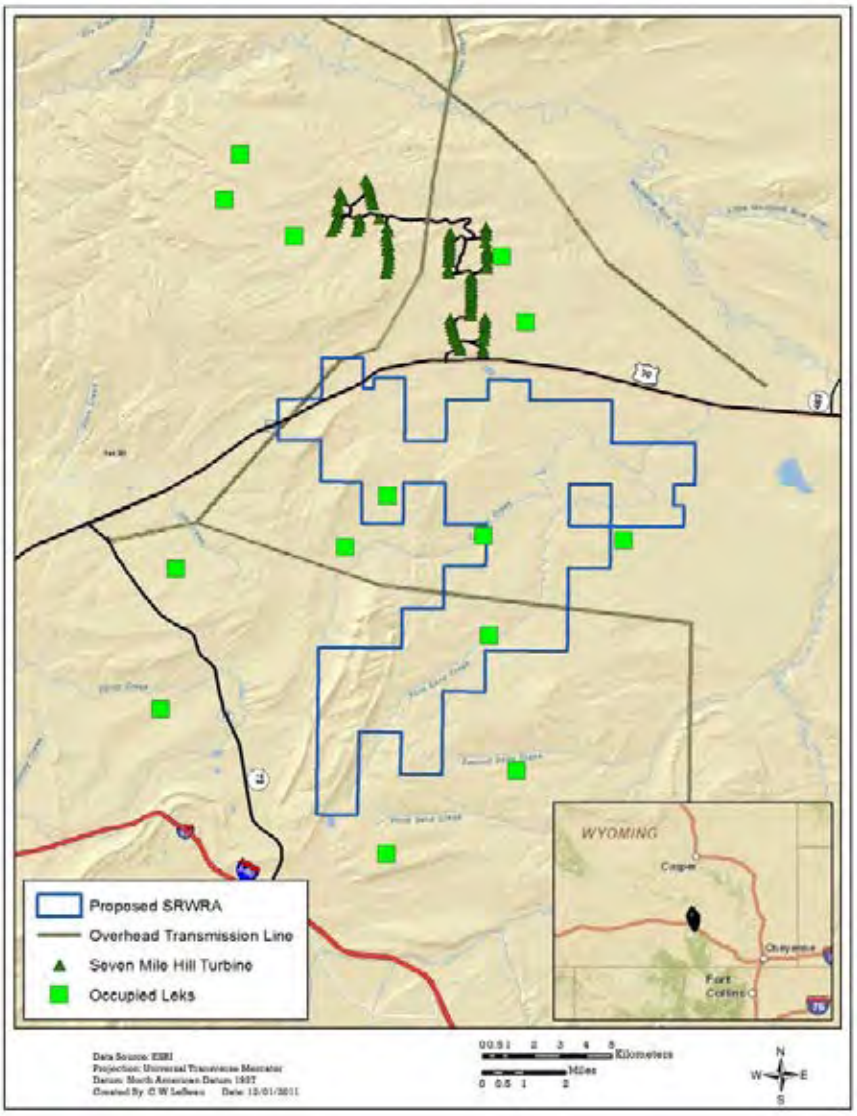



Figure 1-1. Seven Mile Hill and Simpson Ridge study areas located in Carbon County, Wyoming, USA. The Seven Mile Hill Wind Energy facility consisted of 79, 1.5-MW wind turbines. The Simpson Ridge study area comprised of the area within and surrounding the Simpson Ridge Wind Resource Area (SRWRA).

# CHAPTER 2

## Greater Sage-Grouse Habitat Selection Relative to Wind Energy Infrastructure in South-Central, Wyoming

In the format for manuscript submittal to the *Journal of Wildlife Management*


## ABSTRACT

The degradation of sagebrush habitats within the range of greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) has been attributed to a number of environmental and anthropogenic influences including agriculture, large-scale wildfires, and energy extraction. The impacts from energy extraction to sage-grouse populations in the form of oil and gas development have been well documented. The increasing demand for renewable energy has prompted a potential new threat to sage-grouse populations in the form of wind energy development. However, it is unknown if wind turbines and the infrastructure associated with wind energy development will impact the habitat selection patterns of sage-grouse populations. I hypothesized that sage-grouse selected for habitats farther from wind energy infrastructure, particularly wind turbines, during three biologically meaningful periods. In 2009 and 2010, I captured and radio-marked 50 sage-grouse within an existing wind energy facility and 66 within an area not impacted by wind energy development. I monitored the marked sage-grouse via radio-telemetry during the nesting, brood-rearing, and summer periods to document habitat selection. I utilized binary logistic regression to predict the odds of habitat selection within both study areas. I used forward model selection and Akaike's information criterion to identify the best predictive model within both study areas. I validated each top model using K-fold cross validation. Lastly, I created resource selection functions to depict areas of varying levels of habitat selection. The presence of turbines did not influence sage-grouse nest site selection or

brood-rearing habitat selection. However, sage-grouse appeared to select for habitats in close proximity to wind turbines during the summer period. These results may be related to the fact that areas near turbines are comprised of high quality habitats that were used extensively by sage-grouse prior to development of the SMH wind energy facility; however without the collection of pre-development data, it is difficult to speculate the reasons for these selection patterns. The results of my habitat selection modeling did not support my hypothesis that sage-grouse avoid wind turbines during the nesting, brood-rearing, and summer periods. I caution the interpretations of these results because of the strong site fidelity exhibited by sage-grouse and the inherent time lags associated with population-level response to anthropogenic infrastructure as seen in oil and gas developments. However, these results provide valuable insights into the short-term impacts to sage-grouse distribution influenced by wind energy development.

**INTRODUCTION**

Large home ranges and complex habitat selection patterns are characteristic of many greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) populations (e.g., Doherty et al 2008, Atamian et al. 2010, Carpenter et al. 2010). The addition of wind energy infrastructure (hereafter, infrastructure) including turbines, roads, and transmission lines may displace sage-grouse from suitable or desired habitat. From 1984 to 2010, 19 studies examined displacement effects on prairie grouse species from energy development and 12 of these studies were specific to sage-grouse (Hagen 2010). However, none of these studies were specific to the displacement effects of wind energy infrastructure on sage-grouse species.

Displacement impacts similar to those found for sage-grouse from oil and gas development is a growing concern for sage-grouse occupying habitats in close proximity to wind energy development. Some scientists speculate that the skyline created from infrastructure may

displace sage-grouse hundreds of meters or even kilometers from their normal range (USFWS 2003, NWCC 2004). Changing movements may result in selection of poorer quality habitats, ultimately reducing population fitness. If birds are displaced, it is unknown whether in time, local populations may become acclimated to elevated structures. The USFWS argues that placement of tall man-made structures, such as wind turbines, in occupied prairie grouse habitat may result in a decrease in habitat suitability (USFWS 2004). In addition to the displacement from turbines, overhead transmission lines, a type of infrastructure associated with wind energy development, might displace sage-grouse populations. Overhead transmission lines provide perches for avian predators of sage-grouse including ravens (*Corvus corax*) and golden eagles (*Aquila chrysaetos*; Steenhof et al. 1993) and it is assumed that increased predation or indirect impacts from raptors may occur to sage-grouse populations (Ellis 1984, Coates and Delehanty 2010). Although the potential exists for wind turbines to displace greater sage-grouse from occupied habitat, well-designed studies examining the potential impacts of wind turbines on greater sage-grouse are lacking (Johnson and Holloran 2010).

The purpose of my study was to investigate the effect of wind energy infrastructure on sage-grouse distribution and habitat selection patterns. Specifically, I investigated sage-grouse habitat selection during three biologically meaningful periods that included nesting, brood-rearing, and summer within an existing wind energy facility and in comparison to an adjacent, non-developed area. I hypothesized that sage-grouse avoided infrastructure, specifically turbines, when selecting for nesting, brood-rearing, and summer habitats. This information is critical in planning future wind energy development facilities that occur within occupied sage-grouse habitats.

**STUDY AREA**

My study area included the Seven Mile Hill (SMH) study area, which was influenced by infrastructure, and the non-impacted Simpson Ridge (SR) study area. The SMH and SR study areas were separated by U.S. Highway 30/287; however, the minimum distance between SMH and SR occupied leks was approximately 8.5 km. Sage-grouse movements between study areas were relatively low (5% of all marked sage-grouse [6] and 3% of all locations [64] from sage-grouse captured from one of the 2 study areas were documented in the other study area). Consequently, sage-grouse that were captured on leks north of U.S. Highway 30/287 were included in the SMH analysis area and sage-grouse captured south of U.S. Highway 30/287 were included in the SR analysis area. In addition, the leks on SMH were in closer proximity to turbines than those at SR. Because of the general lack of movement by sage-grouse and the difference in infrastructure between the 2 areas, I considered SMH the impacted area and SR the control. Please refer to Chapter 1 for detailed descriptions of each study area (see Fig. 1-1).

**METHODS**

I used binary logistic regression to estimate resource selection functions (RSF) within the SR and SMH study areas to identify the odds of female sage-grouse habitat selection as a function of environmental and infrastructure covariates (Manly et al. 2002). I defined habitat selection (i.e., aka resource selection) as the process by which a sage-grouse chooses habitat components to use (Johnson 1980). Logistic regression is widely used and is a valuable tool to estimate resource selection functions, which are commonly used to evaluate wildlife habitat relationships (Johnson et al. 2006, Manly et al 2002). Animals select particular resource units within available habitats to satisfy particular life requirements. The used resource units can be compared to available resource units to estimate resource selection of that animal (Manly et al. 2002). The results of this comparison can be incorporated into an RSF, which is defined as any function that is

proportional to the probability of use by an animal (Manly et al. 1993, 2002). I used RSF's to predict the odds of habitat selection by sage-grouse during the three seasons within both study areas.

**Field Methods**

I captured 116 female sage-grouse by spotlighting and use of hoop nets (Giesen et al. 1982, Wakkinen et al. 1992) on roosts surrounding leks during the 2009 and 2010 breeding seasons. Initial capture efforts were centered within SR during the first study year (2009) where 50 sage-grouse females were targeted and 25 were targeted within SMH. During the second study season (2010) the target sample size increased to 40 at SMH and 45 at SR. I attempted to capture grouse at all accessible active lek sites within 16 km of the SMH wind turbines proportionately to the number of males attending those leks. I aged, weighed (0.1-g precision), acquired blood samples (year 2009 only), and fitted each captured grouse with a 22-g necklace-mounted radio transmitter with a battery life of 666 days (Advanced Telemetry Systems, Isanti, MN). I then released each radio-marked female grouse at the point of capture and marked the location using a hand held global positioning system (GPS) unit.

I relocated each radio-marked female at least twice each week during the prelaying and nesting period (Apr through Jun); once every week for brooding females during the brood-rearing period (hatch through 15 Aug); and, at least once per week during the summer (Jun through 1 Sep) periods for all barren females (e.g., females that were unsuccessful in producing or raising young or were not currently nesting or raising young). Marked sage-grouse were monitored primarily from the ground using hand-held receivers. I determined sage-grouse locations by triangulation or homing until visibly observed and classified radio-locations as breeding, nesting, brood-rearing, or summer. I estimated triangulation locations by taking two

vectors in the direction of the signal. In addition, I estimated the triangulation error by placing 6 test collars for each technician throughout both project areas and estimated the mean telemetry error between the actual and estimated locations recorded by each technician. The mean error telemetry rate was incorporated into the habitat selection modeling effort. I employed aerial telemetry to locate missing birds throughout the study period.

I determined nesting success for each radio-marked female sage-grouse from long range triangulation at least every third day throughout the nesting season, late April through 15 June. I assumed females were nesting when movements became localized. Nests were located using a progressively smaller concentric circle approached by walking circles around the radio signal using the signal strength as an indication of proximity (Holloran and Anderson 2005). Once I visually confirmed the female in an incubating position, the location of the observer was recorded with a GPS and a photograph was taken of the habitat surrounding the incubating hen. All future monitoring of the nest was made from remote locations (>60 m) using long distance triangulation to minimize potential disturbance. Once a nest location was established, I conducted incubation monitoring on an alternate-day schedule to determine nesting fate. For each nest and re-nest, data were collected on timing of incubation and nest success. All nest locations were mapped using a hand-held GPS. I considered a nest that successfully hatched (i.e., eggs with detached membranes) ≥1 egg to be a successful nesting attempt. Nests that failed to successfully hatch ≥1 egg were considered failed nesting attempts whose fates included predation (avian, mammal, and unknown) and abandoned. Females that were unsuccessful in their first nesting attempt were monitored three times per week to determine possible re-nesting attempts. I monitored females that were unsuccessful in their first or second nesting attempt at least once each week through 1 September in 2009 and 2010.

I located radio-marked females that successfully hatched ≥1 egg each week through 15 August 2009 and 2010 to evaluate brood-rearing habitat selection. I categorized the brood-rearing period as early (hatch through 14 days post-hatch; Thompson et al. 2006) or late (35 days post-hatch; Walker 2008). Females were considered successful through the early brood-rearing period if ≥1 chick survived to two weeks post-hatch; chick presence during this period was established either through visual confirmation of a live chick or the brooding female's response to the researcher (e.g., chick protective behavior exhibited). I determined fledging success (late brood success) for those females who were successful in early brood-rearing by assessing whether a female was brooding chicks through nighttime spotlight surveys conducted on days 35 and 36 post-hatch (Walker 2008). Similar to sage-grouse with unsuccessful nests, sage-grouse that were unsuccessful during either the early or late brood-rearing period were monitored twice each week through 31 August.

**GIS Covariates**

I developed a suite of covariates to estimate the odds of sage-grouse selecting nest sites, brood-rearing habitat, and summer habitat within both study areas. Major roads included paved highways: U.S. Highway 30/287 traversed east-west separating SR from SMH; Wyoming State Highway 72 traversed north-south through the SR study area; and Interstate 80 traversed east-west south of the SR study area (see Fig. 1-1). The SMH study area included wind turbines and access roads, whereas SR did not. I digitized major roads and overhead transmission lines (230 kV wooden H-frame) using aerial satellite imagery and ArcMap 10 (ESRI 2011). Turbine locations were obtained from PacifCorp, the operators of the Seven Mile Hill Wind Energy Facility.

Environmental covariates included vegetation and topography features within both study areas. Vegetation layers used in my analysis were remote-sensed sagebrush products developed by Homer et al. (2012). This dataset used a combination of methods to integrate 2.4 m QuickBird, 30 m Landsat TM, and 56 m AWiFS (Advanced Wide Field Sensor) imagery into the characterization of four primary continuous field components (percent bare ground, percent herbaceous cover, percent litter, and percent shrub cover) and four secondary components (three subdivisions of shrub cover —percent sagebrush (*Artemisia* spp.), percent big sagebrush (*A. tridentata* spp.), and percent Wyoming big sagebrush (*A. t. wyomingensis*)—and shrub height (Homer et al. 2009, 2012; Table 2-1). Landscape features included elevation, slope, and terrain ruggedness all of which I calculated from a 10 m National Elevation Dataset (USGS, EROS Data Center, Sioux Falls, SD). Terrain ruggedness captured the variability in slope and aspect into a single measure ranging from 0 (no terrain variation) to 1 (complete terrain variation; Sappington et al. 2005; Table 2-1).

**Model development**

I included distance to each infrastructure and each environmental covariate in developing my habitat selection models (Table 2-1). In addition to the linear term for the distance to each anthropogenic feature, I also included the quadratic terms and decay functions (-*exp*[*distance*]/decay distance) because in many instances animals may avoid features up to a certain point, but beyond this point the affect is less realized (Carpenter et al. 2010). Lastly, I included distance to nearest occupied lek as a covariate because sage-grouse are known to select habitats in the vicinity of their leks (Aldridge and Boyce 2007). Also, I included this covariate to account for the spatial correlation between the distance to nearest lek and turbines (i.e., 3 of 5 leks were located within 1.6 km of turbines at SMH).

I used nest locations and locations obtained during the brood-rearing period (hatch through 35 days post-hatch) and 1 June – 31 August for the summer period to model sage-grouse habitat selection throughout both study areas. The sage-grouse populations within both study areas were non-migratory (movements were <10 km between or among seasonal ranges), utilizing similar habitats during all annual life cycles (Connelly et al. 2000, Fedy et al. 2012). More specifically, sage-grouse may select different habitats between the early brood period and late brood-rearing periods (Connelly et al. 1988, Kirol et al. 2012). The shift in habitats from early to late brood is dependent on the habitat available to the brooding females and chicks. Brood habitat selection during the early brood and late brood period within both study areas was not characterized by multiple habitats as determined in other more migratory populations where brood selection shifts from xeric to more mesic areas (Connelly et al. 1988, Kirol et al. 2012). Thus, to increase sample sizes, I combined early and late brood locations to estimate habitat selection during the entire brood-rearing period (Aldridge and Boyce 2007).

Because there were a limited number of locations (≤20 per season) for each marked sage-grouse, I pooled each individual's data within seasons and across years and employed a Type I study design where habitat selection and availability were estimated at the population level (Thomas and Taylor 2006). However, to estimate precision of final estimated model coefficients, individual grouse were treated as the primary sampling units (Thomas and Taylor 2006) through bootstrapping to estimate confidence intervals (Manly 2007). The form of the RSF used was (Manly et al. 2002),

$$w(x) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k),$$

where $w(x)$ represents the odds of selection, the $x$'s were model covariates and $\beta$ were coefficients to be estimated.

Defining the scale and amount of available habitat is an important step in modeling habitat selection for any species (Thomas and Taylor 2006). I investigated sage-grouse habitat selection at a landscape level during each of the seasons. It is recommended that the available habitat for a landscape level habitat selection study should be based on the distribution of radio-collared animals (McClean et al. 2008). Subsequently, I created a 100% minimum convex polygon (MCP) surrounding all observed locations within each study area and representative of life stages to define available habitat (Gillies et al. 2006, Carpenter et al. 2010, Kirol 2012). There were no areas within each MCP that were considered not to be available habitat to sage-grouse (i.e., sagebrush rangeland at low-to-moderate relief that did not include trees).

A geographic information system (GIS) was used to randomly generate available locations at 5 times the number of total observed locations per season (Baasch et al. 2009). The average values representing each environmental feature were extracted at 3 different radii scales, the mean telemetry error rate (0.30 km), the median distance between consecutive year's nests from 2009 to 2010 within both study areas (0.46 km), and the median distance traveled between monitoring intervals during the brood-rearing and summer period (1.0 km). The median movement distance was 1.0 km during brood-rearing and 1.6 km during the summer season; however, I used 1.0 km based on findings from previously published sage-grouse habitat selection studies (Aldridge and Boyce 2007, Carpenter et al. 2010).

Prior to model development, I tested whether each pair of continuous covariates were linearly related using Pearson's correlation analysis. Many of the covariates were correlated with one another ($r \geq |0.6|$). Rather than removing correlated covariates, I allowed for all covariates to compete against each other in a modified forward model selection procedure. However, two highly correlated covariates ($r \geq |0.6|$) were not allowed in the same model. The best

approximating model was identified by comparing the Akaike's information criterion (AIC*c* adjusted for small sample sizes; Burnham and Anderson 2002). The forward model selection procedure continued until the AIC*c* score among models did not change or until the model reached a maximum of 5 covariates (Burnham and Anderson 2002). The model having the lowest AIC*c* and a ΔAIC*c* value ≥4 from the next approximating model was considered the top model (Burnham and Anderson 2002, Arnold 2010). To address model uncertainty in competing models, I model averaged across the 90% confidence set of competing models to estimate the final parameters of the top model to produce more robust estimates (Burnham and Anderson 2002, Arnold 2010).

I used a 90% CI to test levels of confidence in my parameter estimates (alpha level = 0.10). Parameter estimate CI's not containing 0.0 were considered statistically different. Confidence intervals for each coefficient were estimated using a bootstrapping technique where the used locations were randomly sampled with replacement and the final model or modeled averaged estimates was refit to the new sample of used locations and the original available locations (Manly et al. 2002, Manly 2007). I used 1,000 bootstrap iterations to identify the lower and upper confidence limits for each estimate. The value at the $5^{th}$ percentile of the 1,000 estimates represented the lower limit of a 90% confidence limit and the value at the $95^{th}$ percentile represented the upper confidence limit (i.e., the "percentile method"; McDonald et al. 2006). I created marginal effects plots using the estimated parameters and their associated CI's from the top model in each period and study area to show the marginal effect of selected variables. I calculated odds ratios [$(\exp(\beta_0)-1)*100$] from coefficients in the final RSF models and used these to interpret the effect and magnitude of each covariate on sage-grouse habitat selection (McDonald et al. 2006). Odds ratios describe the estimated percent change in odds of

selection for a 1-unit change in a predictor variable. Odds ratios were not calculated for covariates with both linear and quadratic effects because odds ratios for quadratic effects depend on values of other variables. Negative odds ratios indicated a decrease in the odds of selection and positive odds ratios indicated an increase.

After estimating the final model for each period and study area, I predicted odds of selection across both study areas. I placed a 100 m x 100 m grid on the landscape within each MCP to make the predictive maps. I extracted habitat covariates associated with each grid cell based on the representative scale of each covariate included in the top logistic regression models. These values represented the various covariates measured at each habitat unit or grid cell. Lastly, I calculated RSF values and placed them into 5 quantile bins to represent progressively selected habitats.

I validated the top models using a K-fold cross-validation process (Boyce et al. 2002) to assess how well the top models performed among a set of apportioned data. I randomly allocated the used locations into 5 equal-sized groups. Leaving out one set of used data (K; testing), I re-estimated the coefficients in the top models using the available locations and the K-1 groups (training) of used locations. The re-estimated model was then used to make predictions to the available locations and used locations from group K. I binned all predictions into 10 classes of equal size using percentiles, and the number of used points in each class was compared to the class rank (1 = lowest, 10 = highest predicted odds of selection) using a Spearman's rank correlation coefficient. This process was repeated for each of K = 5 groups of used locations. The Spearman's rank correlation coefficients ($r_s$) were averaged to test how well the top model performed on the set of apportioned data.

**RESULTS**

I recorded 2,659 locations (SMH, $n$ = 1,063; SR, $n$ = 1,596) from 116 female sage-grouse (SMH, $n$ = 50, SR, $n$ = 66) during the two study years and during all life stages. Sage-grouse habitat selection was generally concentrated around leks (i.e., within an average of 2.6 km of a lek) within both study areas, especially during the nesting and brood-rearing periods. Sage-grouse captured within SR tended to have a greater distribution compared to sage-grouse captured at SMH; however, leks within SR had a larger distribution than the leks within SMH.

**Nest Site Selection**

I used 94 identified nest locations (SMH, $n$ = 42; SR, $n$ = 52) in my nesting habitat selection analysis. One nest of a female captured at SR was observed within SMH, but was not included in the habitat selection analysis because I did not consider that female to be influenced by wind energy development.

Nest site selection within both study areas differed and included multiple environmental and anthropogenic covariates. The top model for SMH included percent shrub and herbaceous cover, elevation, and distance to nearest lek and major road. There was some model uncertainty between the top two models within SMH (i.e., <4 $\Delta$AIC$c$), thus the final parameters were estimated by model averaging the top two models (Table 2-2). The SR model included only 2 covariates: shrub height (cm) and distance to nearest transmission line and was ≥4 $\Delta$AIC$c$ from the next approximating model (Table 2-2). Distance to nearest turbine was not in the top SMH nest site selection model and adding distance to nearest turbine to the top SMH model did not improve model fit ($\Delta$AIC$c$ = 2.10) or have a significant slope ($\beta$ = -0.04; 90% CI: -0.32–0.24).

The estimated odds of sage-grouse nest site selection within SMH was 81.6% (90% CI: 38.9–159.6%) higher with every 1.0% increase in shrub cover within a 0.30 km radii (Table 2-3; Fig. 2-1). In addition, the odds of selecting a nest site within SMH was 39.2% lower for every

1.0 km increase from nearest occupied lek (90% CI: 27.9–56.1%; Table 2-3; Fig. 2-1). Nest site selection increased by 16.4% with every 1.0 km increase in distance to a major road (90% CI: 4.0–29.5%; Table 2-3; Fig. 2-1). Nest site selection increased by 2.1% with every 1.0 m increase in elevation (90% CI: 1.2–3.3%; Table 2-3; Fig. 2-1). Lastly, percent herbaceous cover was included in the top model; however, the estimated parameter was not significant (90% CI: -2.1–51.1%; Table 2-3; Fig. 2-1).

Shrub height and distance to transmission line were included in the top SR model. The estimated odds of selection increased by approximately 10.1% for every 1 cm increase in shrub height within a 0.30 km radii, but decreased by approximately 15.3% for every 1.0 km increase in distance from nearest transmission line (90% CI: 5.0–16.2% and 7.9–23.4%, respectively; Table 2-3, Fig. 2-2).

Nest site selection was highest in the western portion of the SMH study area and highest in the area surrounding the overhead transmission lines at SR (Fig. 2-3; Fig. 2-4). Lastly, the 5-fold validation method used for the top model for each study area indicated that the SMH top model had good overall predictive ability (average $r_s$ = 0.67); however, the predictive ability for the SR top model was lower (average $r_s$ = 0.49), but still better than random chance.

**Brood-rearing Habitat Selection**

I included 347 early and late brood-rearing locations (SMH, $n$ = 139; SR, $n$ = 209) from 30 brooding females (SMH, $n$ =13; SR, $n$ = 17) in the brood-rearing habitat selection analysis. Habitat and anthropogenic covariates included in the top models differed between both study areas; however, percent bare ground and herbaceous cover were in the top models for each study area. The quadratic form of distance to nearest overhead transmission line, elevation, and percent shrub cover were included in the top SMH brood-rearing model (Table 2-4). The next best

approximating model observed at both study areas was greater than approximately 4 ΔAIC*c* values from the top model (Table 2-4). Similar to SMH, distance to nearest overhead transmission line was also included in the SR top model; however, it retained its linear form. Distance to major road and percent litter cover were also included in the top SR model. I experienced some model uncertainty with the top two models being ≤4 ΔAIC*c* from each other thus I model averaged these two competing models to estimate the final models (Table 2-4). Distance to nearest turbine, was not included in the top model for SMH; however, it did compete with all other covariates during the forward model selection procedure. Adding distance to nearest turbine to the top model within SMH did not improve model fit (i.e., ΔAIC*c* = 0.63; $\beta$ = 0.12; 90% CI: -0.39 to 0.61).

The estimated odds of sage-grouse selecting brood-rearing habitat within SMH increased as distance from nearest overhead transmission line increased up to 4.7 km (90% CI: 2.2–18.5 km, then declined (Table 2-5; Fig. 2-5). Brood-rearing habitat selection decreased by approximately 13.1% for every 1.0% increase in percent bare ground within a 0.46 km radii (90% CI: 8.6–17.5%; Table 2-5; Fig. 2-5). In addition, brood-rearing habitat selection increased by 96.5% and 52.7% for every 1.0% increase in percent herbaceous and shrub cover within a 1.0 km radius (90% CI: 27.8–260.0% and 1.1–158.0%), respectively (Table 2-5; Fig. 2-5).

The SR brood-rearing data supported a model that included distance to nearest transmission line and major road and percent herbaceous cover; however, substantial variability of these covariates, indicated by the inclusion of 0.0 within the CI's, existed across individual birds (Table 2-5; Fig. 2-6). The estimated odds of selecting brood-rearing habitat within SR decreased by 3.3% for every 1.0% increase in percent bare ground cover within 0.30 km (90% CI: 1.1–5.6%; Table 2-6; Fig. 2-6). However, brood-rearing habitat selection increased by 11.4%

for every 1.0% increase in percent litter within 0.46 km (90% CI: 2.0–20.7%; Table 2-5; Fig. 2-6).

Habitats west and east of the wind turbines at SMH had the highest odds of habitat selection during the brood-rearing season (Fig. 2-7). Habitats surrounding the overhead transmission line and in the center of SR were estimated as having the highest probability of brood-rearing habitat selection (Fig. 2-8). Lastly, the 5-fold cross-validation for the top models within the SMH and SR study areas indicated that the final top models had overall good predictive abilities (average $r_s = 0.94$ and $r_s = 0.74$, respectively).

**Summer Habitat Selection**

I included 1,961 summer locations (SMH, $n = 796$; SR, $n = 1,165$) from all female sage-grouse (SMH, $n = 66$; SR, $n = 50$) in the summer habitat selection analysis. The distance to major roads, distance to nearest occupied lek, and percent bare ground formed the top models for each study area. Distance to nearest turbine and elevation were additional covariates included in the SMH top model. Percent herbaceous cover and Wyoming big sagebrush cover were also included in the SR top model. The next approximating model observed at both study areas was greater than approximately 40 $\Delta$AIC$c$ values from the top model (Table 2-6).

The estimated odds of selecting summer habitat within SMH decreased by approximately 26.5% for every 1.0 km increase in distance from nearest occupied lek and by 22.4% for every 1.0 km increase in distance to nearest turbine (90% CI: 15.0– 38.7% and 10.7–33.3%, respectively; Table 2-7, Fig. 2-9). Summer habitat selection increased by 17.1% for every 1.0 km increase in distance from nearest major road (90% CI: 7.3–29.0%; Table 2-7; Fig. 2-9). In addition, summer habitat selection decreased by 7.3% for every 1.0% increase in percent bare ground cover within 0.30 km (90% CI: 5.4–9.4%; Table 2-7, Fig. 2-9). Lastly, summer habitat

selection increased by 0.76% for every 1 m increase in elevation (90% CI: 0.3–1.3%; Table 2-7, Fig. 2-9).

Similar to SMH, the odds of selecting summer habitat within SR decreased by approximately 22.5% for every 1.0 km increase in distance from nearest occupied lek and by 12.9% for every 1.0% increase in percent bare ground cover within 1.0 km (90% CI: 10.4–35.3 and 8.0–17.6%, respectively; Table 2-7, Fig. 2-10). In addition, summer habitat selection increased as distance to nearest major road increased up to 8.7 km (90% CI: 1.2–32.0 km), then declined (Fig. 2-10). Lastly, summer habitat selection decreased by 13.4% with every 1.0% increase in percent herbaceous cover and increased by 34.2% with every 1.0% increase in Wyoming big sagebrush cover within 1.0 km (90% CI: 4.0–23.1and 7.3–78.4%, respectively; Table 2-7; Fig. 2-10).

Similar to nest and brood occurrence, the odds of summer habitat selection was highest within habitats west and east of the wind turbines at SMH; however much of these habitats occurred in close proximity to turbines (Fig. 2-11). In addition, summer habitats with the highest odds of selection occurred throughout much of the area within SR; however, most of this habitat occurred within the center of the study area in close proximity to occupied leks (Fig. 2-12). Lastly, the 5-fold cross-validation method used on the top models within the SMH and SR study areas indicated that the final top models had overall strong predictive abilities (average $r_s$ = 0.88 and average $r_s$ = 0.91, respectively).

**DISCUSSION**

The proximity to wind turbines did not influence nest site or brood-rearing habitat selection, but the odds of summer selection increased in habitats closer to wind turbines. In addition, the top models without distance to nearest turbines (i.e., habitat covariates only) experienced some

variability between study areas suggesting the control area used in my analysis may not have been an adequate control. If SR was a true control for SMH then I would expect to see consistent models and consistent effects of individual environmental covariates among the study areas. Because this was not realized in my analysis, I have to caution the effectiveness of SR being a true control area for SMH. The inadequacy of the SR as being a true control to SMH may be attributed to the limitations of the vegetation covariates used in my analysis. The vegetation covariates were obtained from remotely sensed data and subsequently may be subject to high variability in some of the estimates. I was limited to remote sensed data and many of these covariates were linearly correlated. Expanding the covariates included in my analysis to include habitat data from different sources might explain some of the model variability.

Another potential bias in my study was the lack of pre-development data to accurately describe the habitat selection patterns of sage-grouse prior to the addition of wind energy infrastructure. Knowledge of the selection patterns prior to development provides researchers a baseline measurement to compare future selection patterns post development. Having the knowledge of pre-development data would also better validate SR as being a true control for SMH. For example, there may be some variability in the habitat selection patterns between study areas, but this may be attributed to sage-grouse being displaced from higher quality habitats to poorer quality habitats within SMH. Future studies evaluating the effects of wind energy on sage-grouse habitat selection patterns should consider multiple years of pre-development data to fully understand the potential changes in habitat selection patterns. In addition, multiple studies that account for the effects of spatial variation among different sage-grouse populations will be necessary to fully understand the extent of the potential impacts to sage-grouse from wind energy development.

**Nest Site Selection**

Few similarities existed between the top models of nest site selection within SMH and SR. Percent shrub cover was an important predictor within SMH; similarly shrub height was important within the SR study area. Shrub components have also been an important predictor for nest site selection for sage-grouse in other studies (Holloran and Anderson 2005, Hagen et al. 2007, Doherty et al. 2010). Sage-grouse selected for nest sites closer to occupied leks and avoided major roads within SMH. In addition, sage-grouse selected for nesting habitat closer to transmission lines within SR.

Sage-grouse are known to avoid habitats influenced by anthropogenic features (Lyon and Anderson 2003, Holloran et al. 2010). The transmission lines within the SR study area have existed for over 10 yrs and the quality of the habitat surrounding these transmission lines may outweigh the potential risk to sage-grouse from perching raptors (Ellis 1984). In addition, the selection closer to transmission lines may be attributed to the extent of available habitat used in my analysis (Fig. 2-3, Fig. 2-4). I further explored this relationship with a post hoc analysis where I reduced the available habitat to include the area within a 75% fixed kernel home range (Worton 1989). After re-estimating the final model using only the used and random locations within the modified available habitat, I observed a similar effect for shrub height and distance to nearest transmission line as in the original model, suggesting that the habitat I considered to be available using a 100% MCP sufficiently characterized habitat for the nest site selection.

Distance to turbine was not included in the SMH top model for nest site selection and when added to the top model it did not improve model fit (i.e., slope coefficients were not significant at the 90% CI level and AIC*c* scores did not improve). Sage-grouse selecting nesting sites seem to be uninfluenced by the presence of turbines within SMH.

The differences between the SMH and SR study areas could be related to the suite of covariates used in my analysis. The predictive power indicated by the K-fold validation was the lowest for nest site selection further suggesting the covariates used in my analysis may not have been sufficient at estimating the variability of nest site selection between both study areas. Nest site selection was estimated at a larger landscape-level scale where habitat covariates were measured remotely. The landscape-level scale is important for identifying priority nesting habitats but selection patterns can be strongly influenced with the knowledge of local-scale habitat variables that cannot currently be mapped in GIS (Doherty et al. 2010). Also, generation of different covariates may be useful to better estimate the variation in nest site selection between the two study areas.

**Brood-rearing Habitat selection**

Similar to nest site selection, brood-rearing habitat selection top models were different between SMH and SR. Specifically, sage-grouse within SMH selected for brood-rearing habitats farther away from transmission lines. However, much of the habitat surrounding the transmission lines located within the SMH study area was mostly comprised of a greater percent bare ground, which is not characteristic of sage-grouse brood-rearing habitats (Connelly et al. 2000, Aldridge and Boyce 2007) and percent bare ground was represented as a negative effect in the top brood-rearing selection model (i.e., odds of selection increased in habitats with less bare ground). Distance to nearest transmission line was included in the top brood-rearing model for SR; however there was substantial variability across individual birds. Similarly, herbaceous cover was included within both the SR and SMH top models, but herbaceous cover within SR had high variability at predicting the odds of occurrence.

The selection pattern within SMH was consistent with other sage-grouse studies where brooding areas consistently have higher grass or herbaceous cover (Holloran 1999, Thompson et al. 2006, Hagen et al. 2007). However, brooding sage-grouse in both study areas avoided habitats that consisted of a higher percentage of bare ground and selected for habitats that consisted of a higher percentage of shrub cover (SMH) and litter (SR). Broods selected habitats with greater sagebrush cover in southeastern Alberta (Aldridge and Boyce 2007), across Wyoming (Thompson et al. 2006), and south-central Wyoming (Kirol et al. 2012), which was consistent with the SR and SMH study areas. Distance to nearest turbines was not included in the SMH top model for brood-rearing habitat selection and when added to the top model it did not improve model fit (i.e., slope coefficients were not significant at the 90% CI and $AIC_c$ scores did not improve).

**Summer Habitat Selection**

Unlike the SR and SMH nest and brood-rearing habitat selection models, similarities existed among the top covariates included in the SMH and SR female summer habitat selection models. The probability of females selecting habitats in the summer increased as distance to nearest lek decreased, percent bare ground decreased, and as distance to nearest major roads increased within both study areas. Distance to nearest lek was included in the modeling because sage-grouse activity during all life stages was relatively close to each lek. It was also included to account for the spatial autocorrelation experienced at SMH where the proximity of leks to turbines may mask the effects of turbines on habitat selection.

Distance to nearest turbine was included in the top SMH summer habitat selection model, but its affect on the odds of selection was different from what was hypothesized. Sage-grouse in the SMH appeared to be selecting for habitats closer to turbines. This could be the result of

strong site fidelity associated with sage-grouse populations (Fischer et al. 1993, Holloran and Anderson 2005). In this case, sage-grouse likely selected habitats closer to turbines prior to construction of the facility and continued to use these habitats 2-yrs post construction. However, the lack of pre-construction data necessary to confirm this relationship limits the interpretation that sage-grouse selected habitats closer to turbines because they used these habitats prior to development.

The results of habitat selection studies are largely a product of defining available habitat. I defined available habitat as the extent of all sage-grouse locations where outlying locations may have a strong influence on selection patterns. I used a post hoc analysis to test whether the selection pattern associated with turbines was a product of my definition of available habitat. I reduced the available habitat to encompass a 75% fixed kernel home range of all summer locations at SMH (Worton 1989). Reapplication of the final model estimated to the home range available habitat showed a similar relationship to the original estimated coefficients where selection increased in habitats closer to turbines; however, this estimate was not significant at the 90% CI level. In addition, there was a similar affect on distance to nearest occupied lek as the original estimate, but it too was insignificant at the 90% CI level. This suggests that selection occurring at a more local scale may not be influenced by turbines or lek locations during the summer period. The post hoc analysis investigating different levels of habitat selection showed some variability in selection patterns suggesting future habitat selection studies investigating the response of wind energy development should consider multiple levels of selection.

The complex life cycles and time lags attributed to sage-grouse populations (Harju et al. 2010, Holloran et al. 2010) make it difficult to conclude or speculate on the cumulative impacts from wind energy infrastructure on sage-grouse habitat selection from my research, which

covered 2 yrs following wind energy development. Additional years of monitoring as well as multiple studies investigating these relationships are needed to fully understand the long term impacts of wind energy infrastructure on sage-grouse populations. However, the results from my study provide insight into the early effects of wind energy infrastructure on sage-grouse nesting, brood-rearing, and female summer habitat selection.

**MANAGEMENT IMPLICATIONS**

Understanding the potential impacts to sage-grouse populations from wind energy development is an important step towards landscape level sage-grouse population management. Information on the influence of wind energy developments on sage-grouse is limited due to the lack of studies. My study is the first study investigating the potential relationship that may exist between sage-grouse and wind energy. Future study efforts should focus on collecting sage-grouse habitat selection data in a before and after control treatment study design to fully understand these relationships. In addition, multiple studies at multiple locations are necessary for future wind developments to occur in sage-grouse occupied habitats. For example, Fedy et al. 2012, described the movements of monitored sage-grouse in Wyoming and discovered there was high variability across study sites suggesting selection and suitable habitat varies depending on individual landscapes. The relatively small movements from nesting areas to summer areas within my study area (average = 4.3 km) suggest that sage-grouse were using habitats that were in close proximity to leks compared to other sage-grouse populations where they exhibit large average interseasonal movements ranging from (3.8–14.4 km; Fedy et al. 2012). Because leks within the SMH study area were in close proximity to the SMH turbines and interseasonal movements were relatively small, sage-grouse in SMH might be influenced by wind turbines for a longer period of time compared to populations that exhibit larger seasonal movements. These

conditions suggest the need to monitor the response of different sage-grouse populations to wind energy development. Further exploration of the productivity parameters including nest success, brood-rearing success, and survival associated with these habitats is necessary to fully understand the potential long-term impacts of wind energy development on sage-grouse habitat selection and the response of sage-grouse populations to wind energy development.

**LITERATURE CITED**

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

Atamian, M. T., J. S. Sedinger, J. S. Heaton, E. J. Blomberg. 2010. Landscape-level assessment of brood rearing habitat for greater sage-grouse in Nevada. Journal of Wildlife Management 74:1533-1543.

Baasch, D. M., A. J. Tyre, J. J. Millspaugh, S. E. Hygnstrom, and K. C. Vercauteren. 2010. An evaluation of three statistical methods used to model resource selection. Ecological Modelling 221:565-574.

Boyce M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Burnham K. P and D. R. Anderson. 2002. Model selection and multimodel Inference: a practical information-theoretic approach: Second edition. Springer-Verlag, New York, New York, USA.

Carpenter J., C. Aldridge, and M. S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 74:1806–1814.

Coates, P. S. and D. J. Delehanty. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. Journal of Wildlife Management 74:240-248.

Connelly, J. W., H. W. Browers, and R. J. Gates. 1988. Seasonal movements of sage grouse in southeastern Idaho. Journal of Wildlife Management 52:116–122.

Connelly, J. W., M.A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967−985.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187−195.

Doherty, K. E., D. E. Naugle, B. L. Walker. 2010. Greater sage-grouse nesting habitat: The importance of managing at multiple scales. Journal of Wildlife Management 74:1544-1553.

Ellis, K. L. 1984. Behavior of lekking sage-grouse in response to a perched golden eagle. Western Birds 15:37–38.

ESRI. 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, California, USA.

Fedy, B. C., C. A. Aldridge, K. E. Doherty, M. O'Donnell, J. L. Beck, B. Bedrosian, M. J. Holloran, G. D. Johnson, N. W. Kaczor, C. P. Kirol, C. A. Mandich, D. Marshall, G. McKee, C. Olson, C. C. Swanson, and B. L. Walker. 2012. Interseasonal movements of greater sage-grouse, migratory behavior, and an assessment of the core regions concept in Wyoming. Journal of Wildlife Management.

Fischer, R. A., W. L. Wakkinen, K. P. Reese, and J. W. Connelly. 1993. Nesting-area fidelity of sage grouse in southeastern Idaho. Condor 95:1038-1041.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887-898.

Hagen, C. A. 2010. Impacts of energy development on prairie grouse ecology: A research synthesis. Pages 96-104 in Transactions of the 75th North American Wildlife and Natural Resources Conference 75. R. E. McCabe and K. A. Stockwell, technical editor. Wildlife Management Institute, Washington, D. C., USA.

Hagen, C. A., J. W. Connelly, and M .A. Schroeder. 2007. A meta-analysis of greater sage-grouse Centrocercus urophasianus nesting and brood-rearing habitats. Wildlife Biology 13:42-50.

Harju, S. M., M. R. Dzialak, R. C. Taylor, L. D. Hayden-Wing, J. B. Winstead. 2010. Thresholds and time lags in effects of energy development on greater sage-grouse populations. Journal of Wildlife Management 74:437–448.

Holloran, M. J. 1999. Sage grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. Thesis, University of Wyoming, Laramie, WY, USA.

Holloran, M. J. and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. The Condor 107:742–752.

Holloran, M. J. B. J. Heath, A . G. Lyon, S. J. Slater, J. L. Kuipers, S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638-649.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Homer, C. G., Aldridge, C. L., Meyer, D. K., Coan, M. J., and Z. H. Bowen. 2009. Multiscale sagebrush rangeland habitat modeling in southwest Wyoming. US Geological Survey, Washington D. C., USA.

Homer, C. G., C. L. Aldridge, D. K. Meyer, and S. J. Schell. 2012. Multi-scale remote sensing sagebrush characterization with regression trees over Wyoming, USA: laying a foundation for monitoring. International Journal of Applied Earth Observation and Geoinformation 14:233–244.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonlad, M. S. Boyce. 2006. Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347-357.

Johnson, G. D. and M. Holloran. 2010. Greater sage-grouse & wind energy development: A review of the issues. Renewable Northwest Project, Portland, OR, USA.

Kirol, C. P. 2012. Quantifying habitat importance for greater sage-grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. Thesis, University of Wyoming, Laramie, WY, USA.

Kirol, C. P., J. L. Beck, J. B. Dinkins, and M. R. Conover. 2012. Microhabitat selection for nesting and brood-rearing by the greater sage-grouse in xeric big sagebrush. The Condor 114:75-89.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486–491.

Manly B. F. J. 2007. Randomization, bootstrap and Monte Carlo methods in biology, Third Edition. Chapman & Hall/CRC, Boca Raton, Florida, USA.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London, UK.

Manly, B., L. McDonald, and D. Thomas. 1993. Resource selection by animals, statistical design and analysis for field studies. Chapman and Hall, London, UK.

McClean, S. A., M. A. Rumble, R. M. King, and W. L. Baker. 1998. Evaluation of resource selection methods with different definitions of availability. Journal of Wildlife Management 62:793-801.

McDonald, T. L., B. F. Manly, R. M. Nielson, L. V. Diller. 2006. Discrete-choice modeling in wildlife studies exemplified by northern spotted owl nightime habitat selection. Journal of Wildlife Management 70:375-383.

National Wind Coordinating Committee (NWCC). 2004. Wind Turbine Interactions with Birds and Bats: A Summary of Research Results and Remaining Questions. Fact Sheet, Second Edition. <http://www.nationalwind.org/publications/default.htm>. Accessed 01 Dec 2010.

Sappington, M. J., K. M. Longshore, and D. B. Thompson. 2005. Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71:1419-1426.

Steenhof, K., M. N. Kochert, and J. A. Roppe. 1993. Nesting by raptors and common ravens on electrical transmission line towers. Journal of Wildlife Management 57: 271-281.

Thomas, D. L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70:324–336.

Thompson, K. M, M. J. Holloran, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2006. Early brood-rearing habitat use and productivity of Greater Sage-Grouse in Wyoming. Western North American Naturalist 66:332−342.

US Fish and Wildlife Service (USFWS). 2003. Interim Guidelines to Avoid and Minimize Wildlife Impacts from Wind Turbines. US Fish and Wildlife Service, Washington, D. C., USA.

US Fish and Wildlife Service (USFWS). 2004. Prairie Grouse Leks and Wind Turbines: US Fish and Wildlife Service Justification for a 5-Mile Buffer from Leks; Additional Grassland Songbird Recommendations. US Fish and Wildlife Service, Washington, D. C., USA.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

Walker, B. L. 2008. Greater sage-grouse response to coal-bed natural gas development and West Nile virus in the Powder River Basin, Montana and Wyoming, USA. Dissertation, University of Montana, Missoula, MT, USA.

Worton, B. J. 1989. Kernel methods for estimating the ultilization distribution in home range studies. Ecology 70:164-168.

Table 2-1. Explanatory anthropogenic and environmental covariates used in model selection for sage-grouse nest site, brood-rearing, and summer habitat selection at the Seven Mile Hill and Simpson Ridge study areas, Carbon County Wyoming, USA, 2009 and 2010 (Homer et al. 2012).

| Covariate | Covariate description |
|---|---|
| Anthropogenic Infrastructure | |
| dist_major_rds | Distance to nearest major road (WYO HWY 72, US HWY 287/30, and I-80)$^2$; km |
| dist_major_rds$^2$ | Distance to nearest major road (WYO HWY 72, US HWY 287/30, and I-80)$^2$; km |
| dist_tline | Distance to nearest overhead transmission line; 230 kV wooden H-frame; km |
| dist_tline$^2$ | Quadratic term for distance to nearest overhead transmission line (km)$^2$ |
| dist_turbine | Distance to nearest turbine (km) |
| dist_turbine$^2$ | Quadratic term for distance to nearest turbine (km)$^2$ |
| Environmental | |
| Bare ground† | Percent bare ground |
| Big_sagebrush† | Percent big sagebrush (*Artemisia tridentata* spp.) cover |
| Elevation | Altitude above sea level (m) |
| Herbaceous† | Percent herbaceous cover |
| Litter† | Percent litter |
| Sagebrush † | Percent sagebrush (*Artemisia* spp.) cover |
| Shrub† | Percent shrub cover |
| Shrub_hgt† | Shrub height (0–253 cm) |
| Slope | Degrees 0-90 |
| Terrain ruggedness | Variability in slope and aspect (0-1; 1 = complete terrain variation; Sappington et al. 2009) |
| Wyoming big sagebrush † | Percent Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) cover |

†Vegetation covariates obtained from Homer et al. 2012.

Table 2-2. Model fit statistics for greater sage-grouse nest site selection at the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010. Models are listed according to the model best fitting the data and ranked by ($\Delta$AIC*c*), the difference between the model with the lowest Akaike's Information Criterion for small samples (AIC*c*) and the AIC*c* for the current model. The value of the maximized log-likelihood function (log[L]), the number of estimated parameters (K), and Akaike's weights ($w_i$) for each model are also presented.

| Model | log[L] | K | AIC*c* | $\Delta$AIC*c* | $w_i$ |
|---|---|---|---|---|---|
| Seven Mile Hill | | | | | |
| shrub300, lek_dist, herbaceous300, elevation460, dist_major_rds | -86.4 | 6 | 185.8 | 0.00 | 0.75 |
| shrub300, lek_dist, herbaceous300, elevation460 | -88.7 | 5 | 188.2 | 2.33 | 0.23 |
| shrub300, lek_dist, herbaceous300 | -94.3 | 4 | 197.1 | 11.22 | 0.00 |
| shrub300, lek_dist | -98.4 | 3 | 203.0 | 17.13 | 0.00 |
| shrub300 | -103.9 | 2 | 211.8 | 26.00 | 0.00 |
| Simpson Ridge | | | | | |
| shrub_hgt300, dist_tline | -130.6 | 3 | 267.4 | 0.00 | 0.97 |
| shrub_hgt300 | -135.1 | 2 | 274.2 | 6.87 | 0.03 |

Table 2-3. Odds ratios, slope coefficients, and 90% confidence intervals (CI) in the sage-grouse top nest site selection model for the Seven Mile Hill and Simpson Ridge study areas in Carbon County, Wyoming, USA, 2009 and 2010. Odds ratios measure the multiplicative change in odds of selection when a covariate changes by 1 unit, assuming all other covariates remain constant.

| Description | Coefficient | 90% CI | | Odds Ratio (%) | 90% CI (%) | |
|---|---|---|---|---|---|---|
| | | Lower | Upper | | Lower | Upper |
| Seven Mile Hill | | | | | | |
| (Intercept) | -51.6 | | | | | |
| Shrub | 0.60 | 0.33 | 0.95 | 81.6 | 38.9 | 159.6 |
| lek_dist | -0.50 | -0.82 | -0.33 | -39.2 | -56.1 | -27.9 |
| Herbaceous | 0.22 | -0.02 | 0.41 | 24.2 | -2.1 | 51.1 |
| Elevation | 0.02 | 0.01 | 0.03 | 2.1 | 1.2 | 3.3 |
| dist_major_rds | 0.15 | 0.04 | 0.26 | 16.4 | 4.0 | 29.5 |
| Simpson Ridge | | | | | | |
| (Intercept) | -3.4 | | | | | |
| shrub_hgt | 0.10 | 0.05 | 0.15 | 10.1 | 5.0 | 16.2 |
| dist_tline | -0.17 | -0.27 | -0.08 | -15.3 | -23.4 | -7.9 |

Table 2-4. Model fit statistics for greater sage-grouse brood selection at the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010. Models are listed according to the model best fitting the data and ranked by (ΔAIC*c*), the difference between the model with the lowest Akaike's Information Criterion for small samples (AIC*c*) and the AICc for the current model. The value of the maximized log-likelihood function (log[L]), the number of estimated parameters (K), and Akaike's weights ($w_i$) for each model are also presented.

| Model | log[L] | K | AIC*c* | ΔAIC*c* | $w_i$ |
|---|---|---|---|---|---|
| Seven Mile Hill | | | | | |
| dist_tline, dist_tline$^2$, bare ground460, herbaceous1000, elevation1000, shrub1000 | -309.9 | 7 | 635.1 | 0.00 | 0.91 |
| dist_tline, dist_tline$^2$, bare ground460, herbaceous1000, elevation1000 | -313.5 | 6 | 640.0 | 4.92 | 0.08 |
| dist_tline, dist_tline$^2$, bare ground460, herbaceous1000 | -316.9 | 5 | 644.5 | 9.45 | 0.01 |
| dist_tline, dist_tline$^2$, bare ground460 | -323.4 | 4 | 655.3 | 20.22 | 0.00 |
| dist_tline, dist_tline$^2$ | -343.4 | 3 | 693.1 | 57.99 | 0.00 |
| Simpson Ridge | | | | | |
| dist_tline, litter460, dist_major_rds, herbaceous1000, bare ground300 | -518.4 | 6 | 1049.8 | 0.00 | 0.81 |
| dist_tline, litter460, dist_major_rds, herbaceous1000 | -521.1 | 5 | 1052.9 | 3.15 | 0.17 |
| dist_tline, litter460, dist_major_rds | -524.2 | 4 | 1056.9 | 7.06 | 0.02 |
| dist_tline, litter460 | -527.4 | 3 | 1061.0 | 11.19 | 0.00 |
| dist_tline | -530.9 | 2 | 1065.9 | 16.08 | 0.00 |

Table 2-5. Odds ratios, slope coefficients, and 90% confidence intervals (CI) for covariates in the sage-grouse top brood-rearing selection model for the Seven Mile Hill and Simpson Ridge study areas in Carbon County, Wyoming, USA, 2009 and 2010. Odds ratios measure the multiplicative change in odds of selection when a covariate changes by 1 unit, assuming all other covariates remain constant. Odds ratios were not calculated for covariates involved with a quadratic effect because they were dependent on values of other covariates.

| Description | Coefficient | 90% CI | | Odds Ratio (%) | 90% CI (%) | |
|---|---|---|---|---|---|---|
| | | Lower | Upper | | Lower | Upper |
| Seven Mile Hill | | | | | | |
| (Intercept) | 19.3 | | | | | |
| dist_tline | 1.12 | NA | NA | NA | NA | NA |
| dist_tline$^2$ | -0.12 | -0.25 | -0.03 | NA | NA | NA |
| Bare ground | -0.14 | -0.19 | -0.09 | -13.1 | -17.5 | -8.6 |
| Herbaceous | 0.68 | 0.25 | 1.28 | 96.5 | 27.8 | 260 |
| Elevation | -0.01 | -0.02 | 0.00 | -1.1 | -2.28 | -0.14 |
| Shrub | 0.42 | 0.01 | 0.95 | 52.7 | 1.1 | 158 |
| Simpson Ridge | | | | | | |
| (Intercept) | -1.0 | | | | | |
| dist_tline | -0.12 | -0.39 | 0.07 | -11.0 | -32.1 | 7.4 |
| Litter | 0.11 | 0.02 | 0.19 | 11.4 | 2.0 | 20.7 |
| dist_major_rd | 0.09 | -0.05 | 0.28 | 9.2 | -4.4 | 33.0 |
| Herbaceous | -0.09 | -0.28 | 0.01 | -9.0 | -24.6 | 1.1 |
| Bare ground | -0.03 | -0.06 | -0.01 | -3.3 | -5.6 | -1.1 |

Table 2-6. Model fit statistics for greater sage-grouse summer selection at the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010. Models are listed according to the model best fitting the data and ranked by ($\Delta$AIC*c*), the difference between the model with the lowest Akaike's Information Criterion for small samples (AIC*c*) and the AIC*c* for the current model. The value of the maximized log-likelihood function (log[L]), the number of estimated parameters (K), and Akaike's weights ($w_i$) for each model are also presented.

| Model | log[L] | K | AIC*c* | $\Delta$AIC*c* | $w_i$ |
|---|---|---|---|---|---|
| Seven Mile Hill | | | | | |
| lek_dist, bare ground300, dist_major_rds, dist_turbine, elevation1000 | -1880.4 | 7 | 3774.1 | 0.00 | 1.00 |
| lek_dist, bare ground300, dist_major_rds, dist_turbine | -1915.1 | 6 | 3841.0 | 66.9 | 0.00 |
| lek_dist, bare ground300, dist_major_rds, | -1959.0 | 5 | 3926.7 | 152.6 | 0.00 |
| lek_dist, bare ground300 | -1983.4 | 3 | 3973.4 | 199.3 | 0.00 |
| lek_dist | -2045.0 | 2 | 4094.3 | 320.3 | 0.00 |
| Simpson Ridge | | | | | |
| lek_dist, bare ground1000, dist_major_rds, dist_major_rds$^2$, herbaceous1000, Wyoming_sagebrush1000 | -2625.4 | 7 | 5266.1 | 0.00 | 1.00 |
| lek_dist, bare ground1000, dist_major_rds, dist_major_rds$^2$, herbaceous1000 | -2648.2 | 6 | 5309.3 | 43.2 | 0.00 |
| lek_dist, bare ground1000, dist_major_rds, dist_major_rds$^2$ | -2688.7 | 5 | 5388.6 | 122.6 | 0.00 |
| lek_dist, bare ground1000 | -2780.3 | 3 | 5567.2 | 301.1 | 0.00 |
| lek_dist | -2963.4 | 2 | 5931.1 | 665.0 | 0.00 |

Table 2-7. Odds ratios, slope coefficients, and 90% confidence intervals (CI) for covariates in the sage-grouse top summer selection model for the Seven Mile Hill and Simpson Ridge study areas in Carbon County, Wyoming, USA, 2009 and 2010. Odds ratios measure the multiplicative change in odds of selection when a covariate changes by 1 unit, assuming all other covariates remain constant. Odds ratios were not calculated for covariates involved with a quadratic effect because they were dependent on values of other covariates.

| Description | Coefficient | 90% CI | | Odds Ratio (%) | 90% CI (%) | |
|---|---|---|---|---|---|---|
| | | Lower | Upper | | Lower | Upper |
| Seven Mile Hill | | | | | | |
| (Intercept) | -11.9 | | | | | |
| lek_dist | -0.31 | -0.49 | -0.16 | -26.5 | -38.7 | -15.0 |
| bare ground | -0.08 | -0.10 | -0.06 | -7.3 | -9.4 | -5.4 |
| dist_major_rds | 0.16 | 0.07 | 0.26 | 17.1 | 7.3 | 29.0 |
| dist_turbine | -0.25 | -0.41 | -0.11 | -22.4 | -33.3 | -10.7 |
| elevation | 0.01 | 0.00 | 0.01 | 0.76 | 0.27 | 1.3 |
| Simpson Ridge | | | | | | |
| (Intercept) | 5.63 | | | | | |
| lek_dist | -0.25 | -0.43 | -0.11 | -22.5 | -35.3 | -10.4 |
| bare ground | -0.14 | -0.19 | -0.08 | -12.9 | -17.6 | -8.0 |
| dist_major_rds | 0.40 | NA | NA | NA | NA | NA |
| dist_ major_rds$^2$ | -0.02 | -0.05 | 0.00 | NA | NA | NA |
| herbaceous | -0.14 | -0.26 | -0.04 | -13.4 | -23.1 | -4.0 |
| wygenis | 0.29 | 0.07 | 0.58 | 34.2 | 7.3 | 78.4 |

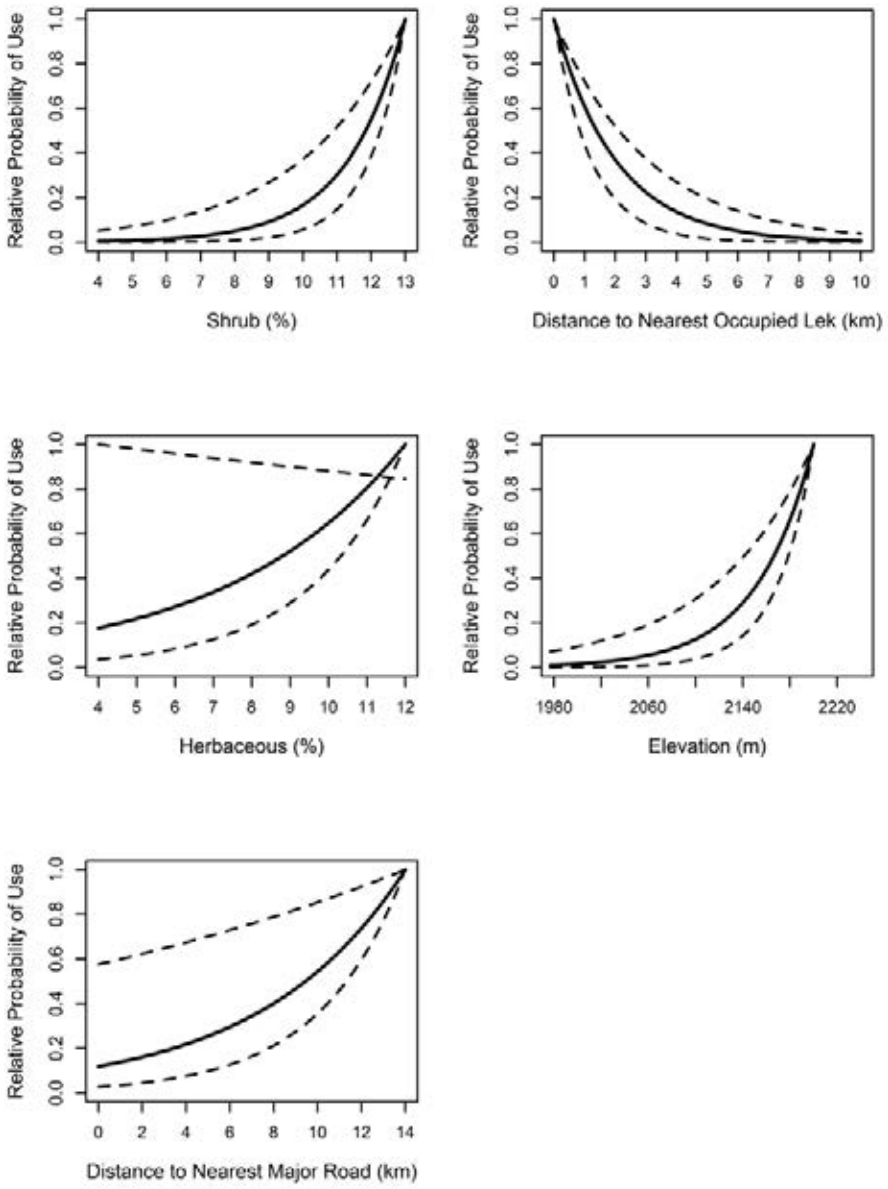



Figure 2-1. Odds ratios or relative probability of sage-grouse nest site selection and 90% confidence intervals (dashed lines) within the Seven Mile Hill study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value. Overlapping confidence limits indicate a non-significant estimate.

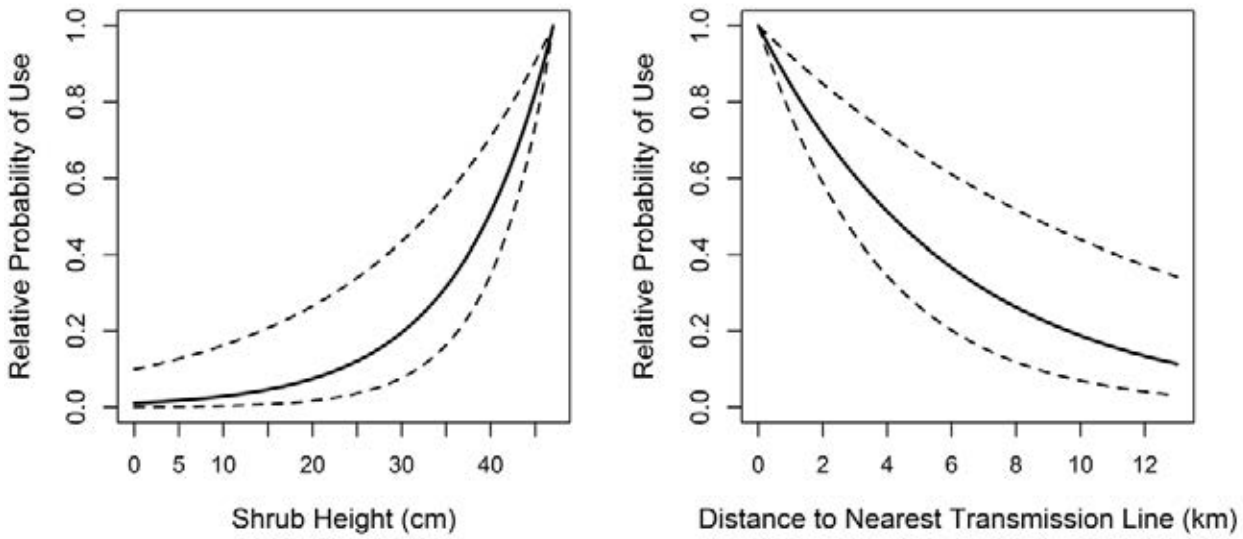



Figure 2-2. Odds ratios or relative probability of sage-grouse nest site occurrence and 90% confidence intervals (dashed lines) within the Simpson Ridge study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value.

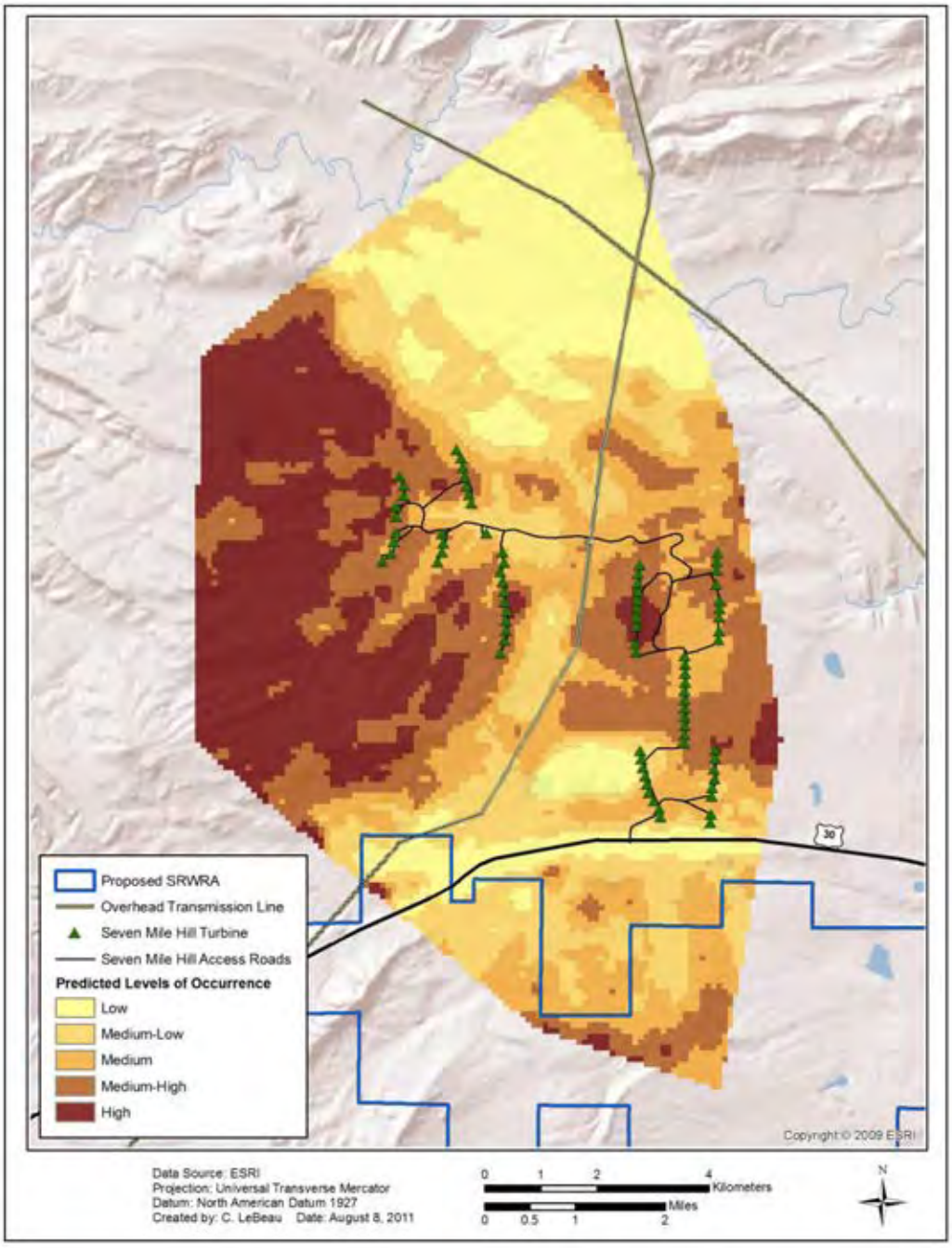



Figure 2-3. Predicted nesting habitat used within a 129 km$^2$ minimum convex polygon by sage-grouse within the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010.

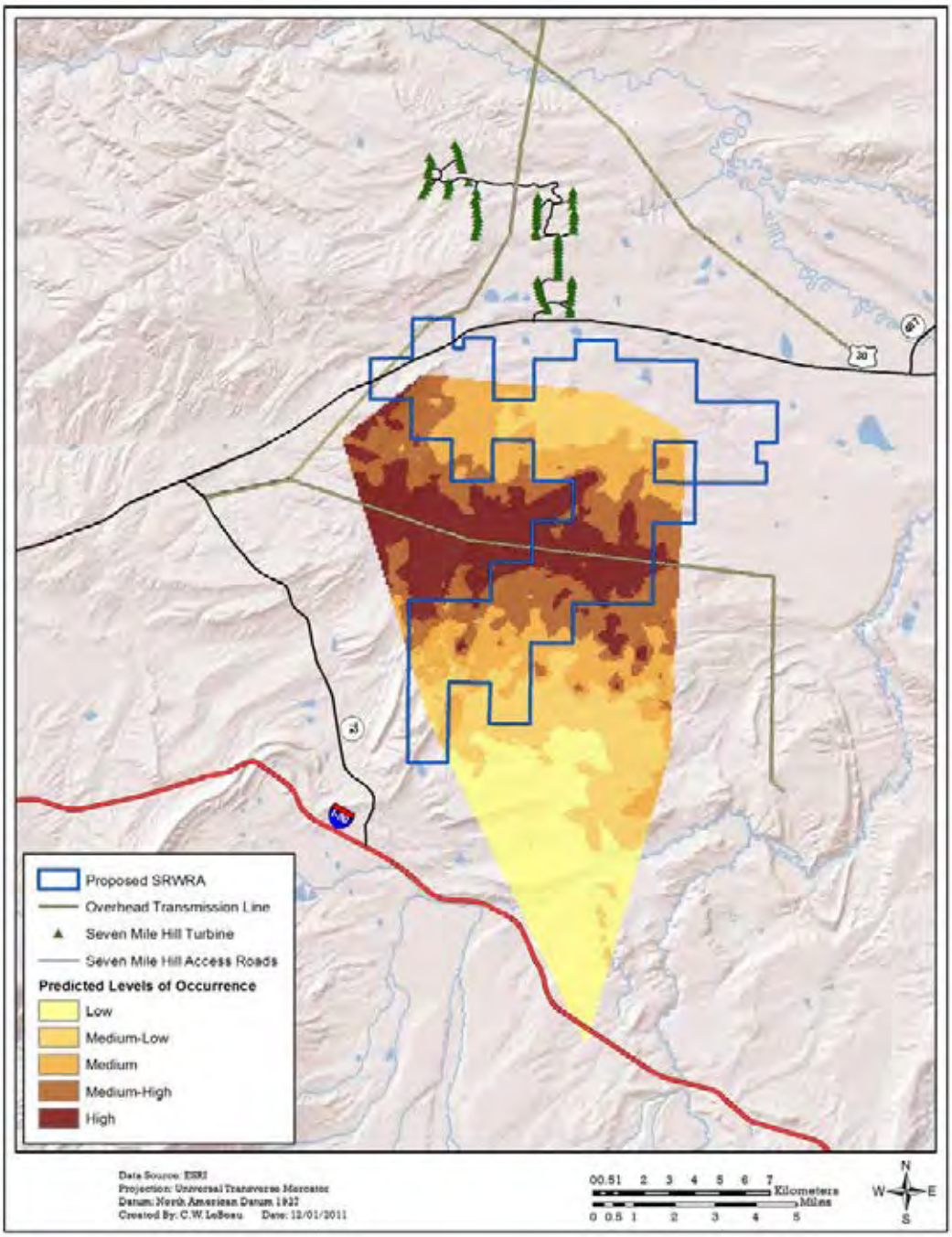



Figure 2-4. Predicted nesting habitat used within a 217 km$^2$ minimum convex polygon by sage-grouse within the Simpson Ridge Study area, Carbon County, Wyoming, USA, 2009 and 2010.

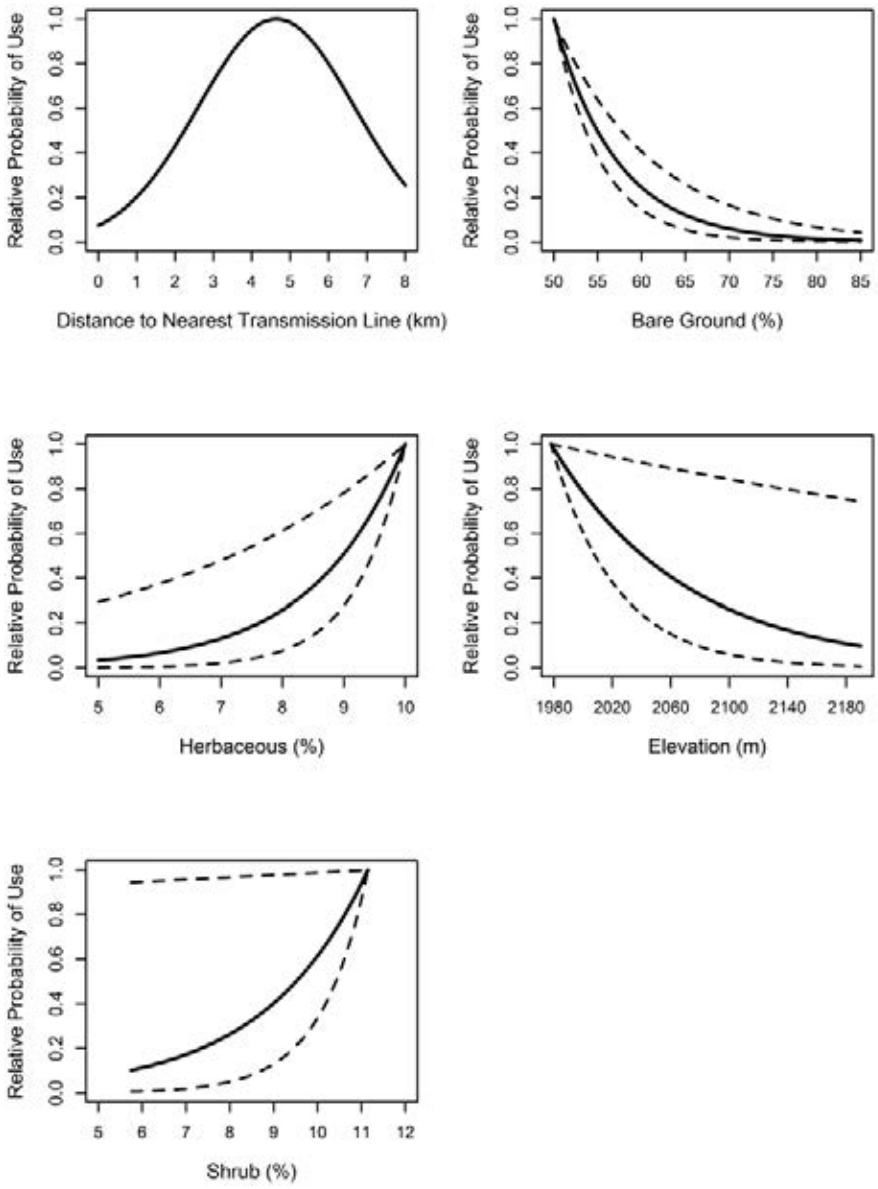



Figure 2-5. Odds ratios or relative probability of sage-grouse brood-rearing selection and 90% confidence intervals (dashed lines) within the Seven Mile Hill study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. Confidence intervals were not calculated for distance to transmission line because confidence intervals for quadratic effects depend on values of other covariates.

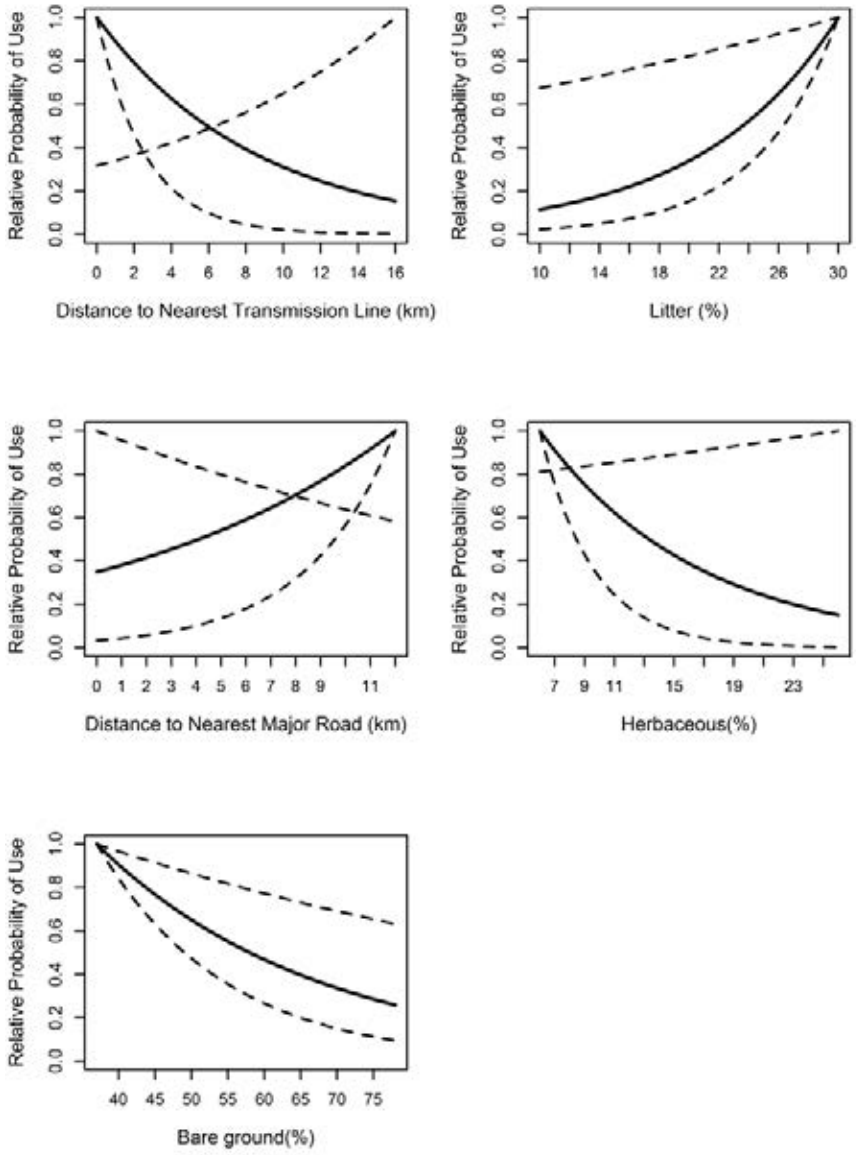



Figure 2-6. Odds ratios or relative probability of sage-grouse brood-rearing occurrence and 90% confidence intervals (dashed lines) within the Simpson Ridge study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value. Overlapping confidence limits indicate a non-significant estimate.

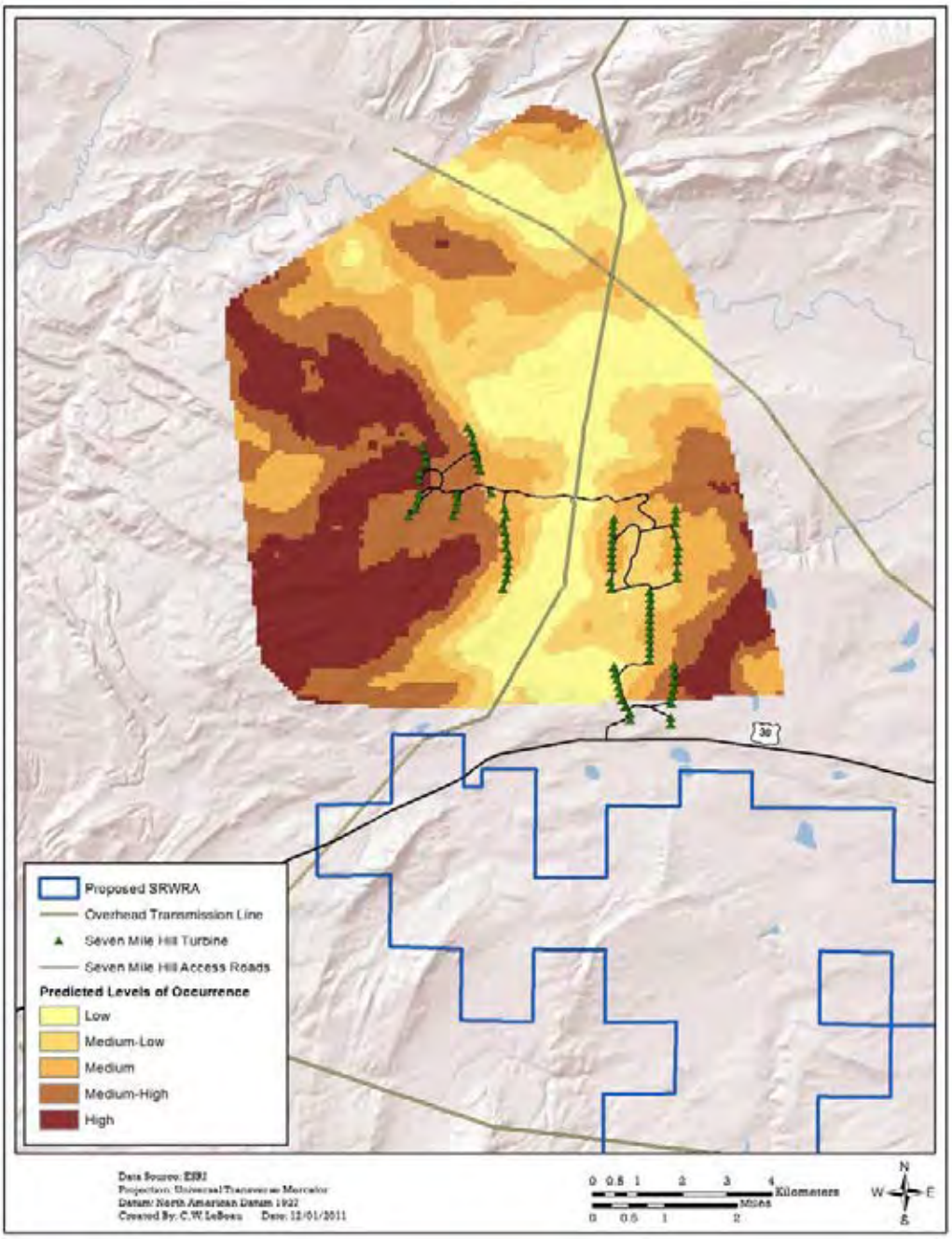



Figure 2-7. Predicted brood-rearing habitat used within a 126 $km^2$ minimum convex polygon by sage-grouse within the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010.

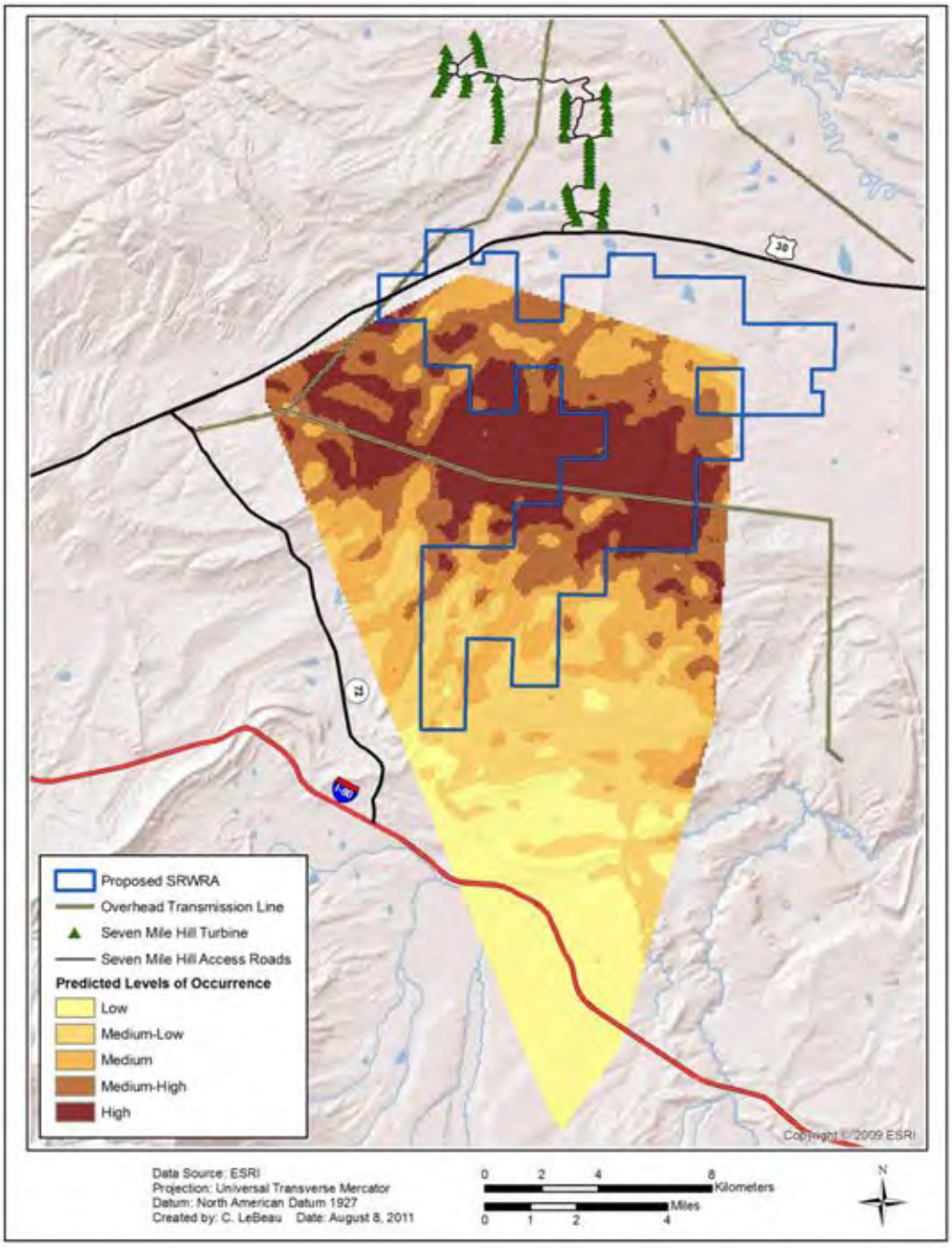



Figure 2-8. Predicted brood-rearing habitat used within a 650 $km^2$ minimum convex polygon by sage-grouse within the Simpson Ridge study area, Carbon County, Wyoming, USA, 2009 and 2010.

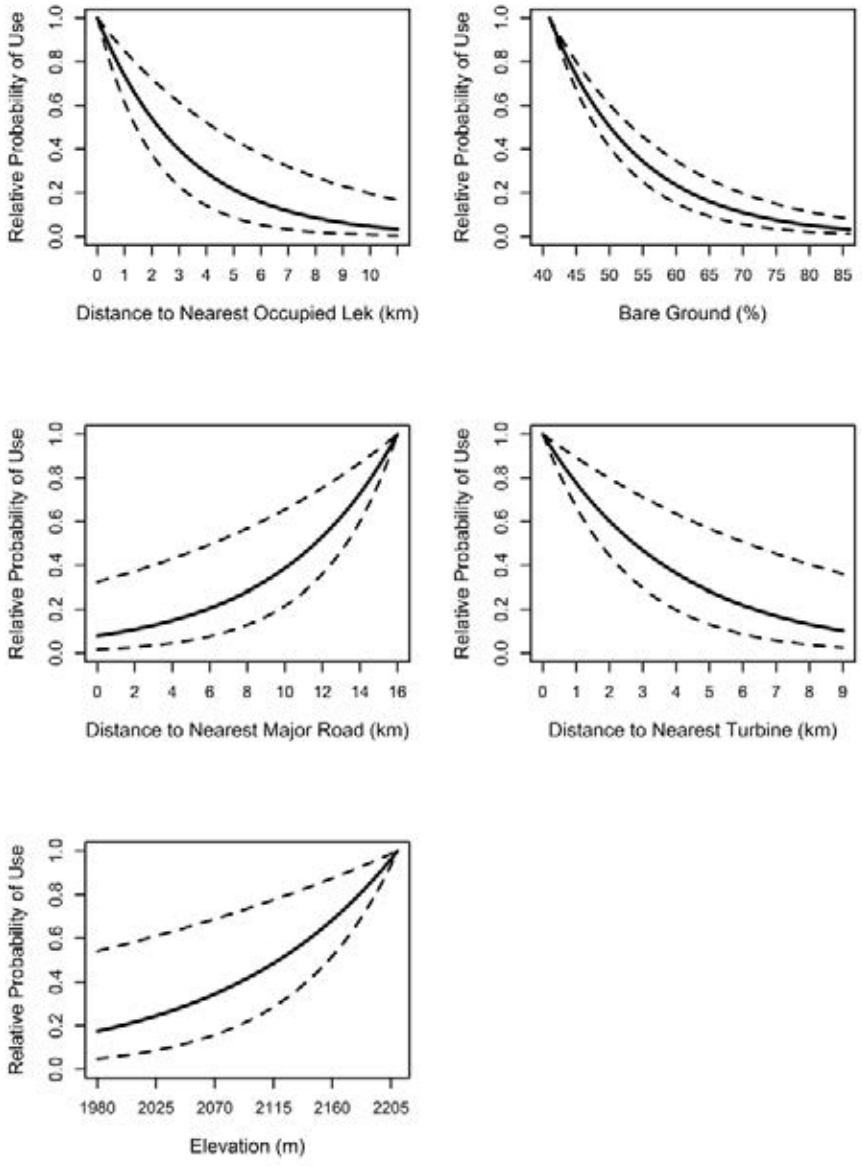



Figure 2-9. Odds ratios or relative probability of female sage-grouse summer occurrence and 90% confidence intervals (dashed lines) within the Seven Mile Hill study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value.

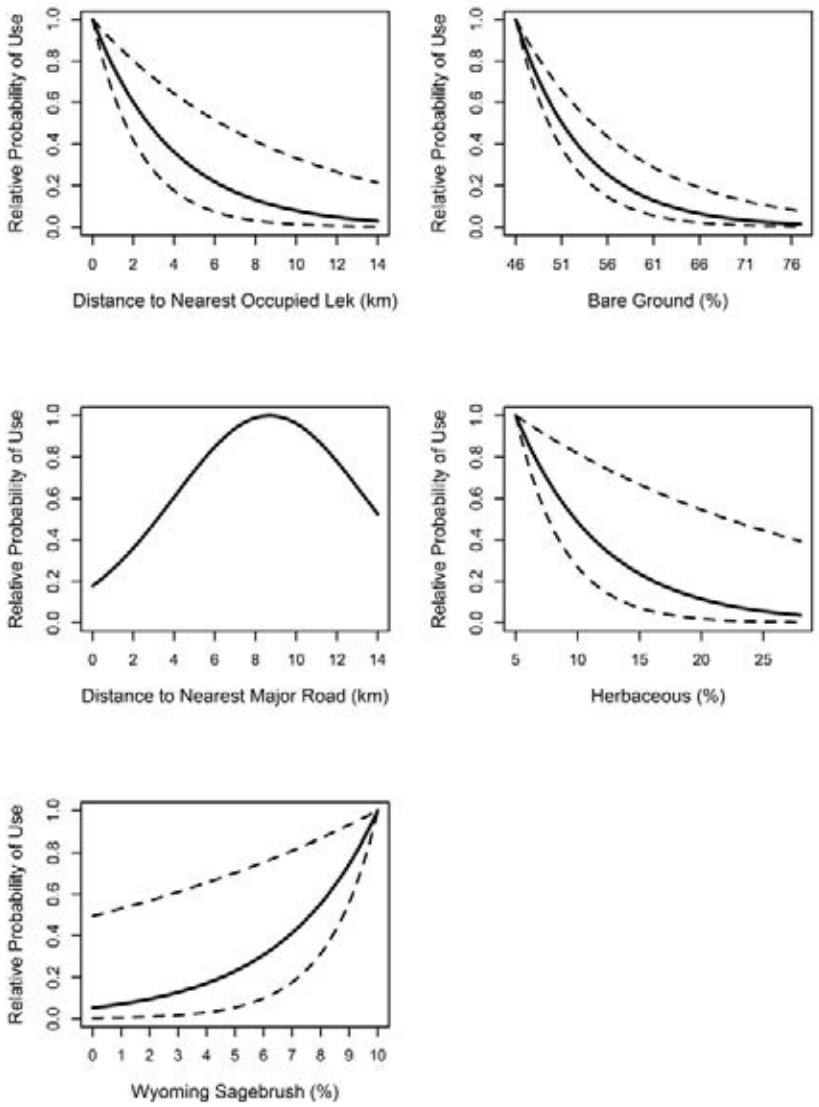



Figure 2-10. Odds ratios or relative probability of female sage-grouse summer occurrence and 90% confidence intervals (dashed lines) within the Simpson Ridge study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value. Confidence intervals were not calculated for distance to major road because confidence intervals for quadratic effects depend on values of other covariates.

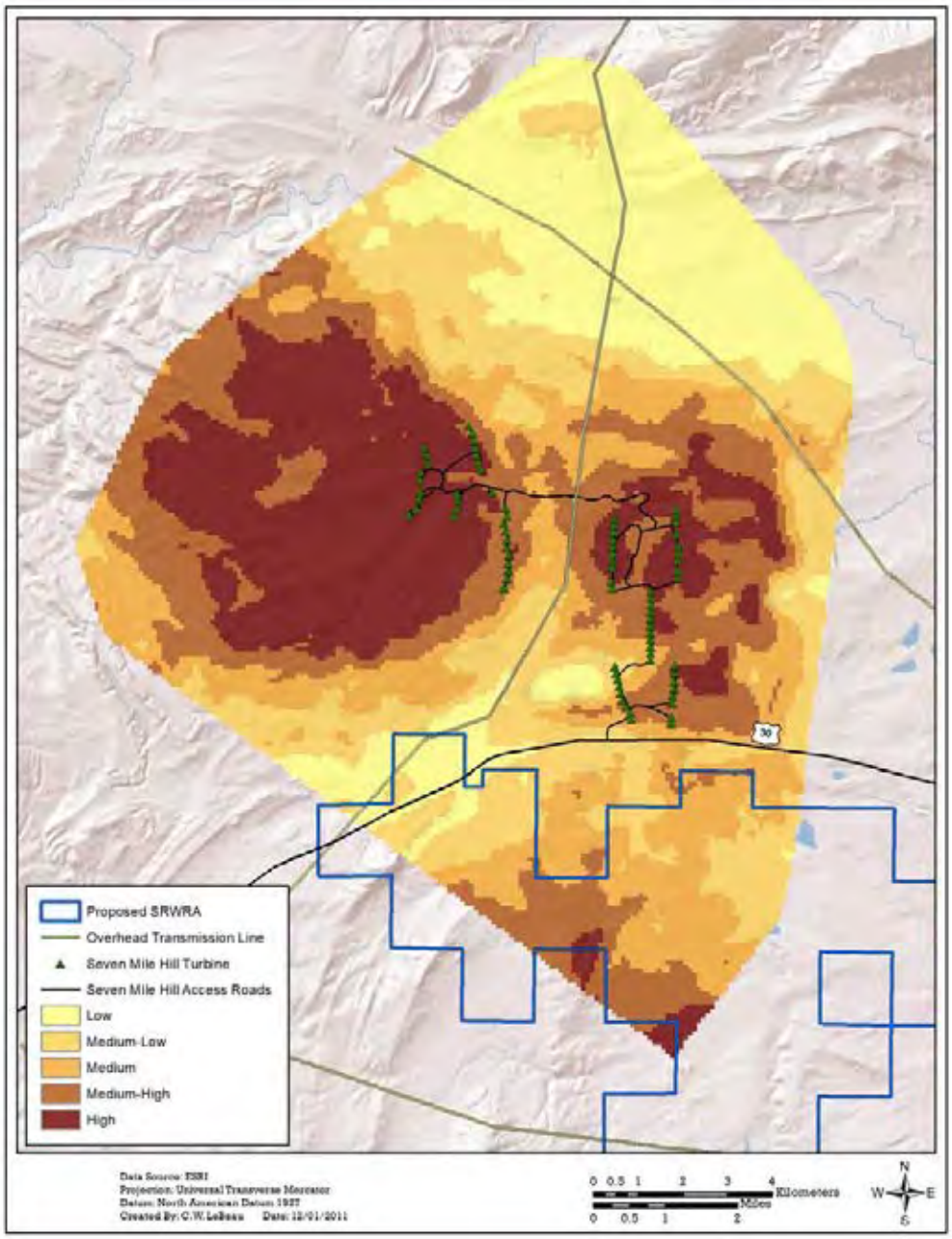



Figure 2-11. Predicted summer habitat used within a 243 km$^2$ minimum convex polygon by sage-grouse within the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010.

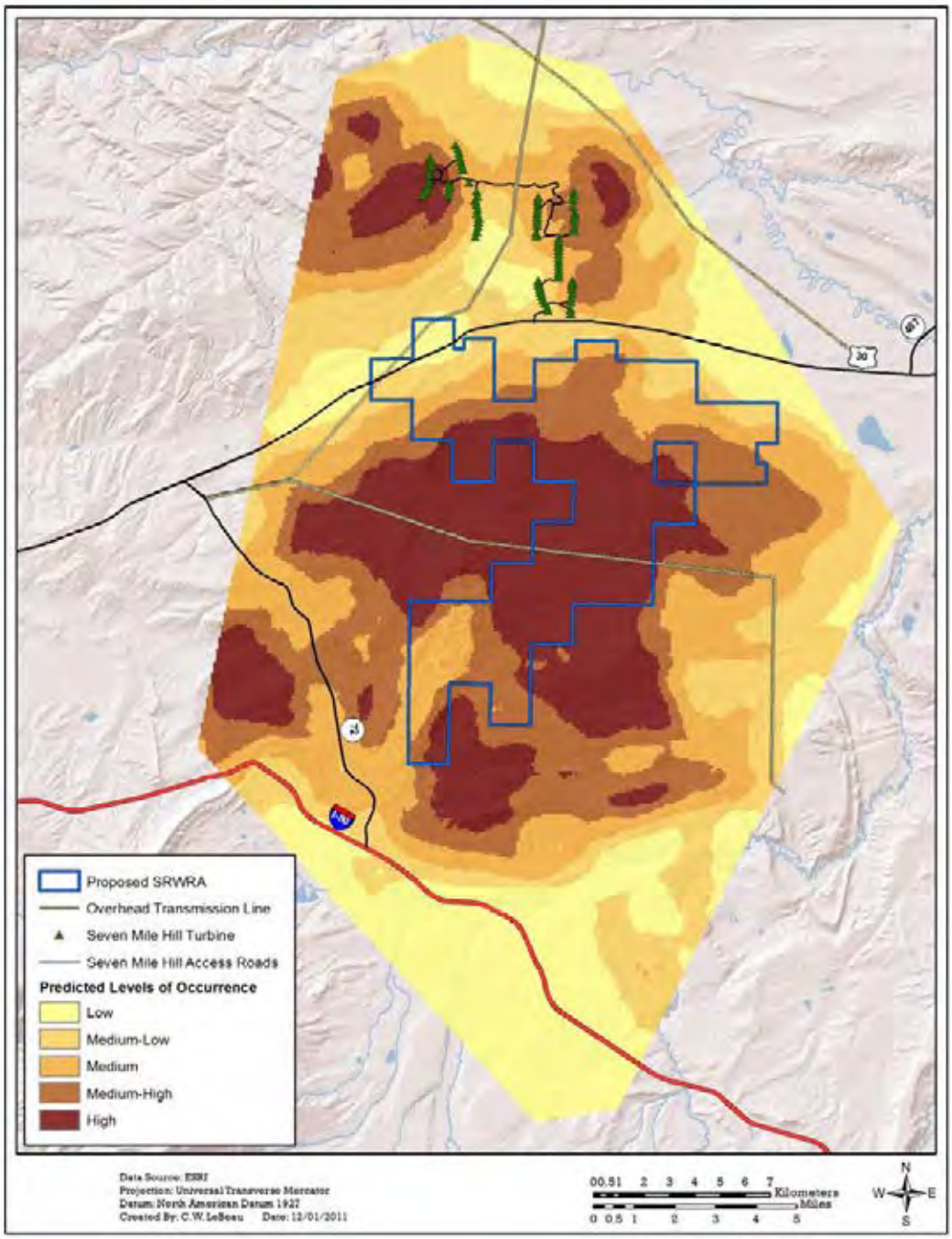



Figure 2-12. Predicted summer habitat used within a 751 km$^2$ minimum convex polygon by sage-grouse within the Simpson Ridge study area, Carbon County, Wyoming, USA, 2009 and 2010.

# CHAPTER 3

## Greater Sage-grouse Fitness Parameters Associated with Wind Energy Development

In the format for manuscript submittal to the *Journal of Wildlife Management*


## ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*) are experiencing population declines in much their current range. Population declines are directly related to changes in greater sage-grouse fitness parameters including nest success, brood success, and female survival. The overall fitness of an individual ultimately determines if the individual is contributing to the viability of a population. Reduced fitness leads to population declines because of the lack of the individual's contribution to the population. Reduced fitness in greater sage-grouse populations have been attributed to a decrease in habitat suitability caused by invasive plant species, increased predation, and energy extraction activities. More recently, the increased demand for clean renewable energy has raised concerns about the impacts to greater sage-grouse fitness parameters in habitats occupied by wind turbines. However, little is known about these potential impacts and mine is the first study to estimate short-term impacts from wind energy development on greater sage-grouse fitness parameters. I hypothesized greater sage-grouse fitness parameters decreased with increasing proximity to wind energy infrastructure particularly wind turbines. I identified 88 nests from 2009 to 2010 within the Simpson Ridge and Seven Mile Hill study areas. In addition, I monitored 31 females during the brood-rearing period to assess brood survival. Lastly, I identified 45 mortalities of adult females within both study areas. I utilized Cox proportional hazard regression to model nest survival and used the Andersen and Gill survival model to estimate female survival and brood survival relative to wind turbines. I used forward model

selection and Akaike's information criterion to determine optimal models for each fitness parameter. I used Schoenfeld residuals to test for non-proportional hazards in the top model. The results from the survival time analysis indicated the risk of a brood or nest failing increased within habitats of close proximity to wind turbines. In addition, I detected no variation in female survival relative to wind infrastructure. Future wind energy development should consider the increased risk of brood and nest failure within habitats of close proximity to turbines. Identifying nesting and brood-rearing habitats within close proximity to wind energy developments is critical when estimating potential impacts to overall population fitness.

**INTRODUCTION**

The population demographics of greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) are unique among upland game bird species (Connelly et al. 2011). Sage-grouse have relatively low reproductive rates (Connelly et al. 2000); low winter mortality (Wik 2002, Zablan 2003), high annual survival (Holloran 1999), and many populations are migratory (Connelly et al. 1988, 2000, Schroeder et al. 1999; Fedy et al. 2012). These demographics are variable among subpopulations across the species' range due to changes in environmental gradients and anthropogenic influences (Connelly et al. 2011).

Nest success is an important vital rate of sage-grouse populations and can be used to assess trends in population productivity. Nest success is defined as the probability of a nest hatching one or more eggs successfully (Rotella et al. 2004). Poor nest success has often been related to sage-grouse population declines (Crawford and Lutz 1985, Gregg et al. 1994, Schroeder et al. 1999). The average nest success rate for sage-grouse in 29 studies using radio-telemetry was 46% (range: 15–86%), and was widely dependent on region, habitat conditions, and study design (Connelly et al. 2011). Nest success also differs from unaltered habitats (61%

of studies reported ≥50% and 22% of studies reported <40% overall nest success) to altered habitats (17% of studies reported ≥50% and 42% of studies reported <40% overall nest success; Connelly et al. 2011).

Peak egg-laying and incubation occurs from March through mid-June, with renesting lasting into early July (Gregg 2006, Schroeder et al. 1999). Mean sage-grouse clutch size ranges from 6.3 to 9.1 eggs (Schroeder et al. 1999). Female sage-grouse exhibit high fidelity to nesting areas (Holloran and Anderson 2005, Fischer et al. 1993). They are known to nest on average 2.1 km from undisturbed leks of capture and 4.1 km from disturbed leks of capture in southwestern Wyoming (Lyon and Anderson 2003). In Wyoming, nests that are not located in close proximity to other nests and situated closest to leks tend to be more successful (Holloran and Anderson 2005). Nest propensity is variable across the species range averaging 78% (Connelly et al. 2011). Furthermore, adult females tend to have higher nest initiation rates than yearlings (Connelly et al. 2004) and female sage-grouse may renest (mean: 30% in the western portion of the species range) following their failed first nesting attempt (Connelly et al. 2011).

In addition to nesting success, early and late brood success is a key parameter in assessing sage-grouse population demographics because juvenile survival impacts overall population productivity (Crawford et al. 2004, Connelly et al. 2011). Beck et al. (2006) provided estimates that indicate juvenile survival equals adult survival after 10 weeks of age, suggesting that nesting and early brood-rearing success are critical drivers of population change. I defined early brood success as the proportion of broods that survived 14 days post hatch (Thompson et al. 2006) and late brood success as the proportion of broods that survived 35 days post hatch (Walker 2008).

Sage-grouse chick survival during the early brood period (18 days post hatch) has been estimated to be 44% in southeastern Oregon and northern Nevada (Rebholz 2007), and 39% through day 28 in south-central Oregon and northern Nevada (Gregg 2006). Chick survival during the late brood period (35 days post hatch) has been estimated to be 33–50% in northeastern Wyoming and southeastern Montana (Walker 2008) and 76.2% (40 days post hatch) in southeastern Wyoming (Kirol 2012). Early brood activity occurs in the vicinity of nesting locations (mean distance from nest in southwestern Wyoming was 1.1 km; Lyon 2000), with the habitat characterized as having a healthy sagebrush (*Artemisia* spp.) overstory and herbaceous understory containing insects critical to chick survival (Johnson and Boyce 1990). When landscapes become desiccated around midsummer, brooding hens often migrate 5-82 km from early brood-rearing habitat (Klebenow and Gray 1968, Wallestad 1971, Connelly et al. 1988, Fisher et al. 1997) to more forb rich habitat, usually higher in elevation where pockets of moisture still remain (Klebenow 1969). These brooding habitats are widely variable and in many cases are dependent on yearly weather conditions (Patterson 1952, Dalke et al. 1963, Connelly et al. 1988, Gregg et al. 1993, Wallestad 1971).

Sage-grouse declines are at least partially explained by lower annual survival of female sage-grouse and in the case of oil and gas development, the impacts to survival result in population-level declines (Holloran 2005). Sage-grouse are characterized as having high annual survival compared to other upland game birds. Annual survival rates of adult female sage-grouse in Wyoming were estimated to be 48–78% (Holloran 1999, 2005). Seasonal survival is variable for both male and female sage-grouse, but is highest during the winter (88–100%; Wik 2002, Beck et al. 2006) and lowest during the spring (57%, March-June; Connelly et al. 2000), summer, and fall (Connelly et al. 2000, Wik 2002).

The purpose of my study was to investigate the affect of wind energy infrastructure on sage-grouse fitness parameters. Specifically, I investigated sage-grouse nest, brood, and female survival in relation to wind energy infrastructure including turbines, roads, and transmission lines. I hypothesized that sage-grouse nest, brood, and female survival decreased as proximity to infrastructure, specifically turbines, increased. This information is critical to provide for use in planning future wind energy development sites that occur within occupied sage-grouse habitats.

## STUDY AREA

My study area was consistent with Chapters 1 and 2 in this thesis. Observed nests, brood locations, and mortality locations were combined between years and study areas for my survival analysis (see Fig. 1-1).

## METHODS

### Field Methods

I captured 116 female sage-grouse by spotlighting and use of hoop nets (Giesen et al. 1982, Wakkinen et al. 1992) on roosts surrounding leks during the 2009 and 2010 breeding seasons. Initial capture efforts were centered within SR during the first study year (2009) where 50 sage-grouse females were targeted and 25 were targeted within SMH. During the second study season (2010) the target sample size increased to 40 at SMH and 45 at SR. I attempted to capture grouse at all accessible active lek sites within 16 km of the SMH wind turbines proportionately to the number of males attending those leks. I aged, weighed (0.1-g precision), acquired blood samples (year 2009), and fitted each captured grouse with a 22-g necklace-mounted radio transmitter with a battery life of 666 days (Advanced Telemetry Systems, Isanti, MN). I then released each radio-marked female grouse at the point of capture and marked the location using a hand held global positioning system (GPS) unit.

I relocated each radio-marked female at least twice each week during the prelaying and nesting period (Apr through Jun); once every week for brooding females during the brood-rearing period (hatch through 15 Aug); and, at least once per week during the summer (Jun through 1 Nov) periods for all barren females (i.e., females that were unsuccessful in producing or raising young or were not currently nesting or raising young). Marked sage-grouse were monitored primarily from the ground using hand-held receivers. I determined sage-grouse locations by triangulation or homing until visibly observed and classified radio-locations as breeding, nesting, brood-rearing, or summer. Triangulation locations were estimated by taking two vectors in the direction of the signal. In addition, I estimated the triangulation error by placing 6 test collars for each technician throughout both project areas and estimated the mean telemetry error between the actual and estimated locations. The mean error telemetry rate was incorporated into the habitat selection modeling effort. I employed aerial telemetry to locate missing birds throughout the study period.

I determined nesting success for each radio-marked female sage-grouse from long range triangulation at least every third day throughout the nesting season, late April through 15 June. I assumed females were nesting when movements became localized. Nests were located using a progressively smaller concentric circle approached by walking circles around the radio signal using the signal strength as an indication of proximity (Holloran and Anderson 2005). Once I visually confirmed the female in an incubating position, the location of the observer was recorded with a GPS and a photograph was taken of the habitat surrounding the incubating hen. All future monitoring of the nest was made from remote locations (>60 m) using long distance triangulation to minimize potential disturbance. Once a nest location was established, I conducted incubation monitoring on an alternate-day schedule to determine nesting fate. For

each nest and re-nest, I collected data on timing of incubation and nest success. All nest locations were mapped using a hand-held GPS. A nest that successfully hatched (i.e., eggs with detached membranes) ≥1 egg was considered a successful nesting attempt. Nests that failed to successfully hatch ≥1 egg were considered failed nesting attempts whose fates included predation (avian, mammal, and unknown) and abandoned. Females that were unsuccessful in their first nesting attempt were monitored three times per week to determine possible re-nesting attempts. Females that were unsuccessful in their first or second nesting attempt were monitored twice each week through 1 November in 2009 and 2010.

I located radio-marked females that successfully hatched ≥1 egg each week through 15 August 2009 and 2010 to evaluate brood-rearing habitat selection. I categorized the brood-rearing period as early (hatch through 14 days post-hatch; Thompson et al. 2006) or late (35 days post-hatch; Walker 2008). Females were considered successful through the early brood-rearing period if ≥1 chick survived to two weeks post-hatch; chick presence during this period was established either through visual confirmation of a live chick or the brooding female's response to the researcher (e.g., chick protective behavior exhibited). I determined fledging success (late brood success) for those females who were successful in early brood-rearing by assessing whether a female was brooding chicks through nighttime spotlight surveys conducted on days 35 and 36 post-hatch (Walker 2008). Similar to sage-grouse with unsuccessful nests, sage-grouse that were unsuccessful during either the early or late brood-rearing period were monitored twice each week through 31 August.

**GIS Covariates**

I developed a suite of covariates to estimate the variability in nest, brood, and female survival within both study areas. Anthropogenic features included major roads, transmission lines, and

turbines. Major roads included paved highways: U.S. Highway 30/287 traversed east-west separating SR from SMH; Wyoming State Highway 72 traversed north-south through the SR study area; and Interstate 80 traversed east-west south of the SR study area (see Fig. 1-1). The SMH study area included wind turbines and access roads whereas the SR did not. Major roads and overhead transmission lines were digitized using aerial satellite imagery and ArcMap 10 (ESRI 2011). Turbine locations were obtained from PacifCorp, the operators of the SMH Wind Energy Facility.

Environmental covariates I considered included vegetation and topographic features within both study areas. Vegetation layers used in the analysis were remote sensed sagebrush products developed by Homer et al. (2012). This dataset used a combination of methods to integrate 2.4 m QuickBird, 30 m Landsat TM, and 56 m AWiFS (Advanced Wide Field Sensor) imagery into the characterization of four primary continuous field components (percent bare ground, percent herbaceous cover, percent litter, and percent shrub cover) and four secondary components (three subdivisions of shrub cover —percent sagebrush (*Artemisia* spp.), percent big sagebrush (*A. tridentata* spp.), and percent Wyoming big sagebrush (*A. t. wyomingensis*)—and shrub height, using regression classification (Homer et al. 2009, 2012; Table 3-1). Landscape features included elevation, slope, and terrain ruggedness all of which were calculated from a 10 m National Elevation Dataset (USGS, EROS Data Center, Sioux Falls, SD). Terrain ruggedness captured the variability in slope and aspect into a single measure ranging from 0 (no terrain variation) to 1 (complete terrain variation; Sappington et al. 2005; Table 3-1).

**Survival Parameters**

The most common method used to estimate nest survivorship is the Mayfield method (Mayfield 1961, 1975, Burhans et al. 2002, Liebeziet and George 2002, Nur et al. 2004); however, this

method cannot be used to statistically model nest failure in relation to a set of quantitative covariates or measure the joint effects of covariates (Johnson 1979, Nur et al. 2004). A more commonly used method to relate survival to a set of covariates is to use survival time analysis or more specifically, Cox proportional hazard models (Cox 1972). Cox proportional hazard models examine the relationship of multiple explanatory variables to the probability of nest, brood, and female survival for each individual (Therneau and Grambsch 2000). The Cox proportional hazard assumes that each covariate associated with each individual is equal to the average value of that covariate for the entire sample population and the events for the individuals are independent of each other. Violating this assumption creates non-proportional hazards. The Cox proportional hazard models produces risk ratios or hazard ratios that can be used to compare the effects of different levels of a particular covariate of interest (i.e., distance to nearest turbine) on the risk of failure (i.e., nest, brood, and female death). I used survival time analysis to estimate the effects of wind energy infrastructure on nest, brood, and female survival.

I assessed nest survival during the 26 day incubation period during the 2009 and 2010 nesting seasons (Schroeder et al. 1999, Aldridge and Boyce 2007). Nests observed within both study areas were combined into one sample. Re-nests are a result of failed nesting attempts and including re-nests assumes the bird is the sampling unit and not individual nests; therefore, re-nests were excluded from estimates of apparent nest success and survival. Events or failures occurred when the sage-grouse abandoned its nest or its nest was depredated. Abandoned nests thought to be caused by the researcher were not included in the survival analysis because of the potential biased associated with that nest. I estimated nest fate date using the last known monitoring interval as well as the condition of the nest to estimate the event date as well as the type of predator (mammalian or avian). Nests that were successful through the 26 day period

were censored (Nur et al. 2004). I used Cox proportional hazards to estimate the effects of wind energy infrastructure on nest survival (Nur et al. 2004, Aldridge and Boyce 2007, Liebezeit et al. 2009).

In addition to nest survival, I estimated brood survival within both study areas. Female sage-grouse successfully hatching at least 1 egg during the nesting season were monitored at least once each week from time of hatch to 35 days post hatch; however, to determine brood survival I assessed the presence of chicks with hens at least 2 times during the first 14 days of the brood-rearing period and one final time at the end of the 35 day brood-rearing period. All early and late brood-rearing locations from both study areas and years were combined and included in the survival modeling. Events or failures occurred when no chicks were observed or the female did not act as if she had chicks during either one of the checks. I estimated the fate date using the last monitoring interval where chick survival was assessed. Broods that were successful through the 35 day period were censored (Nur et al. 2004). I used weekly monitoring intervals during this period to assess brood survival. The first monitoring interval began directly after a successful hatched nest and ended 37 days post hatch (Walker 2008). Intervals that recorded multiple observations were grouped and their corresponding covariates were averaged.

Lastly, I modeled female sage-grouse survival from time of capture to 31 October during both years. Female sage-grouse were monitored at least once each week during this period, thus I assessed weekly survival for all monitored sage-grouse. Events or mortalities occurred when I confirmed mortality via telemetry. I estimated fate date by the condition of the carcass and last known monitoring interval. I grouped intervals that recorded multiple observations and averaged their corresponding covariates.

**Model Development**

I estimated nest survival using Cox proportional hazards (Cox 1972); however, I used the Anderson-Gill model (A-G; Anderson and Gill 1982), a formulation of the Cox proportional hazards model, to model brood and female survival. The A-G model accommodates left and right censored observations, continuous and categorical covariates that may vary during monitoring, and discontinuous intervals of risk, which are the product of missed observations or measurements (Therneau and Grambsch 2000, Johnson et al. 2004). The A-G model uses a counting process style of data input where each subject is represented as a series of observations with time intervals (i.e., sage-grouse brood location during a single monitoring interval). This allowed me to incorporate varying degrees of habitat units used throughout the interval of risk.

I used a forward model selection procedure to identify the effects of wind energy infrastructure on nest, brood, and female survival. Because many of my covariates were correlated ($r \geq |6|$), I allowed for each covariate to compete with each other in a forward selection procedure. However, I did not allow two correlated variables to be included in any one model. I included an indicator variable for which study area the sage-grouse was captured from (SMH=1, SR= 0) and the age of the sage-grouse (adult = 1, juvenile = 0) to determine if age or study area was influencing survival. In addition, the average values representing each environmental feature were extracted at 3 different radii scales, the mean telemetry error rate (0.30 km), the median distance between consecutive year's nests from 2009 to 2010 within both study areas (0.46 km), and the median distance traveled between monitoring intervals during the brood-rearing and summer period (1.0 km). The median movement distance was 1.0 km during brood-rearing and 1.6 km during the summer season; however, I used 1.0 km based on findings from previously published sage-grouse habitat selection studies (Aldridge and Boyce 2007, Carpenter et al. 2010). Kirol (2012) found the SD of shrub height to be an important predictor of nest survival in

south-central Wyoming; subsequently I included the SD of shrub height, shrub, and sagebrush in my modeling procedure.

I identified the best approximating model by comparing the adjusted Akaike's Information Criterion (AIC*c*; Burnham and Anderson 2002) values between models to identify the model with the lowest AIC*c* value. The top model was identified to be at least 4 ΔAIC*c* values from the next approximating model (Arnold 2010). I model averaged across the 90% confidence set of competing models to estimate the final parameters of the top model to produce more robust estimates and to address model uncertainty in competing models (Burnham and Anderson 2002, Arnold 2010). I calculated hazard ratios and 90% hazard ratio confidence intervals to interpret the magnitude of habitat and anthropogenic variables on an individual nest, brood, or female sage-grouse's daily or weekly hazard during the nesting, brooding-rearing, and female survival periods. Estimates that included 0.0 within their 90% confidence interval were considered insignificant (alpha level = 0.10). I used survival curves to illustrate the varying degree of risk as a function of the top model covariates (Johnson et al. 2004, Therneau and Grambsch 2000). I applied the coefficients generated from the top survival model to a logistic regression equation to predict the odds of survival from 2009 through 2010 at both study areas (Johnson et al. 2004).

Lastly, I used Schoenfeld residuals (Schoenfeld 1982) to assess model fit (Therneau et al. 1990). Scoring Schoenfeld residuals can be a powerful technique to test for non-proportional hazards for continuous variables (Grambsch and Therneau 1994). Schoenfeld residuals for each covariate in the top model are defined for every individual that has a failure event (Kleinbaum and Klein 2005). For the proportional hazard assumption to hold true, the Schoenfeld residuals for a particular covariate would not be related to survival time. I ranked the Schoenfeld residuals

for each covariate in the order of event failures (i.e., the individual with the first event gets a value of 1, and so on; Kleinbaum and Klein 2005). I plotted the ranked Schoenfeld residuals for each covariate and for the top model as a whole against time to inspect the distribution of the residuals. I fitted a line to the residuals to test for a nonzero slope. A nonzero slope indicated heterogeneity in the residuals thus, rejecting the null hypothesis that the correlation between the Schoenfeld residuals and survival time was zero. Rejection of the null hypothesis indicates that the proportional hazard assumption was violated.

## RESULTS

### Nest Survival

I located 95 nests in 2009 and 2010 (SR, $n$ = 53; SMH, $n$ = 42). During both study years, nesting propensity, the number of females observed initiating a nesting attempt, ranged from 59.4% (90% CI: 43.3–74.0%) to 77.3% (90% CI: 58.0–90.6%) within both study areas. SR had more nests during both study years compared to SMH; however, SMH had 6 re-nest attempts compared to 1 re-nest attempt at SR.

Two of the 6 observed re-nests within SMH were successful and the 1 re-nest observed within SR was unsuccessful. Nest success was similar in 2009 and 2010 within both study areas, ranging from 41.9% to 42.9% at SR and from 31.6% to 35.3% at SMH. Overall, nest success at SR (42.3%; 90% CI: 30.7–54.6%, $n$ = 52) was higher than at SMH (33.3%; 90% CI: 20.5–48.3%, $n$ = 36); however, the difference in the means was not statistically different. Nest hatch dates ranged from 26 May to 28 June (mean = 1 Jun) for all assumed first nesting attempts and from 29 June to 2 July (mean = 30 Jun) for all second nesting attempts.

During the 2009 and 2010 monitoring seasons, 16 first nesting attempt nests were initiated within 1.6 km of wind turbines at SMH; the five nests closest to turbines were located

137 m, 231 m, 248 m, 257 m, and 333 m from the nearest turbine. Four of the 16 nests (25.0%) within 1.6 km of turbines were successful, but none of the 5 nests closest to turbines were successful.

The proximity of the observed nests to each infrastructure feature varied throughout the study area. The mean distance to major roads and SMH turbines was greater for all successful nests (6.5 km [90% CI: 5.5–7.4 km] and 8.3 km [90% CI: 6.3–10.2 km], respectively) compared to failed nests (5.6 km [90% CI: 5.1–6.2 km] and 6.6 km [90% CI: 5.4–7.9 km], respectively); however, these differences were not statistically different.

*Model Fit*.—Eighty-eight sage-grouse nests were used in Cox proportional hazard modeling. The median duration of failed nesting attempts was estimated at 12 days. Results of the univariate model estimating differences in survival among study areas indicated that study area did not influence nest survival (hazard ratio = 1.2, 90% CI: 0.76–1.9). Three models including environmental and anthropogenic covariates were within 2.5 $\Delta$AIC*c* of each other. I model averaged the three competing models to estimate the final parameters for the top model (Burnham and Anderson 2002; Table 3-2). The top model relating environmental and anthropogenic features to sage-grouse nest survival included the standard deviation of shrub height (cm) within 0.30 km of a nest and distances (km) to nearest turbine and nearest overhead transmission line (Table 3-2).

The risk or the odds of a nest failing increased by 11.1% [(exp($\beta_0$)-1)*100] with every 1.0 km increase in the distance to nearest overhead transmission line (90% CI: 10.1–12.1%; Table 3-3; Fig. 3-1). The risk of a nest failing decreased by 14.4% for every 1 cm increase in the SD of shrub height (cm) within 0.30 km of a nest (90% CI: 13.1–15.8%; Table 3-3; Fig. 3-1). Similarly, the risk of a nest failing decreased by 6.2% as distance from turbine increased by 1 km

(90% CI: 5.9–6.5%). More specifically, as distance increased from turbines, the risk of failure decreased by 17.5% ($e^{3(-0.064)}$) at 3.0 km to 47.3% at 10.0 km ($e^{10(-0.064)}$) from the nearest turbine (Table 3-3; Fig. 3-1).

A sage-grouse nest with poor survival would be located in habitats with higher levels of risk. These habitats would consist of a lower standard deviation (SD) of shrub height (5.6 cm, value at the 25$^{th}$ percentile) within 0.30 km, farther from an overhead transmission line (4.9 km, 75$^{th}$ percentile), and closer to turbines (2.0 km, 25$^{th}$ percentile; Fig. 3-2). Habitats with good survival would consist of a higher SD of shrub height (8.8 cm, 75$^{th}$ percentile) within 0.30 km, closer to overhead transmission lines (1.3 km, 25$^{th}$ percentile), and farther from turbines (11 km, 75$^{th}$ percentile; Fig. 3-2). The Cox proportional hazard model predicted a mean survival rate of 45.6% (SE = 0.084; 90% CI: 31.8–59.4%) for nests located in poor habitat conditions and 81.5% (SE = 0.053; 90% CI: 72.7–90.2%) for nests located in more favorable habitat conditions (Fig. 3-2). Spatially, habitats closer to turbines had higher odds of a nest failing than habitats farther from turbines (Fig. 3-3). Lastly, there was no evidence of non-proportional hazards for any of the 3 covariates included in the top model (*P* ranged from 0.22 [turbine] to 0.65 [SD of shrub height]) suggesting that nest failures were independent of each other. In addition, a global test was also calculated for the model as a whole and it too showed no evidence of non-proportional hazards ($P = 0.60$).

**Brood Survival**

Thirty-one females were monitored during the brood-rearing period in 2009 and 2010 (SMH $n$ = 13; SR $n$ = 18). Early brood-rearing success was relatively high during both study years, ranging from 92.3% in 2009 and 66.7% in 2010 (SR) to 100% in 2009 and 2010 (SMH). Of the successful early brood females, 11 broods were successful through the late brood-rearing period

in 2009 (9 within SR and 2 within SMH) and 8 were successful in 2010 (4 within SR and 4 within SMH). Late brood-rearing success was similar during both study years (2009 = 61.1%; 90% CI: 39.4–79.5%; 2010 = 80.0%; 95% CI: 49.0–95.6%). In addition, over the 2-year period, late brood-rearing success was 22% greater in the SR study area than in SMH (SMH = 54.5%; 90% CI: 27.8–79.2%, *n* = 11; SR =76.5, 90% CI: 53.6–91.0%, *n* = 17); however there was no statistical difference in the means. The total number of chicks observed ranged from 11 (2009 SMH) to 36 (2010 SR) chicks per study area and year. Brood size (the number of chicks observed per successful late brood-rearing female) ranged from 3.3 chicks/female (SMH 2010) to 5.5 chicks/female (SMH 2009). During both study years, productivity (number of chicks per female in the marked sample) was greater within SR than within SMH (0.18; 90% CI: 0.05–0.32).

*Model Fit*.—Two broods were censored due to an immediate mortality or the marked female was no longer trackable. Results of the univariate model estimating differences in survival among study areas indicated that broods located within the SMH study area were 2.9-times more likely to fail than broods within SR (hazard ratio = 2.9; 90% CI: 1.1–7.6). The top model ($\Delta$AIC*c* = 5.08) relating environmental and anthropogenic features to sage-grouse brood survival included distance to nearest turbine (km), terrain ruggedness (scale = 0.46 km), and the percent shrub cover within 1.0 km of a brood location (Table 3-2). The next best approximating model differed by $\geq 5$ $\Delta$ AIC*c* from the top ranked model (Burnhman and Anderson 2002, Arnold 2010).

The risk or odds of a brood failing increased approximately 5 fold with every 1-unit increase in terrain ruggedness within 0.46 km of a brood location (hazard ratio = 4.8; 90% CI: 2.1–11.3; Table 3-3; Fig. 3-4). The risk of a brood failing increased approximately 3 fold with

every 1.0% increase in percent shrub cover within 1.0 km of a brood location (hazard ratio = 3.0; 90% CI: 1.5–6.2; Table 3-4; Fig. 3-4). Lastly, the risk of a brood failing decreased by 38.1% with every 1.0 km increase in distance from nearest turbine (hazard ratio = 0.619; 90% CI: 18.6–52.9%; Table 3-3; Fig. 3-4). More specifically, while holding other covariates constant, the effect of a 0.50 km increase in distance to nearest turbine decreased the risk of brood failure by 21.3%. As distance increased from turbine, the relative risk of failure decreased from 76.2% at 3 km to 97.8% at 8 km from the nearest turbine (Fig. 3-4). Spatially, habitats closer to turbines had higher odds of a brood failing than habitats farther from turbines (Fig. 3-5). Lastly, there was no evidence of non-proportional hazards for any of the 3 covariates included in the top model (*P* ranged from 0.29 [rugged460] to 0.80 [turbine]) suggesting that brood failures were independent of each other. In addition, a global test calculated for the model as a whole showed no evidence of non-proportional hazards ($P = 0.20$).

**Female Survival**

During the study, 45 of 116 (38.8%) radio-marked birds died. I recorded 31 mortalities in SR (15 in 2009 and 16 in 2010) and 14 within SMH (5 in 2009 and 9 in 2010). Although cause of death could not be determined for all mortalities, 13 were determined to be killed by avian predators and 16 were determined to be killed by mammalian predators. In 2009, 3 dead radio-collared females that did not exhibit any signs of trauma were submitted to the Wyoming State Veterinary Lab in Laramie, Wyoming to be examined for the presence of West Nile virus. Two of the 3 female sage-grouse tested positive for West Nile virus and all were located within the SR study area. The median distance of mortality locations to each infrastructure feature varied from 4.0 km (overhead transmission line), to 6.7 km (major roads), to 8.7 km (turbine). The mean female

survival rate at SMH was 28.0% (90% CI: 18.1–40.4%) compared to 47.0% (90% CI: 36.5–57.7%) at SR.

*Model Fit*.–A total of 1,417 locations, 23 monitoring intervals, and 45 mortalities were used to model female sage-grouse survival. Eight mortality events were censored because they occurred within 2 weeks of capture. The univariate model estimating differences in female survival among study areas indicated that study area (SMH vs. SR) did not influence female survival (hazard ratio = 0.84; 90% CI: -0.73–0.36). Adult females were 1.3-times more likely to die than juvenile females (hazard ratio = 1.3; 90% CI: 0.75–2.2). I experienced some model uncertainty and modeled averaged the 95% confidence set of top models (Table 3-2).The top model ($\Delta$AIC$c$ = 0.55) relating environmental and anthropogenic features to female survival included distance (km) to nearest major road and overhead transmission line (Table 3-2). However, this model (AIC$c$ = 378.9) was not more explanatory (within 4 AIC$c$ points) than the null model (AIC$c$ = 379.3), suggesting none of the predictors I used were adequate to explain the variation in survival within my study (Table 3-2). However, the risk of female mortality during the survival period increased by 21.0% with every 1.0 km increase in distance from major roads (90% CI: 16.4–24.9%; Table 3-3, Fig. 3-6). Similarly, the risk of mortality increased by 9.4% with every 1.0 km increase in distance from transmission line (90% CI: 8.5–10.2%; Table 3-3, Fig. 3-6). Spatially, habitats closer to transmission lines had a higher odds of survival than habitats farther from transmission lines (Fig. 3-7). There was no evidence of non-proportional hazards for any of the 2 covariates included in the top model ($P$ = 0.86 for major roads and $P$ = 0.81 for overhead transmission line) suggesting that summer mortalities were independent of each other. In addition, a global test was also calculated for the model as a whole and it too showed no evidence of non-proportional hazards ($P$ = 0.95).

## DISCUSSION

I investigated the potential influence of wind energy development 2 yrs post development, particularly wind turbine influences on sage-grouse nests, broods, and female survival because these parameters have the greatest effect on sage-grouse population growth (Taylor et al. 2012). More specifically, female survival and brood survival, in that order, have the greatest effect on sage-grouse population growth rate (Taylor et al. 2012). I hypothesized that risk of failure increased for nests and broods that were in close proximity to turbines. In addition, I hypothesized that the risk of female mortality increased as proximity to turbines decreased. I determined that the risk of sage-grouse nest and brood failure increased as proximity to turbines increased using Cox proportional hazards and the Andersen-Gill formulation of Cox proportional hazards. Overall female survival was not influenced by proximity to turbines or any other landscape habitat feature used in the analysis; however, female survival was highest around transmission lines throughout the study area.

The reason for the decreased nest and brood survival within habitats in close proximity to turbines is unknown but may be attributed to increased predation (Coates and Delhanty 2010) due to the presence of human development and edge effects (Batary and Baldi 2004). The lack of concurrent predator monitoring makes it difficult to speculate why there is a decrease in survival closer to turbines. The incorporation of different covariates (i.e., predator densities, noise, and detailed weather data) may further explain the variation in survival among sage-grouse occurring in habitats with close proximity to wind energy.

Nest success within SMH (33.3%) was similar to other sage-grouse studies that reported nest success in other habitats influenced by other forms of energy development (<40%; Connelly et al. 2011). Nest success at SR (42.3%) was slightly higher than at SMH (33.3%), but not as

high as the majority of studies in unaltered habitats (11 of 18 [61%] of studies reported ≥50%; Connelly et al. 2011).

Survival time analysis or Cox proportional hazard modeling is becoming a widely used and effective tool to predict nest survivorship in avian species (Liebezeit et al. 2009, Nur et al. 2004, Kirol 2012). Survival time analysis has been incorporated into sage-grouse studies as an effective modeling procedure aimed at identifying risky habitats and specific covariates influencing nest and brood survival (Aldridge and Boyce 2007, Moynahan et al. 2007, Herman-Brunson et al. 2009, Kolada et al. 2009). Logistic regression (Holloran et al. 2005) and the Mayfield method (Mayfield 1961, 1975) are also two other common methods for estimating nest survivorship; however they have some limitations. Logistic regression is commonly used when analyzing nest success in avian species (Holloran et al. 2005, Nur et al. 2004); however, it may be inefficient and in some cases may introduce bias into the analyses because nests with uncertain fates must be excluded from the analysis (Manolis et al. 2000). The Mayfield method (Mayfield 1961, 1975) is the most common method at estimating nest survivorship in avian studies; however, it is met with several restrictive and unrealistic assumptions including nest failure is constant over time, homogeneity of failure probability, and independence of outcome among nests (Dinsmore et al. 2002, Nur et al. 2004). Unlike logistic regression and the Mayfield method, survival time analysis accounts for these assumptions.

The results of my nest survival time analysis indicated that nest survival within both study areas was influenced by proximity to turbines and the variation in shrub height. The risk of nest failure increased as proximity to turbines decreased and as the variation in shrub height decreased. Similar sage-grouse nest survival studies indicated that the risk of nest failure was positively influenced by greater shrub cover, higher grass height, grass cover, and greater

variation in the Normalized Difference Vegetation Index (NDVI; Aldridge and Boyce 2007, Moynahan et al. 2007, Herman-Brunson et al. 2009, Kolada et al. 2009). Only one of these studies included covariates explaining the influence of energy development on sage-grouse nest survival; however it was not significant at predicting nest survival (Aldridge and Boyce 2007). My models predicting nest survival provide good predictive power and insight into the spatial variation of nest survival in relation to wind energy development, particularly wind turbines.

Another important fitness parameter that I modeled was brood survival. I used a formulation of Cox proportional hazards model (Andersen-Gill) to estimate brood survival within both study areas. The A-G model incorporates time-varying covariates when predicting survivorship. Aldridge and Boyce (2007) utilized Cox proportional hazards to model chick survival to 56 days. Similarly, Gregg and Crawford (2009) modeled chick survival to 28 days with the Cox model. Cox proportional hazards are appropriate for estimating survival because there are no time varying covariates (i.e., nest covariates are constant during the incubation period or monitoring interval). Cox proportional hazards model can model brood survival (Aldridge and Boyce 2007, Gregg and Crawford 2009); however, this methodology does not allow for time-dependent covariates that may vary in magnitude with time. The Cox proportional hazard model assumes that left or right censored observations are represented over the entire monitoring interval. Thus, it does not take into account the multiple habitats a sage-grouse potentially uses during the brood-rearing period. The A-G formulation of the Cox model accommodates multiple monitoring intervals and subsequently accounts for multiple habitat characteristics represented during the brood-rearing survival period (Therneau and Grambsch 2000).

The results of my brood survival analysis indicated that the risk of a brood failing increased as proximity to turbines increased, as terrain ruggedness increased, and percent shrub cover increased. Of the studies that utilized Cox survival model, brood survival was positively correlated with grass cover (Gregg and Crawford 2009), risk of failure increased in habitats with higher visible oil and gas well density within 1.0 km, and failure increased in habitats with higher CTI (soil moisture index; Aldridge and Boyce 2007).

Lastly, estimating adult female survival is useful in understanding animal population trends because it compares the cumulative effects of environmental conditions or anthropogenic influences to the overall persistence of the population or the growth rate ($\lambda$). Sage-grouse declines are at least partially explained by lower annual survival of female sage-grouse and in the case of oil and gas development, the impacts to survival result in population-level declines (Holloran 2005).

I used the A-G model to estimate female survival in summer in relation to wind energy infrastructure. The top model did not differ from the null model suggesting the covariates I measured within both study areas did not detect any variability in survival across the landscape. However, the risk of mortality decreased in habitats with close proximity to transmission lines and major roads. Similar to my study, Moynahan et al. (2006) found no support for inclusion of landscape-level habitat variables in modeling monthly annual survival rates of sage-grouse in Montana.

**MANAGEMENT IMPLICATIONS**

Mine is the first study to evaluate short term effects of wind energy infrastructure, specifically turbines, on sage-grouse fitness parameters. The presence of turbines negatively impacted sage-grouse nest and brood survival, whereas the presence of turbines did not appear to be affecting

female survival. Future wind energy project placement should consider the increased levels of risk to sage-grouse broods and nests within habitats of close proximity to wind turbines. Although I did not determine actual thresholds, increased levels of risk to these fitness parameters appeared to increase up to 5.0 km from turbines. Identifying nesting and brood-rearing habitats prior to construction and operation of wind energy facilities will provide valuable information as to the possible affect of the facility on sage-grouse nest and brood survival. Furthermore, placing wind turbines at least 5 km from nesting and brood-rearing habitat should reduce negative influences from wind energy infrastructure on sage-grouse nest and brood survival.

**LITERATURE CITED**

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

Anderson, P. K. and R. D. Gill. 1982. Cox's regression model for counting processes: a large sample study. The Annals of Statistics 10:1100–1120.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Infromation Criterion. Journal of Wildlife Management 74:1175-1178.

Batary, P. and A. Baldi. 2004. Evidence of an edge effect on avian nest success. Conservation Biology 18:389-400.

Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070–1078.

Burhans, D. E., D. Dearborn, F. R. Thompson III, and J. Faaborg. 2002. Factors affecting predation at songbird nests in old fields. Journal of Wildlife Management 66:240-249.

Burnham K. P and D. R. Anderson. 2002. Model selection and multimodel Inference: a practical information-theoretic approach: Second edition. Springer-Verlag, New York, New York, USA.

Carpenter J., C. Aldridge, and M. S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 74:1806–1814.

Coates, P. S. and D. J. Delehany. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. Journal of Wildlife Management 74:240-248.

Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53-69 in S. T. Knick and J. W. Connelly, editor. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38. University of California Press, Berkeley, California, USA.

Connelly, J. W., H. W. Browers, and R. J. Gates. 1988. Seasonal movements of sage grouse in southeastern Idaho. Journal of Wildlife Management 52:116–122.

Connelly, J. W., M.A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967−985.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Cheyenne, Wyoming, USA.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society Series B-Statistical Methodology 34:187−220.

Crawford, J. A. and R. S. Lutz. 1985. Sage grouse population trends in Oregon, 1941-1983. Murrelet 66:69–74.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Witson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2–19.

Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity and management of sage grouse in Idaho. Journal of Wildlife Management. 27:811−841.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476-3488.

ESRI. 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, California, USA.

Fedy,B. C., C. L. Aldridge, K. E. Doherty, M. O'Donnell, J. L. Beck, B.Bedrosian, M. J. Holloran, G. D. Johnson, N. W. Kaczor, C. P. Kirol, C. A.Mandich, D. Marshall, G. McKee, C. Olson, C. C. Swanson, and B. L.Walker. 2012. Interseasonal movements of greater sage-grouse, migratory behavior, and an assessment of the core regions concept in Wyoming. Journal of Wildlife Management 76:1062-1071.

Fischer, R. A., W. L. Wakkinen, K. P. Reese, and J. W. Connelly. 1993. Nesting-area fidelity of sage grouse in southeastern Idaho. Condor 95:1038-1041.

Fischer, R. A., W. L. Wakkinen, K. P. Reese, and J. W. Connelly. 1997. Effects of prescribed fire on movements of female sage-grouse from breeding to summer ranges. Wildlife Society Bulletin 109:82–91

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Grambsch, P. M., and T. M. Therneau. 1994. Proportional hazards test and diagnostics based on weighted residuals. Biometrika 81:515-526.

Gregg, M. A. 2006. Greater sage-grouse reproductive ecology: linkages among habitat resources, maternal nutrition, and chick survival. Dissertation, Oregon State University, Corvallis, USA.

Gregg, M. A., and J. A. Crawford. 2009. Survival of greater sage-grouse chicks and broods in the Northern Great Basin. Journal of Wildlife Management 73:904-913.

Gregg, M. A., J. A. Crawford, and M. S. Drut. 1993. Summer habitat use and selection by female sage grouse (Centrocercus urophasianus) in Oregon. Great Basin Naturalist 53:293–298.

Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetational cover and predation of sage grouse nests in Oregon. Journal Wildlife Management 58:162–166.

Herman-Brunson, K. M., K. C. Jensen, N. W. Kaczor, C. C. Swanson, M. A. Rumble, and R. W. Klaver. 2009. Nesting ecology of greater sage-grouse *Centrocercus urophasianus* at the eastern edge of their historic distribution. Wildlife Biology 15:395-404.

Holloran, M. J. 1999. Sage grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. Thesis, University of Wyoming, Laramie, USA.

Holloran, M. J. 2005. Greater sage-grouse (Centrocercus urophasianus) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Holloran, M. J. and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. The Condor 107:742–752.

Holloran, M. J. B. J. Heath, A . G. Lyon, S. J. Slater, J. L. Kuipers, S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638-649.

Homer, C. G., Aldridge, C. L., Meyer, D. K., Coan, M. J., and Z. H. Bowen. 2009. Multiscale sagebrush rangeland habitat modeling in southwest Wyoming. US Geological Survey, Washington D. C., USA.

Homer, C. G., C. L. Aldridge, D. K. Meyer, and S. J. Schell. 2012. Multi-scale remote sensing sagebrush characterization with regression trees over Wyoming, USA: laying a foundation for monitoring. International Journal of Applied Earth Observation and Geoinformation 14:233–244.

Johnson, C. J., M. S. Boyce, C. C. Schwartz, and M. A. Haroldson. 2004. Modeling survival: application of the Andersen-Gill Model to Yellowstone grizzly bears. Journal of Wildlife Management 68:966–978.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651-661.

Johnson, D. H. 1980. The comparsion of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Johnson, G. D., and M. S. Boyce. 1990. Feeding trials with insects in the diet of sage grouse chicks. Journal of Wildlife Management 54:89–91.

Kirol, C. P. 2012. Quantifying habitat importance for greater sage-grouse (Centrocercus urophasianus) population persistence in an energy development landscape. Thesis, University of Wyoming, Laramie, USA.

Klebenow, D. A. 1969. Sage grouse nesting and brood habitat in Idaho. Journal of Wildlife Management 33:649–662.

Klebenow, D. A., and G. M. Gray. 1968. Food habits of juvenile sage grouse. Journal of Range Management 21:80–83.

Kleinbaum, D. G., and M. Klein. 2005. Survival analysis, a self-learning text, Second Edition. Springer Sceince+Business Media, Inc, New York, New York, USA.

Kolada, E. J., M. L. Casazza, and J. S. Sedinger. 2009. Ecological factors influencing nest survival of greater sage-grouse in Mono County, California. Journal of Wildlife Management 73:1341-1347.

Liebezeit, J. R. and T. L. George. 2002. Nest predators, nest site selection, and nesting success of the dusky flycatcher in a managed ponderosa pine forest. Condor 104:507-517.

Liebezeit, J. R., S. J. Kendall, S. Brown, C. B. Johnson, P. Martin, T. L. McDonald, D. C. Payer, C. L. Rea, A. Streever, A. M. Wildman, and S. Zack. 2009. Influence of human development and predators on nest survival of tundra birds, Arctic Coastal Plain, Alaska. Ecological Applications 19:1628-1644.

Lyon, A. G. 2000. The potential effects of natural gas development on sage grouse near Pinedale, Wyoming. Thesis, University of Wyoming, Laramie, USA.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486–491.

Manolis, J. C., D. E. Andersen, and F. J. Cuthbert. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. Auk 117:615-626.

Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255-261.

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2006. Factors contributing to process variance in annual survival of female greater sage-grouse in Montana. Ecological Applications 16:1529-1538.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in northcentral Montana. Journal of Wildlife Management 71:1773-1783.

Nur, N., A. L. Holmes, and G. R. Geupel. 2004. Use of survival time analysis to analyze nesting success in birds: an example using loggerhead shrikes. Condor 106:457-471.

Patterson, R. L. 1952. The sage grouse in Wyoming. Wyoming Game and Fish Commission and Sage Books. Denver, Colorado, USA.

Rebholz, J. L. 2007. Influence of habitat characteristics on greater sage-grouse reproductive success in the Montana Mountains, Nevada. Thesis, Oregon State University, Corvallis, USA.

Rotella, J. J., S. J., Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187–205.

Schoenfeld, D. 1982. Residuals for the propotional hazards regression model. Biometrika 69:239-241.

Schroeder, M.A., J.R. Young, and C.E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Pages 1-28 in A. Pool and F. Gill, editors. The Birds of North America. The Birds of North America, Inc, Philadelphia, Pennsylvania, USA.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336-347.

Therneau T. M. and P. M. Grambsch. 2000. Modeling survival data: Extending the Cox model. Springer-Verlag, New York, New York, USA.

Therneau T. M., P. M. Grambsch, and T. R. Fleming. 1990. Martingale-based residuals for survival models. Biometrika 77:147-160.

Thompson, K. M, M. J. Holloran, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2006. Early brood-rearing habitat use and productivity of Greater Sage-Grouse in Wyoming. Western North American Naturailst 66:332−342.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

Walker, B. L. 2008. Greater sage-grouse response to coal-bed natural gas development and West Nile virus in the Powder River Basin, Montana and Wyoming, USA. Dissertation, University of Montana, Missoula, USA.

Wallestad, R. O. 1971. Summer movements and habitat use by sage grouse broods in central Montana. Journal of Wildlife Management 35:129–136.

Wik, P. A. 2002. Ecology of greater sage-grouse in south-central Owyhee County, Idaho. Thesis. University of Idaho, Moscow, USA.

Zablan, M. A., C. E. Braun, and G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal of Wildlife Management 67:144–154.

Table 3-1. Explanatory anthropogenic and environmental covariates used in modeling of sage-grouse nest, brood, and female survival at the Seven Mile Hill and Simpson Ridge study areas, Carbon County Wyoming, USA, 2009 and 2010.

| Covariates | Variable description |
|---|---|
| Anthropogenic infrastructure | |
| dist_major_rds | Distance to nearest major road [WYO HWY 72, US HWY 287/30, and I-80 (km)] |
| dist_tline | Distance to nearest overhead transmission line (km) |
| dist_turbine | Distance to nearest turbine (km) |
| Environmental | |
| Bare ground† | Percent bare ground |
| Big sagebrush† | Percent big sagebrush (*Artemisia tridentata* spp.) |
| Elevation | Altitude above sea level (m) |
| Herbaceous† | Percent herbaceous cover |
| Litter† | Percent litter |
| Sagebrush†* | Percent sagebrush (*Artemisia* spp.) |
| Shrub†* | Percent shrub cover |
| Shrub_hgt†* | Shrub height (0–253 cm) |
| Slope | Degrees 0-90 |
| Terrain ruggedness | Variability in slope and aspect (0-1; 1 = complete terrain variation; Sappington et al. 2009) |
| Wyoming big sagebrush† | Percent Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) |

*Also included is the standard deviation of these covariates.

†Vegetation covariates obtained from Homer et al. 2012.

Table 3-2. Model fit statistics for greater sage-grouse nest, brood, and survival at the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010. Models are listed according to the model best fitting the data and ranked by (Δ AIC*c*), the difference between the model with the lowest Akaike's Information Criterion for small samples (AIC*c*) and the AIC*c* for the current model. The value of the maximized log-likelihood function (log[L]), the number of estimated parameters (K), and Akaike's weights ($w_i$) for each model are also presented.

| Model | log[L] | K | AIC*c* | Δ AIC*c* | $w_i$ |
|---|---|---|---|---|---|
| Nest Survival | | | | | |
| sd_shrub_hgt, dist_turbine, dist_tline | -213.3 | 4 | 433.1 | 0.00 | 0.44 |
| sd_shrub_hgt, dist_turbine | -214.4 | 3 | 433.1 | 0.1 | 0.43 |
| sd_shrub_hgt | -216.7 | 2 | 435.6 | 2.5 | 0.13 |
| null | -218.7 | 1 | 437.4 | 4.3 | 0.05 |
| Brood Survival | | | | | |
| dist_turbine, terrain ruggedness, shrub | -30.1 | 4 | 66.6 | 0.00 | 0.91 |
| dist_turbine, terrain ruggedness | -33.7 | 3 | 71.6 | 5.0 | 0.07 |
| dist_turbine | -36.6 | 2 | 75.4 | 8.8 | 0.01 |
| null | -38.3 | 1 | 76.5 | 10.0 | 0.01 |
| Female Survival | | | | | |
| dist_major_rds, dist_tline | -187.3 | 3 | 378.9 | 0.00 | 0.55 |
| dist_major_rds | -188.6 | 2 | 379.3 | 0.37 | 0.45 |
| null | -189.7 | 1 | 379.4 | 0.69 | 0.28 |

Table 3-3. Relative risks of sage-grouse for each covariate or risk factor included in the top model for the Seven Mile Hill and Simpson Ridge study areas in Carbon County, Wyoming, USA, 2009 and 2010.

| Covariate | Scale (km) | Estimate | SE | Hazard Ratio [*exp*(Estimate)] | Hazard Ratio 90% CI | |
|---|---|---|---|---|---|---|
| | | | | | Lower | Upper |
| Nest Survival | | | | | | |
| sd_shrub_hgt | 0.30 | -0.16 | -0.01 | 0.86 | 0.84 | 0.87 |
| dist_turbine | NA | -0.06 | -0.01 | 0.94 | 0.94 | 0.94 |
| dist_tline | NA | 0.11 | 0.01 | 1.11 | 1.10 | 1.12 |
| Brood Survival | | | | | | |
| dist_turbine | NA | -0.48 | 0.17 | 0.62 | 0.47 | 0.81 |
| Terrain ruggedness | 0.46 | 1.6 | 0.52 | 4.83 | 2.07 | 11.3 |
| Shrub | 1.0 | 1.1 | 0.43 | 3.03 | 1.49 | 6.16 |
| Survival | | | | | | |
| dist_major_rds | NA | 0.19 | 0.02 | 1.21 | 1.16 | 1.25 |
| dist_tline | NA | 0.09 | 0.01 | 1.09 | 1.09 | 1.10 |

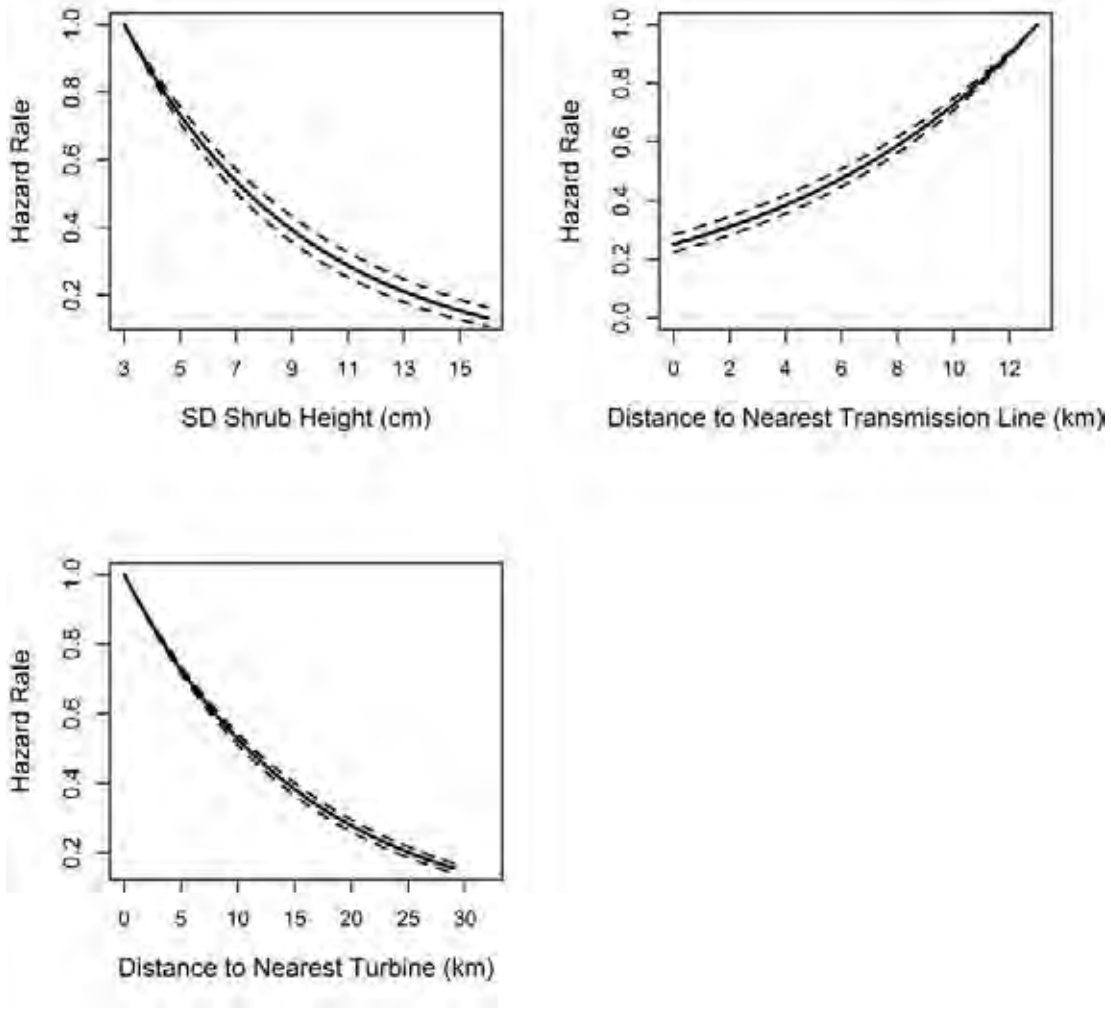



Figure 3-1. Relative hazard rate of nest survival adjusted for the SD of shrub height within 0.30 km, and the distance to nearest turbine and transmission line at the Simpson Ridge and Seven Mile Hill study areas, Carbon County, Wyoming, USA, 2009 and 2010. Dashed lines indicate the lower and upper 90% confidence limits.

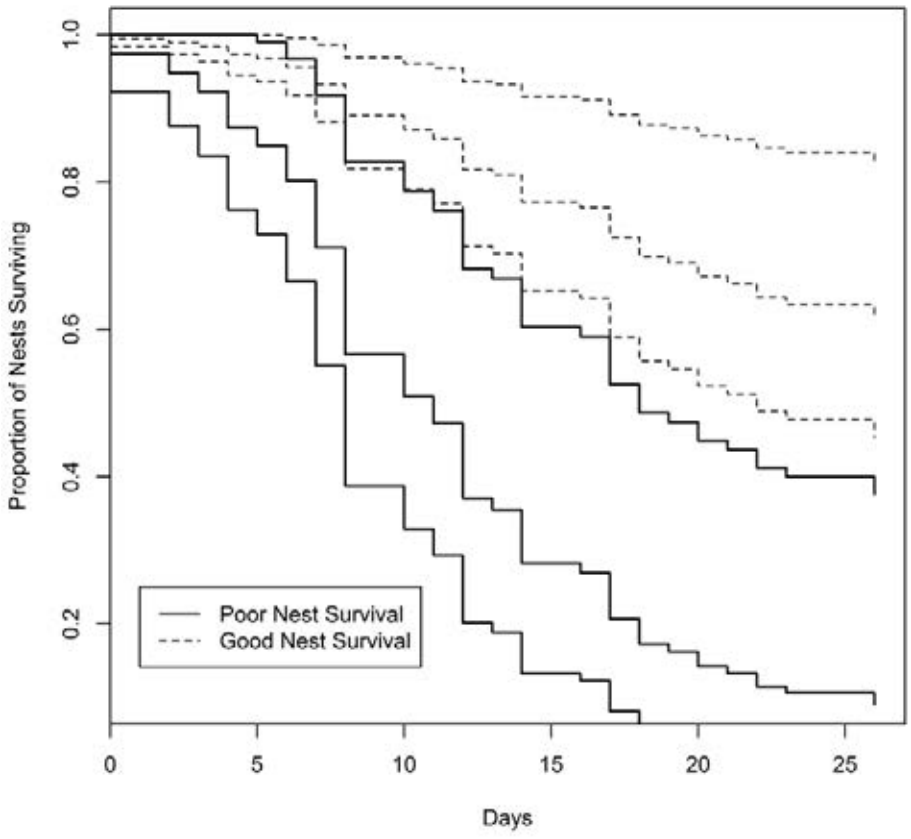



Figure 3-2. Expected nest survival and 90% confidence intervals for nests located in higher risk habitats (closer to turbines, further from transmission lines, and higher SD of shrub height within 0.30 km; poor nest survival) and for nests located in lower risk habitats (good nest survival) within the Simpson Ridge and Seven Mile Hill study areas Carbon County, Wyoming, USA, 2009 and 2010.

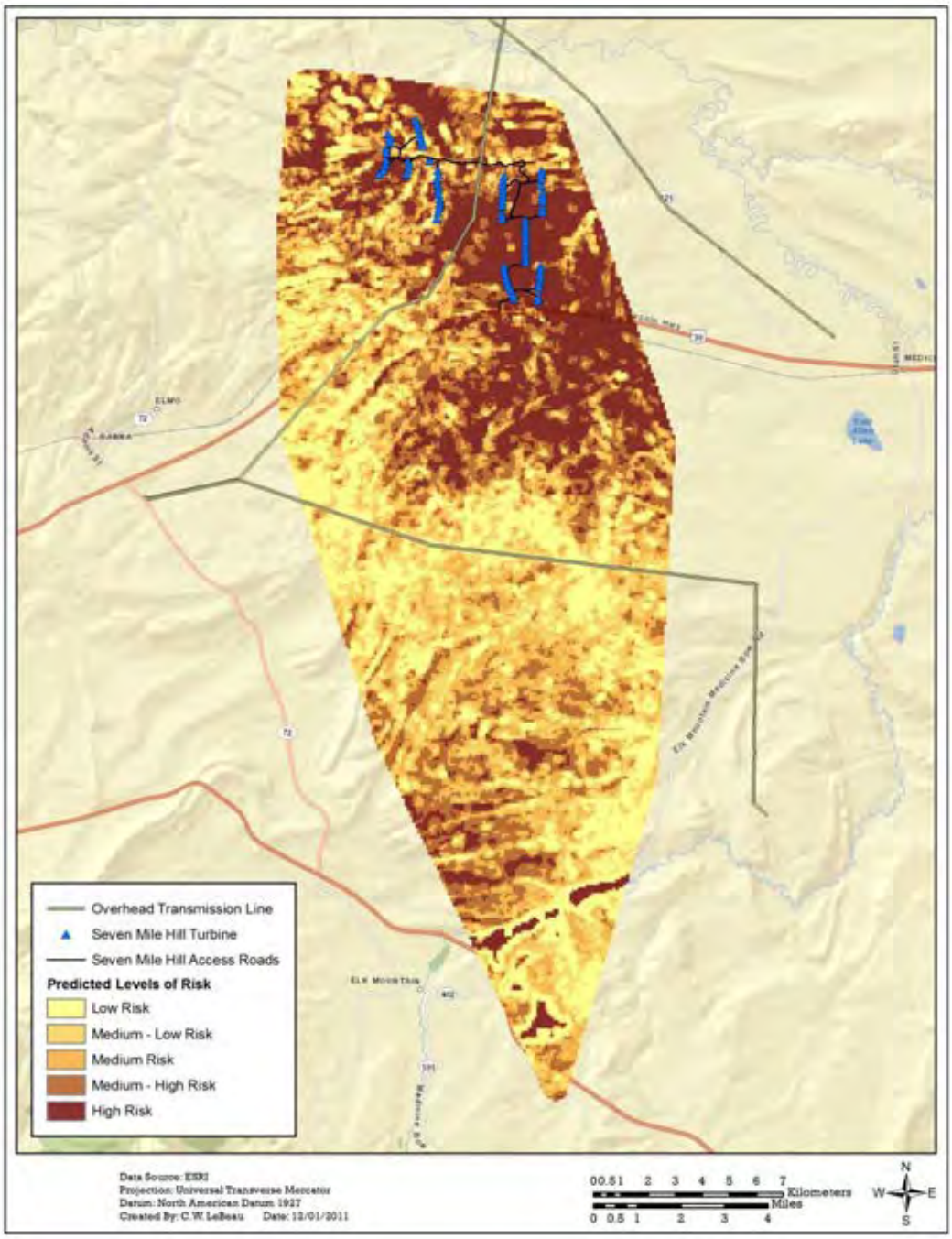



Figure 3-3. Spatial variation in the predicted relative risk of sage-grouse nest failure (low – high) within the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010.

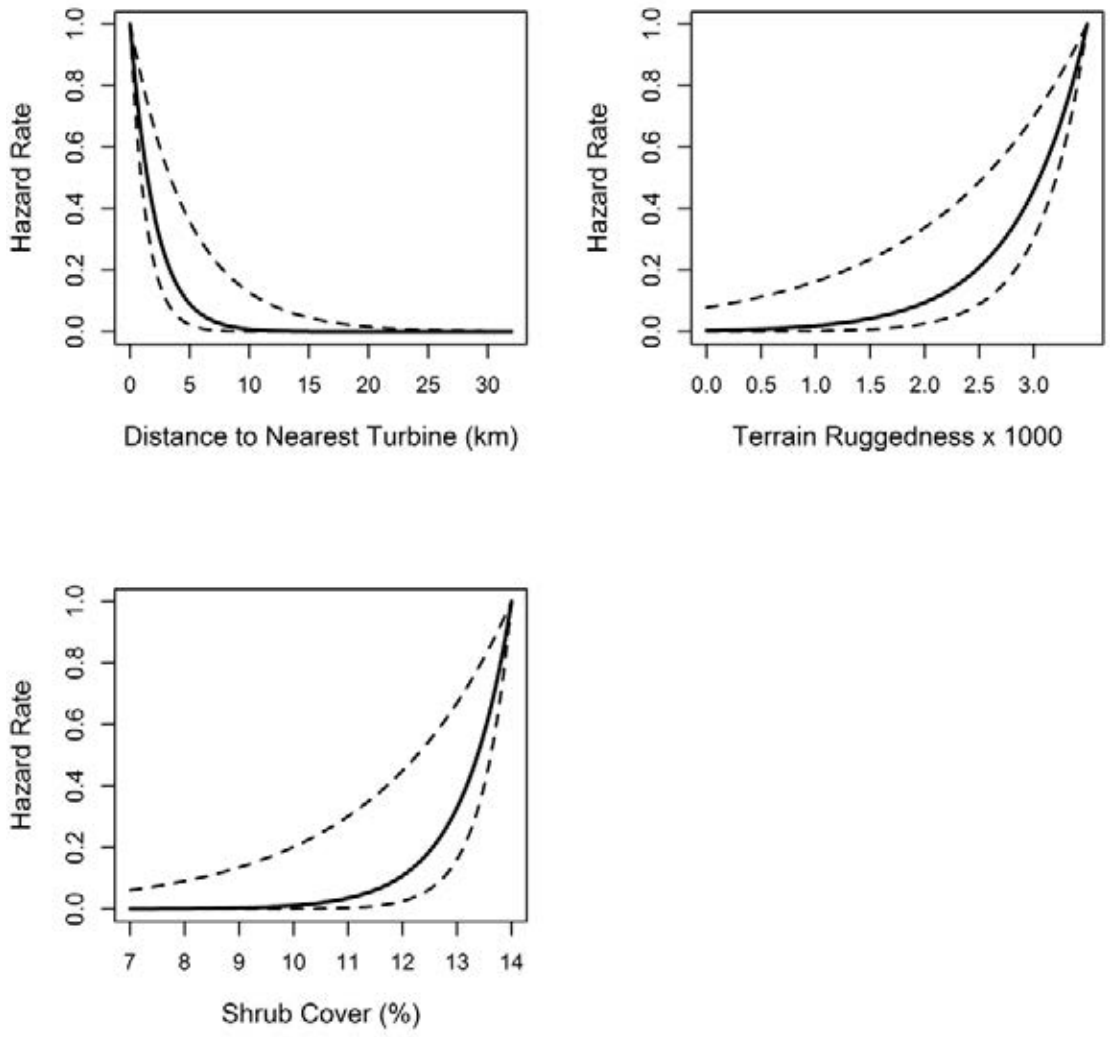



Figure 3-4. Relative hazard rate of brood survival adjusted for distance to nearest turbine, terrain ruggedness, and percent shrub cover at the Simpson Ridge and Seven Mile Hill study areas, Carbon County, Wyoming, USA, 2009 and 2010. Dashed lines indicate the lower and upper 90% confidence limits.

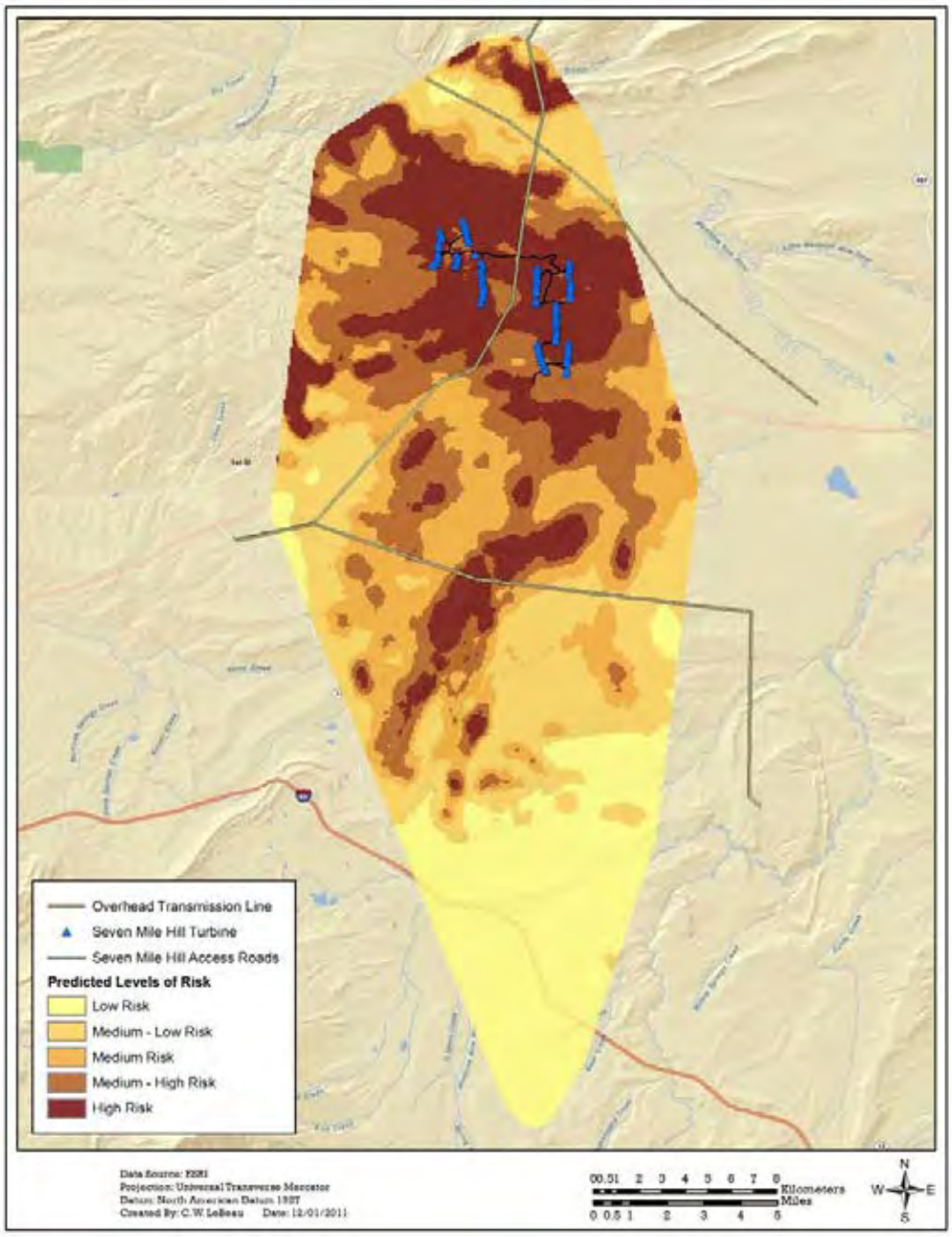



Figure 3-5. Spatial variation in the predicted relative risk of sage-grouse brood failure (low – high) within the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010.

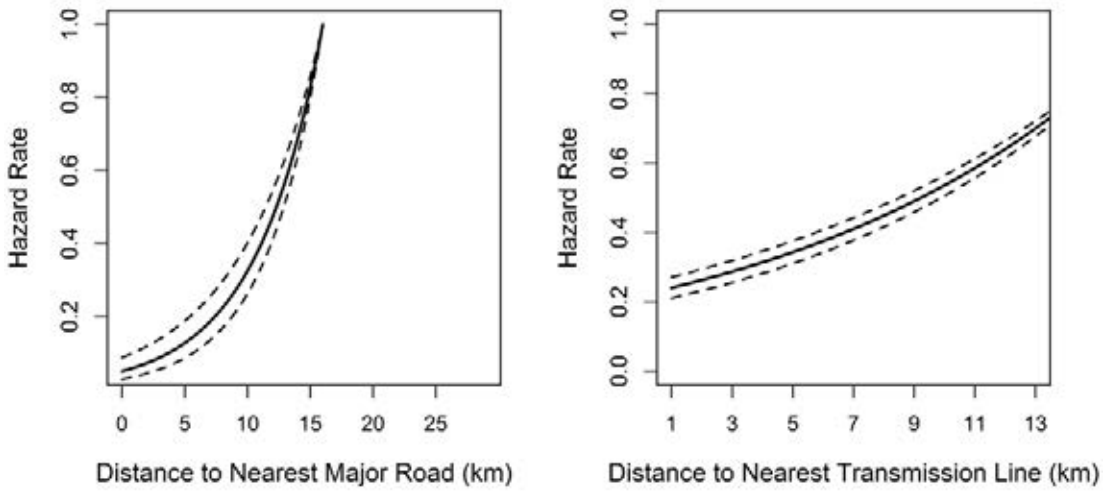



Figure 3-6. Relative hazard rate of female survival adjusted for the distance to nearest major road and distance to nearest overhead transmission line at the Simpson Ridge and Seven Mile Hill study areas, Carbon County, Wyoming, USA, 2009 and 2010. Dashed lines indicate the lower and upper 90% confidence limits.

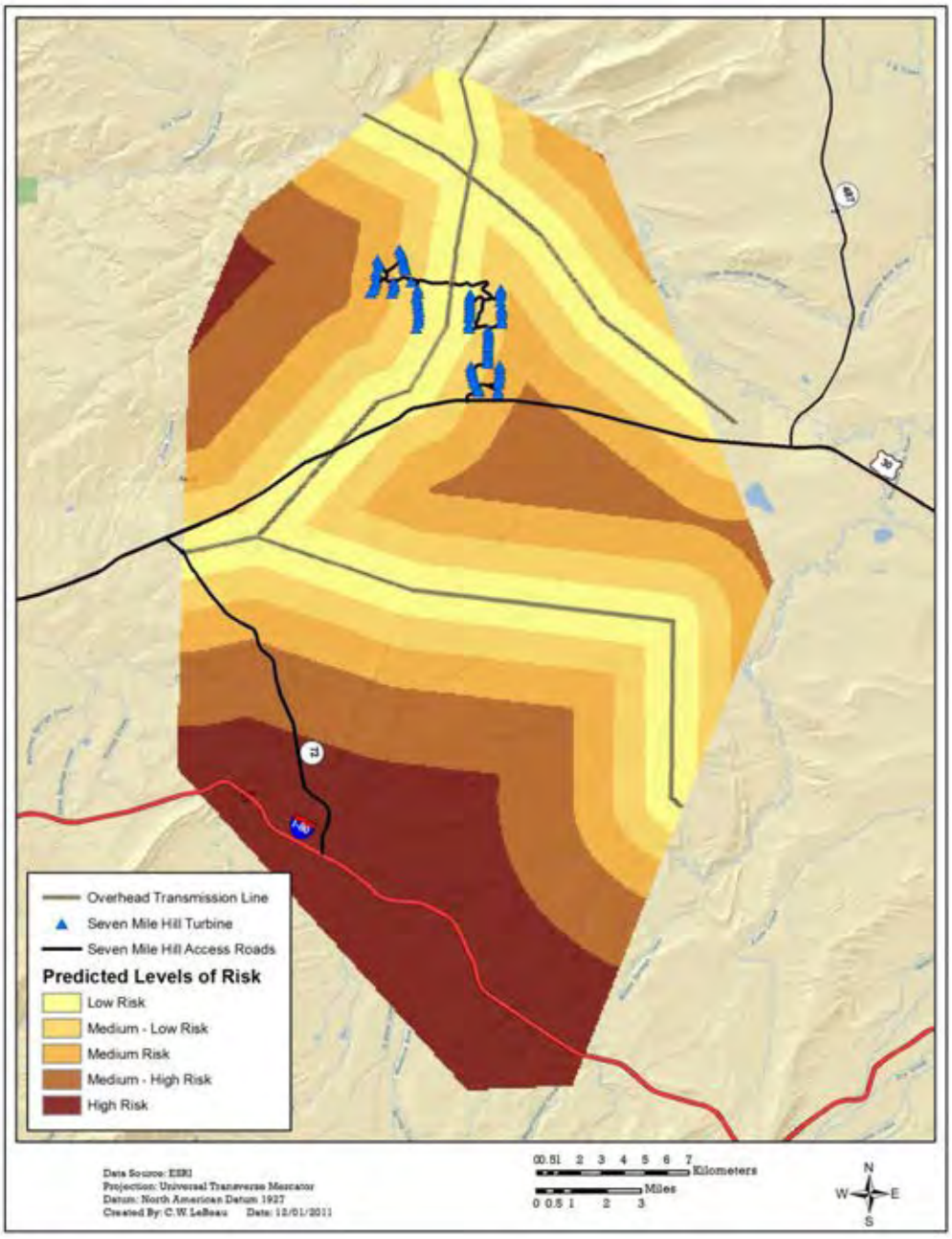



Figure 3-7. Spatial variation in the predicted relative risk of sage-grouse summer mortality (low – high) within the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010.

# CHAPTER 4

## Greater Sage-Grouse Male Lek Attendance Relative to Wind Energy Development

In the format for manuscript submittal to the *Journal of Wildlife Management*


## ABSTRACT

Trends in greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) population abundance are typically indexed through lek counts documenting peak male attendance. Monitoring male lek attendance can provide insight into the viability of sage-grouse populations. Lek counts have been used to assess changes in male attendance rates and male recruitment at leks impacted by anthropogenic features. Impacts to male lek attendance have been documented at leks located in close proximity to oil and gas development. Furthermore, it has been documented that there is a time lag of 2–10 years when measurable affects can be detected at leks impacted by oil and gas development. It is unknown whether the same time lags or degree of impact will occur at leks located in close proximity to wind energy development. My study question focused on whether leks that were spatially proximate to wind energy infrastructure had greater declines in male lek attendance from pre-development to 4 years post development of a wind energy facility. I used a before-after-control-impact study design to assess male lek attendance. Aerial surveys were flown to identify any unknown leks. In addition, 3 lek counts were conducted at each occupied lek identified during the breeding season to determine the peak number of males attending each lek. First, I used ratio of means of lek counts to investigate differences among lek attendance pre and post development of the wind energy facility. Then, I further investigated the changes in lek attendance pre and post development by calculating a disturbance metric for each lek and regressing this metric with male lek attendance using linear

mixed effects models. Leks located within wind energy development experienced a significant decline in male lek attendance from pre development to 4 years post development. However, leks located outside of the wind energy development experienced similar significant declines. The top model derived from the mixed effects linear model included one fixed term (year) and one random component, the effect of individual leks. Leks that were influenced more by wind energy development experienced similar declines as leks with no influence from pre development to 4 years post development. The significant decline in male lek attendance from 1 year pre development to 4 years post development cannot solely be attributed to the presence of the wind energy facility. Impacts from the wind energy facility may not be initially realized due to the time lags associated with sage-grouse breeding populations. More than 4 years of post development monitoring and multiple sites may be necessary to adequately assess greater sage-grouse breeding response to wind energy development.

**INTRODUCTION**

Trends in sage-grouse population abundance are typically indexed through lek counts (Beck and Braun 1980, Connelly and Braun 1997, Walsh et al. 2004). While the use of telemetry is the best method to determine population demographic rates, lek counts provide a good index of breeding population levels and in many cases long-term data sets are available for trend analysis (Connelly and Braun 1997, Connelly et al. 2000*a*). Multiple studies have used lek counts to provide information on sage-grouse breeding populations in response to disturbances including prescribed burning (Connelly et al. 2000*b*) and oil and gas development (Holloran 2005, Walker et al. 2007, Harju et al. 2010, Holloran et al. 2010).

The purpose of my study was to investigate the effect of wind energy infrastructure on sage-grouse peak male lek attendance. Peak male lek attendance was defined as the highest

number of males attending each lek during any of the 3 counts initiated during the breeding season. I used a before-after-control-impact study design (BACI) to evaluate the impacts of wind turbines on male lek attendance (Green 1979, Morrison et al. 2008). BACI study designs consist of knowing what type of impact will occur, when and where it will occur, and having the ability to collect data prior to the impact (Green 1979) at the impacted site and a geographically similar site that remains unaffected (control). I employed this study design to evaluate whether the newly constructed wind turbines reduced male lek attendance at leks located near the facility within 4 years of development. The objectives of this chapter were to (1) estimate a trend in peak male attendance between leks with varying proximity to turbines pre and post-construction of the Seven Mile Hill wind energy facility, and (2) compare those trend(s) to peak male attendance at Simpson Ridge (control site).

## STUDY AREA

The study area used in this chapter is consistent with the first 3 chapters of my thesis. Sage-grouse leks located south of U.S. Highway 30/287 were within the SR study area and leks located north of U.S. Highway 30/287 were within the SMH study area.

## METHODS

### Field Methods

To investigate the effect of wind energy infrastructure on the sage-grouse population, I determined the distribution and number of males at active leks throughout the SMH ($n$ = 5) and SR ($n$ = 9) study areas. I obtained the locations of known historic and existing sage-grouse leks within 6.4 km (twice the distance of non-disturbance around leks suggested by Connelly et al 2000*a*) of the proposed SRWRA located in the SR and the SMH project areas from the Wyoming Game and Fish Department (WGFD) lek database. Because it is important to detect all

leks when comparing lek counts to population trends (Walsh 2004), lek searches, following the methodology outlined by WGFD (Christiansen 2007), were conducted during the 2009 lekking period to detect any unknown leks within both study areas. Aerial surveys were conducted from fixed-wing aircraft flying parallel transects designed to provide full coverage of both project areas. These surveys were conducted during the peak of the lekking season from early April through early May. All mapped historic and existing leks were flown to check for occupancy in spring 2009. I conducted surveys from one-half hour before sunrise to one-half hour after sunrise (Patterson 1952) during optimal weather conditions. Aerial flight transects were oriented north-south and were separated by approximately 1.0 km. Transects were flown at a height of 91 to 137 m above ground level at an approximate speed of 161 kph. I recorded GPS coordinates and the approximate numbers of grouse observed at all located leks. In addition, I obtained lek locations and counts within 18 km (the furthest distance of a lek from the SMH turbines within SMH and SR study areas) of SR and SMH study area because SR may not be an adequate control for SMH because of its close proximity to SMH turbines. In addition, the area encompassing an 18-km radius was selected by Johnson et al. (2011) to evaluate the influence of environmental and anthropogenic features around sage-grouse leks because Connelly et al. (2000*a*) recommended this distance around leks to manage for migratory sage-grouse populations. These 22 leks were considered as the regional population (REG).

Ground surveys were conducted from 2008 to 2012 to count sage-grouse on identified leks within SMH and SR. Lek counts for the regional leks were obtained from WGFD and only included 2008 to 2011. Each active lek located during aerial surveys and known historic lek locations in the survey area were visited 3 times each spring to count the number of sage-grouse using the lek. Ground surveys were spaced a minimum of 7 days apart and occurred during the

lekking period (WGFD 2003). Counts were conducted for a 15–30 minute period in the early morning when the lek was most active. I collected data on the maximum number of birds counted by sex (males, females, unknown), date, time period of observation, and weather information (temperature, wind speed and direction, cloud cover, precipitation; WGFD 2003).

*Analytical Methods*.—Because data were collected at each lek each year, I first estimated the difference in the ratio of means of the peak male lek attendance between 2008 to 2009, 2008 to 2010, 2008 to 2011, and 2008 to 2012 within both study areas using a 500 iteration bootstrapping technique where I sampled counts with replacement from each lek during each year and calculated the ratio of means between the study areas and years. I calculated SE and 90% CI from the SD of the 500 bootstrap iterations. A statistically significant difference (alpha = 0.10; 90% confidence interval [CI] not including 0.0) between pre-construction (2008) and any of the 4 years post-construction of the SMH facility indicated a change in the mean lek attendance and warranted further investigation.

If there was statistically significant difference between any of the study areas then a more complicated linear mixed-effects analysis (Henderson 1950, Goldberger 1962, McLean 1991, Blickley et al. 2012) was used to investigate relationships between lek attendance and disturbance metrics. Mixed models have both fixed and random effects. Fixed effects are identical or constant for all groups (leks) in a population, and random effects are allowed to differ from group to group (Gelman 2005). Random effects assume some type of relationship within a group exists, and in this case we assumed a relationship within individual leks across years. I used the following linear mixed model:

$$R_{ij} = \beta_0 + \beta_1 X_i + \beta_2 Year_j + \omega_i + \varepsilon_{ij} ,$$

where $R_{ij}$ was the attendance count values for each lek *i* (*i*=1,…,14) in year *j* (2008 = 1, 2009 = 2, 2010 = 3, 2011 = 4, and 2012 = 5), $X_i$ was a disturbance covariate measured at lek *i*, $Year_j$ was the effect of year *j*, $\omega_i$ was a random lek effect, $\varepsilon_{ij}$ were error terms for each lek and year assumed to be normally distributed, and $\beta_0$(intercept), $\beta_1$, and $\beta_2$ were fixed-effect coefficients to be estimated.

Fixed-effects (covariates) considered in my analysis included 5 disturbance metrics, which included distance to nearest turbine and the proportion of turbines that overlapped each lek. The distance to nearest turbine was the distance from the center of the lek to the nearest turbine (km). I also included 4 different decay functions (-*exp*[*distance*]/decay distance) representing various decay distances from turbines (i.e. 1.5, 5.0, 10, 15 km). The proportion of overlapping turbines was calculated by buffering each lek by 3.2 km, which is the suggested management area around each lek (Connelly et al. 2000*a*, Walker et al. 2007). I then buffered the individual turbines with their access roads by varying sizes to evaluate various disturbance proportions. These buffer sizes ranged from 0.60 km to 5.0 km and were determined from studies where sage-grouse leks have been impacted by energy development (Table 4-1). The resulting overlapping area(s) were used as covariates to estimate male lek attendance trends. I also included a categorical covariate identifying each study area (1 = SMH and 0 = SR).

In addition to fixed effects, I also included a random effect in the mixed model. Peak male lek attendance varied between leks located within both study areas. Subsequently, male lek attendance over the 4-year period was more likely to be related within individual leks than between leks. For example, lek attendance might consistently be 10–20 males at a lek for a span of 5 to 10 years and another lek might consistently have around 75–100 males attending that lek

over the same time frame. To account for this pseudo-replication (Zuur et al. 2009), I considered individual leks as a random effect in the mixed model.

To estimate the effects of turbines on male lek attendance, I followed a multiple step process that included simple linear regression, mixed modeling, model selection, and goodness-of-fit evaluations. I first used linear regression to investigate if there was an individual lek effect on lek attendance. My response variable was the natural log (*ln*) of peak number of males (hereafter count) and my explanatory variables was year interacting with the turbine disturbance metric. Some leks recorded 0 males, subsequently I added 1 to each count (i.e., *ln*(count+1)). I used residual plots to test for within lek-correlation and heterogeneity of the residuals (Zuur et al. 2009).

If within lek-correlation was present in the linear model further model development using a random intercept would be warranted (Zurr et al. 2009). Model development followed a top-down strategy (Diggle et al. 2002). I compared models using analysis of variance (ANOVA), likelihood ratio tests, and Akaike's information criterion corrected for small sample sizes (AIC*c*; Burham and Anderson 2002, Zuur et al. 2009). I first compared the linear model to a random intercept model using ANOVA and likelihood ratios to determine whether a random intercept for each lek was warranted and if further model development was needed (Zuur et al. 2009). If results of the linear and random intercept model comparison were significantly different I included lek as random effect in a mixed model (Zuur et al. 2009).

I used likelihood ratio tests and maximum likelihood estimation to compare the fixed effects for the nested models. I used ML estimation to determine the optimal fixed structure because models with different fixed effects fitted with REML cannot be compared on the basis of their restricted likelihoods (Pinheiro and Bates 2000, Zuur et al. 2009). The models that

included the interaction of year and disturbance metric to models with no interactions were compared. Models with and without the fixed effects were also compared to estimate the final model. The final model parameters were estimated using REML (Zuur et al. 2009). Lastly, I validated the final model by inspecting the residuals for equal scatter and homogeneity to ensure a good model fit (Zuur et al. 2009). I also utilized a QQ-plot to assess the normality of the residuals and the normality of the random effects (Zuur et al. 2009). Because SR may not be an adequate control for SMH, I estimated mixed models with leks from all three study areas and with only leks from SMH and SR to see if SR was an adequate control. If it was I would see similar effects on lek attendance between the SR and REG leks.

**RESULTS**

Fourteen greater sage-grouse leks were observed during lek surveys in both study areas (5 within SMH and 9 within SR during 2008, 2010, 2011, and 2012 (Table 4-2; Fig. 4-1). Two leks located in SMH were not counted during 2009. During 2008 (pre-development of SMH wind energy facility) the maximum number of male birds present at the occupied leks within the SMH study area ranged from 18 males (Hanna Draw East 2) to 74 males (Missouri John), with a mean count of 36 males per lek. During 2009, 2010, 2011, and 2012 the mean lek counts decreased to 34, 22, 8, and 9 males per lek, respectively at SMH. Similarly to SMH, occupied leks located within SR had a mean count of 37 males/lek, ranging from 0 (Old Percy 2) to 111 males (Old Carbon 35-2) in 2008. The mean male count peaked in 2009 (40 males/lek) then decreased to 23, 20, and 14 males per lek in 2010, 2011, and 2012, respectively (Table 4-2). I included 22 regional leks in my analysis and the mean count ranged from 23 males/lek in 2008 to 7 males/lek in 2011.

Prior to construction in 2008, three leks were located within 1.6 km of the Seven Mile Hill turbines, including the Missouri John, Pine Draw, and Commo 1 leks (Fig. 4-1). In 2008,

130 males were observed on all of these leks combined. In 2009, 103 males were counted on these three leks (Table 4-2). There were 2 additional leks (Hanna Draw East 1 and 2) located >3.2 km; however these leks were not surveyed in 2009 (Table 4-2; Fig. 4-1). In 2010, 2011, and 2012, leks within 3.2 km of the Seven Mile Hill turbines were surveyed. Data collected from 2009 through 2012 represent the first, second, third, and fourth sage-grouse breeding seasons, respectively, after the wind-energy facility became operational. The three leks within 3.2 km were located 0.58, 1.6, and 1.5 km from the nearest wind turbine (Fig. 4-1). The total number of males counted on these three leks decreased from 130 the first year prior to construction (2008), to 33 in 2012 with one lek becoming inactive (i.e., no males observed at the Pine Draw lek in 2012; Table 4-2).

The results from the ratio of means test indicated there was no significant difference from 2008 to 2012 between the three study areas. Regressing the ratio of means for each study area against year indicated no significant difference between the slopes (SMH vs SR = 0.03; SE = 0.05; SMH vs REG = 0.04; SE = 0.07). I did however detect a significant difference in mean male lek attendance from 2008 to 2011 between SMH and SR (Fig. 4-2). I further investigated whether the addition of turbines to SMH had a greater impact on male lek attendance at leks with closer proximity to turbines than leks farther from turbines by using linear mixed effects models.

**Model Development**

The residual plot for the linear regression model indicated unequal scatter of the residuals, thus evidence of within-lek correlation in the data (Fig. 4-3). The likelihood ratio test indicated that the random intercept model including lek as the random term was considerably better than the linear model ($L = 42.56$, $df = 1$, $P < 0.001$). The optimal fixed structure included year interacting with distance to nearest turbine ($\Delta AIC = 0.402$); however, this interaction was insignificant ($\beta =$

0.013; 90% CI: -0.003 –0.03). The final resulting model only included year as the fixed term. The final model showed a significant year effect on male lek attendance. Male lek attendance decreased on average by 25.6% (90% CI: 17.5–32.9%) every year from 2008 to 2012 within leks located at SMH and SR. I observed similar trends when I incorporated the data from the regional leks ($n$ = 22). The interaction between year and distance to turbine was not significant ($\beta$ = -0.003; 90% CI: -0.011–0.006). Male lek attendance at the regional leks decreased on average by 31.4% (90% CI: 24.6–37.7%) every year from 2008 to 2011. Similar to the ratio of means analysis there appeared to be no significant difference in male lek attendance from 1-yr pre construction to 4 years post construction between the three study areas.

**DISCUSSION**

Ratio of means and linear mixed models were used to investigate the trends in peak male attendance at leks impacted by wind turbines. I utilized a BACI study design to detect changes in peak male attendance at leks prior to the construction and operation of the SMH wind energy facility to 4 years post-development. I hypothesized that leks closer to turbines, or leks that had a greater proportion of overlapping wind energy infrastructure, experienced a significant decrease in male lek attendance from pre-construction to 4 years post construction.

Male lek attendance significantly decreased from 2008 to 2012; however, this decrease could not be attributed to the degree of influence by wind turbines or the study area in which each lek resided. Leks located in both study areas and regionally, significantly decreased from 2008 to 2012. The SR study area, which was not influenced by turbines, experienced similar trends from 2008 to 2012 as did the leks located within SMH, the area influenced by wind turbines.

Holloran (2005) assessed peak male lek attendance at 21 leks in southwestern Wyoming over a time period that ranged from 1999 to 2004. Leks located within 5.0 km of oil and gas development had significantly greater annual rates of decline than control leks (Holloran 2005). Male lek attendance has also been shown to be negatively affected within 0.8, 3.2, and 4.8 km of active well surfaces (Walker et al. 2007, Harju et al. 2010). In addition, leks impacted by oil and gas development experience a time lag of when discernible affects on male lek attendance can be measured (Walker et al. 2007, Doherty 2008, Harju et al. 2010). These time lags range from 2–10 years (Harju et al. 2010) and 4 years (Doherty 2008) when effects of oil and gas development can be measured on male lek attendance.

Although the results of my study indicate there was no difference in male lek attendance between leks within and outside of wind energy development, the results from other studies where leks have been impacted by oil and gas development indicate there is a time lag and effects may not be realized until 2–10 years following development. There is only one grouse/wind energy published study I am aware of that assessed male grouse lek attendance relative to wind energy development. Black grouse (*Tetrao tetrix*) in Austria, were not impacted by the wind energy facility the immediate year following construction, but did show considerable declines 4 years after construction suggesting there may be a similar time lag to wind development as oil and gas development in grouse (Zeiler and Grünschachner-Berger 2009). In addition, a review of unpublished studies investigating the impacts to male lek attendance from wind energy development indicated that prairie grouse may continue to use habitats near wind energy developments and may experience similar time lags as oil and gas development (Johnson and Stephens 2011). Further monitoring and inventorying of these leks will be necessary to identify any long-term population trends (Fedy and Aldridge 2011).

**LITERATURE CITED**

Beck, T. D. I., C. E. Braun. 1980. The strutting ground count: variation, traditionalism, management needs. Proceedings of the Western Association of Fish and Wildlife Agencies 60:558–566.

Blickley, J. L., D. Blackwood, and G. L. Patricelli. 2012. Experimental evidence for the effects fo chronic anthropogenic noise on abundance of greater sage-grouse at leks. Conservation Biology 26:461-471.

Burnham K. P and D. R. Anderson. 2002. Model selection and multimodel Inference: a practical information-theoretic approach: Second edition. Springer-Verlag, New York, New York, USA.

Christiansen, T. 2007. Chapter 12: Sage Grouse (*Centrocercus urophasianus*). Pages 12-11 to 12-51 In Handbook of Biological Techniques. Third edition. S. A. Tessmann, edition. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

Connelly J. W., K. P. Reese, R. A. Fischer, and W. L. Wakkinen. 2000*b*. Response of a sage-grouse breeding population to fire in southeastern Idaho. Wildlife Biology 28:90–96.

Connelly, J. W. and C. E. Braun. 1997. Long-term changes in sage-grouse Centrocercus urophasianus populations in western North America. Wildlife Biology 3:123–128.

Connelly, J. W., M.A. Schroeder, A. R. Sands, and C. E. Braun. 2000*a*. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967−985.

Diggle, P. J., P. Heagerty, K. Y. Liang, and S. L. Zeger. 2002. The analysis of longitudinal data. Second Edition. Oxford University Press, Oxford, England.

Doherty, K. 2008. Sage-grouse and energy development: Integrating science with conservation planning to reduce impacts. Dissertation, University of Montana, Missoula, Montana, USA.

Fedy, B. C., and C. L. Aldridge. 2011. The importance of within-year repeated counts and the influence of scale on long-term monitoring of sage-grouse. Journal of Wildlife Management 75:1022-1033.

Gelman, A. (2005). Analysis of varianace - why it is more important than ever. The Annals of Statistics 33:1-53.

Goldberger, A. S. 1962. Best linear unbiased prediction in generalized linear regression model. Journal of American Statistical Association 57:369-375.

Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. Wiley and Sons, New York, New York, USA.

Harju, S. M., M. R. Dzialak, R. C. Taylor, L. D. Hayden-Wing, J. B. Winstead. 2010. Thresholds and time lags in effects of energy development on greater sage-grouse populations. Journal of Wildlife Management 74:437–448.

Henderson, C. R. 1950. Estimation of genetic parameters. The Annals of Mathematical Statistics 21:309-310.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. J. Amundson, and S. T. Knick. 2011. Influence of environmental and anthropogenic features on greater sage-grouse populations, 1997–2007. Pages 407-450 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38. University of California Press, Berkeley, California, USA.

Johnson, D. H. and S. E. Stephens. 2011. Windpower and biofuels: A geen dilemma for wildlife conservation. Pages 131-157 in D. E. Naugle, editor. Wildlife Conservation in Western North America. Island Press, Washington, DC, USA.

McLean, R. A., W. L. Sanders, and W. W. Stroup. 1991. A unified approach to mixed linear models. The American Statistician 45:54-64.

Morrison, M. L., W.M. Block, M. D. Strickland, B. A. Collier, and M. J. Peterson. 2008. Wildlife study design. Second Edition. Springer Press, New York, New York, USA.

Patterson, R. L. 1952. The sage grouse in Wyoming. Wyoming Game and Fish Commission and Sage Books. Denver, Colorado, USA.

Pinheiro, J. and D. Bates. 2000. Mixed effects models in S and S-Plus. Springer-Verlag, New York, New York, USA.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

Walsh, D. P., C. G. White, T. E. Remington, and D. C. Bowden. 2004. Evaluation of the lek-count index for greater sage-grouse. Wildlife Society Bulletin 32:56–68.

Wyoming Game and Fish Department (WGFD). 2003. Wyoming greater sage-grouse conservation plan. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

Zeiler, H.P. and V. Grünschachner-Berger. 2009. Impact of wind power plants on black grouse, *Lyrurus tetrix* in Alpine regions. Folia Zoologica 58:173-182.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

Table 4-1. Disturbance metrics included in the mixed modeling procedure to determine potential extents of impact from turbines to male lek attendance at leks located within the Seven Mile Hill and Simpson Ridge study areas in Carbon County Wyoming, USA, 2008–2012. Metrics were derived from male breeding use areas (0.60 km), identified management areas (3.2 km), or disturbance distances previously determined from oil and gas development.

| Variable | Variable description |
|---|---|
| area_smh | Nominal variable indicating study area the lek was located in (1=SMH, 0=SR). |
| dist_turbine | The distance to nearest turbine from each active lek within both study areas (km). |
| sq_km600 | The proportion of overlapping area within 0.60 km of turbines and a 3.2 km buffer of each lek (CGSSC 2008). |
| sq_km1600 | The proportion of overlapping area within 1.6. km of turbines and a 3.2 km buffer of each lek (1.6 to 2 km, Harju et al. 2010) |
| sq_km3200 | The proportion of overlapping area within 3.2 km of turbines and a 3.2 km buffer of each lek (Connelly et al. 2000*a*) |
| sq_km5000 | The proportion of overlapping area within 5.0 km of turbines and a 3.2 km buffer of each lek (3-5 km Holloran 2005). |

Table 4-2. Maximum counts, yearly averages, and totals of male sage-grouse on occupied leks located within the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2008–2012. Entries of "NA" indicate no count was conducted.

| Lek Name | 2008 | 2009 | 2010 | 2011 | 2012 |
|---|---|---|---|---|---|
| Seven Mile Hill | | | | | |
| Commo 1[a] | 23 | 21 | 18 | 5 | 15 |
| Hanna Draw East 1 | 32 | NA | 27 | 5 | 11 |
| Hanna Draw East 2 | 18 | NA | 11 | 2 | 2 |
| Missouri John[a] | 74 | 62 | 38 | 20 | 18 |
| Pine Draw[a] | 33 | 20 | 14 | 6 | 0 |
| Average | 36 | 34 | 22 | 8 | 9 |
| Total | 180 | 103 | 108 | 38 | 46 |
| Simpson Ridge | | | | | |
| Kyle 63 | 67 | 68 | 64 | 32 | 19 |
| Kyle 65 | 5 | 8 | 4 | 0 | 2 |
| Old Carbon 31 | 28 | 41 | 28 | 23 | 23 |
| Old Carbon 32 | 9 | 33 | 4 | 20 | 12 |
| Old Carbon 34 | 49 | 49 | 31 | 26 | 20 |
| Old Carbon 35 2 | 111 | 88 | 41 | 55 | 22 |
| Old Carbon 37 | 54 | 42 | 28 | 23 | 25 |
| Old Carbon 38 | 10 | 1 | 0 | 0 | 0 |
| Old Percy 2 | NA | 31 | 4 | 3 | 0 |
| Average | 37 | 40 | 23 | 20 | 14 |
| Total | 333 | 361 | 204 | 182 | 123 |

[a]Leks located within 1.6 km of wind turbines at Seven Mile Hill

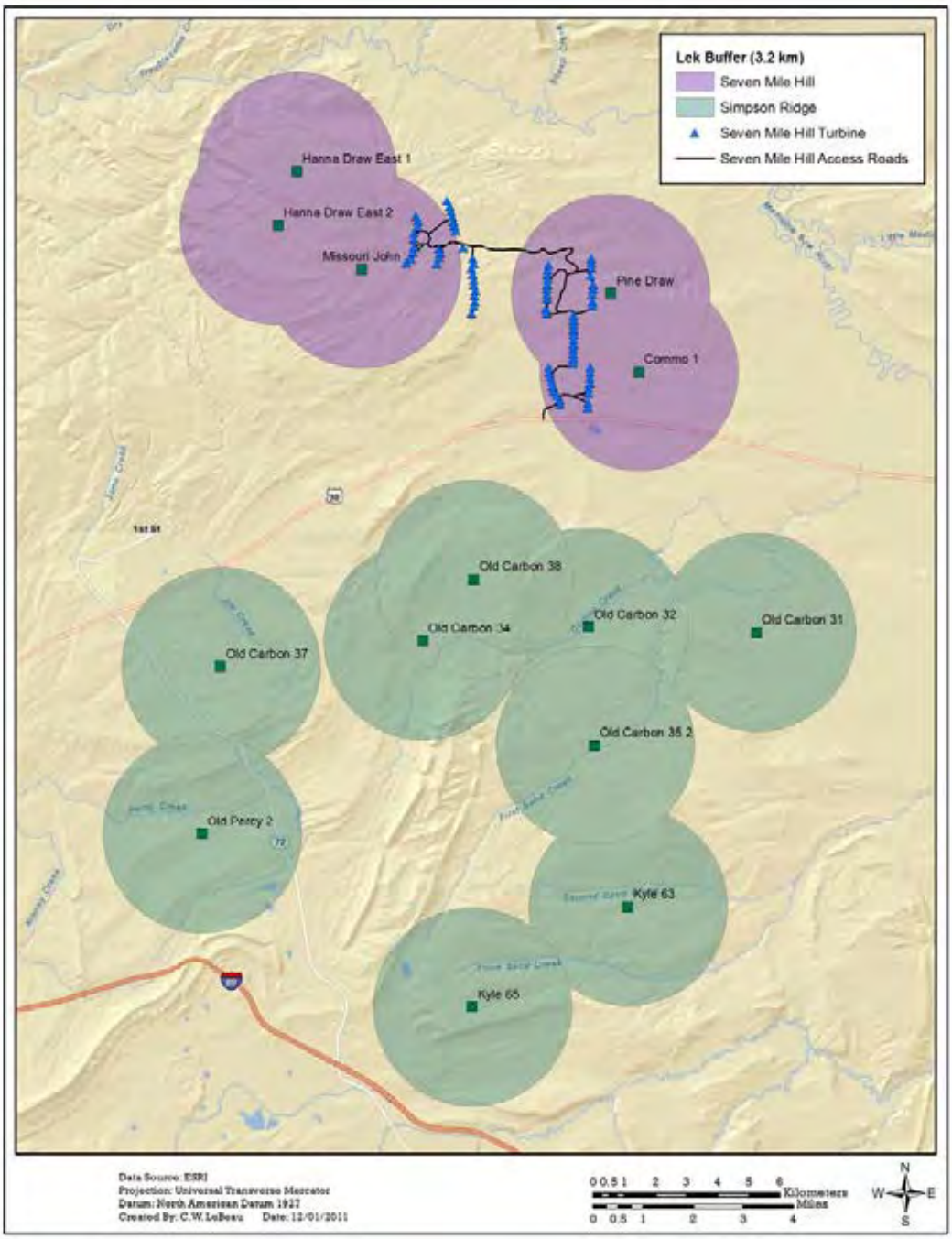



Figure 4-1. Lek locations within the Seven Mile Hill and Simpson Ridge study areas located in Carbon County, Wyoming, USA, 2008–2011.

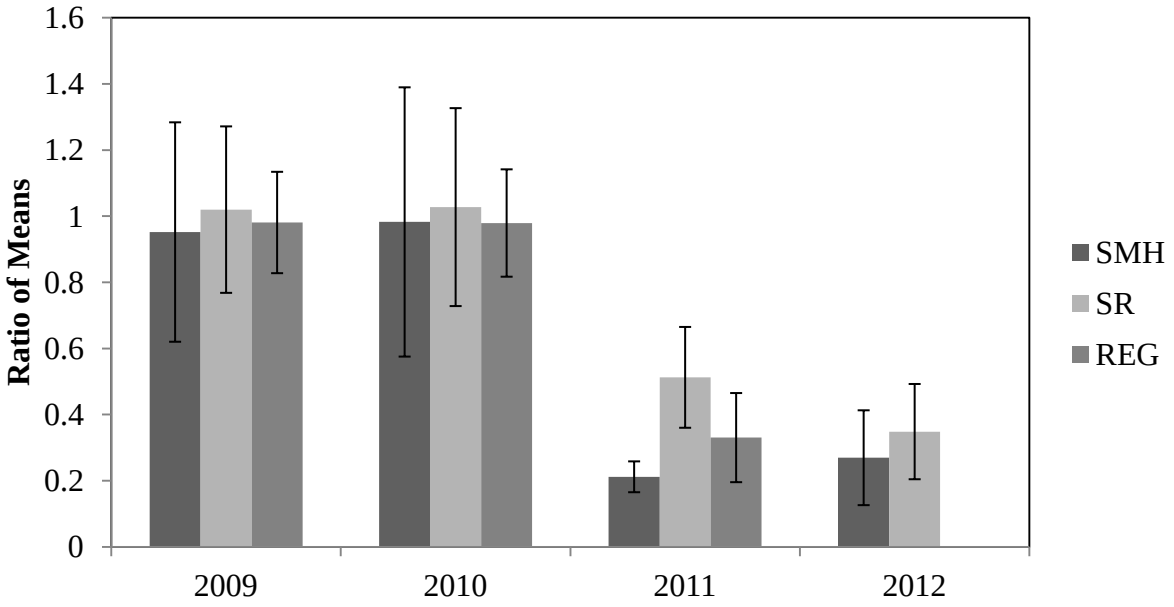



Figure 4-2. Ratio of means (± 90% CI) of peak male lek attendance observed at Simpson Ridge (SR), Seven Mile Hill (SMH), and regional (REG) leks from 2008–2012, Carbon County Wyoming, USA. Pre-development (2008) counts were used as the baseline to detect changes in peak male lek attendance to 4 years post development. The 2012 lek data was not available for the regional lek population at time of publication.

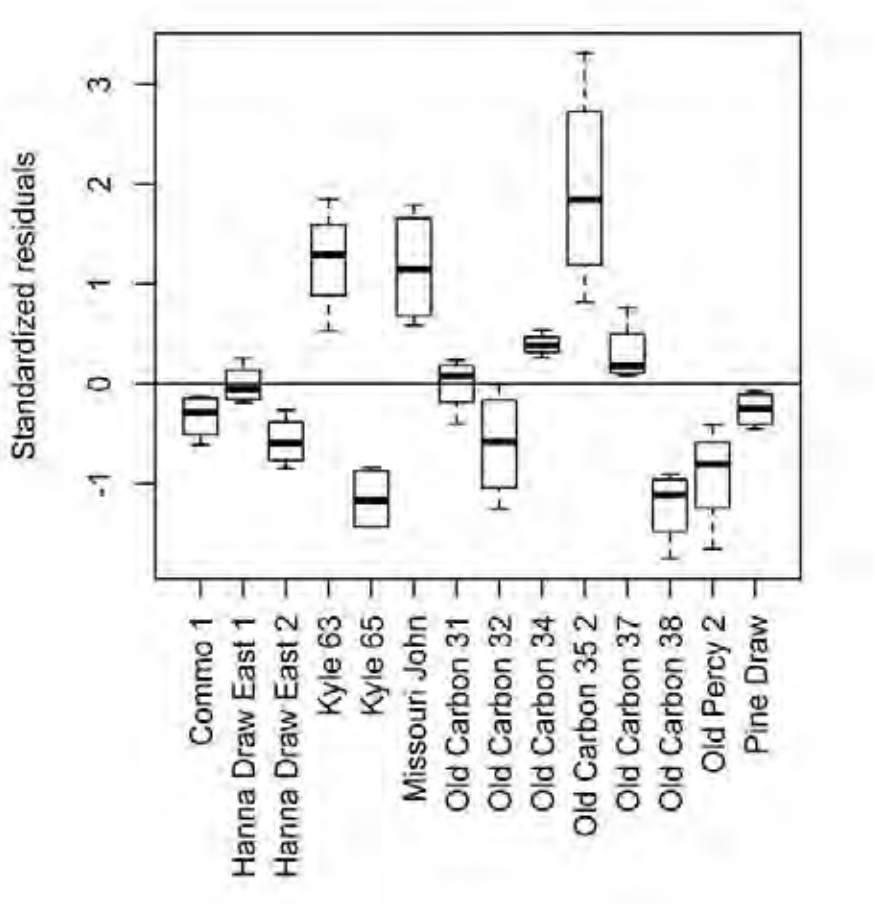



Figure 4-3. The distribution of standardized residuals from the linear regression model comparing male lek attendance to year and study area in Carbon County, Wyoming, USA, 2008–2012. The standardized residuals were plotted against individual leks within both study areas. Leks located above and below the zero residual line indicate within lek correlation. Boxes include the interquartile range (25th–75$^{th}$ percentile) in standardized residuals; horizontal lines inside boxes are median standardized residuals; lower and upper whiskers are standardized residuals extending to 1.5 times the interquartile range.

The Journal of Wildlife Management 78(3):522–530; 2014; DOI: 10.1002/jwmg.679

*Management and Conservation*

# Short-Term Impacts of Wind Energy Development on Greater Sage-Grouse Fitness

**CHAD W. LEBEAU,**[1] *Western EcoSystems Technology, Inc., 415 W. 17th Street, Suite 200, Cheyenne, WY 82001, USA*

**JEFFREY L. BECK,** *Department of Ecosystem Science and Management, University of Wyoming, Dept 3354, 1000 East University Avenue, Laramie, WY 82071, USA*

**GREGORY D. JOHNSON,** *Western EcoSystems Technology, Inc., 415 W. 17th Street, Suite 200, Cheyenne, WY 82001, USA*

**MATTHEW J. HOLLORAN,** *Wyoming Wildlife Consultants, LLC, 1612 LaPorte Avenue, Suite 9, Fort Collins, CO 80521, USA*

**ABSTRACT** Greater sage-grouse (*Centrocercus urophasianus*) are experiencing population declines across much of their current range. Population declines are directly related to changes in greater sage-grouse fitness parameters including nest and brood success, and female survival. Reduced fitness in greater sage-grouse populations has been attributed to a decrease in habitat suitability caused by anthropogenic disturbance factors including energy extraction activities. The increased demand for renewable energy has raised concerns about the impacts of infrastructure associated with wind energy development on greater sage-grouse populations. We hypothesized that greater sage-grouse nest, brood, and adult survival would decrease with increasing proximity to wind energy infrastructure, particularly wind turbines. We monitored 95 nests, 31 broods, and identified 45 mortalities from 116 female greater sage-grouse from 2009 to 2010 at a wind energy facility in south-central Wyoming, USA. We used Cox proportional hazards regression to model nest survival and used the Andersen–Gill survival model to estimate female and brood survival relative to vegetation cover, topography, and distance to wind turbines and other anthropogenic features on the landscape. Results from our survival analysis indicated that the risk of a nest or brood failing decreased by 7.1% and 38.1%, respectively, with every 1.0 km increase in distance from nearest turbine. We detected no variation in female survival relative to wind energy infrastructure. Decreased nest and brood survival was likely the result of increased predation, which may have been a product of anthropogenic development and habitat fragmentation. Future wind energy developments should consider the increased risk of nest and brood failure within habitats of close proximity to turbines. Identifying nesting and brood-rearing habitats within close proximity to proposed wind energy developments is critical when estimating potential impacts to overall population fitness. © 2014 The Wildlife Society.

**KEY WORDS** *Centrocercus urophasianus*, energy development, fitness, greater sage-grouse, survival, wind energy, wind turbines.

Increasing concern for environmental sustainability and the demand for domestic energy has led to a large expansion of renewable wind energy development in the United States. Wind energy development is increasing in prairie habitats with high wind capacity, which has raised concerns over impacts to prairie grouse species including greater sage-grouse (*Centrocerus urophasianus*; hereafter, sage-grouse), sharp-tailed grouse (*Tympanuchus phasianellus*), and lesser (*T. pallidicinctus*) and greater (*T. cupido*) prairie chickens (Kuvlesky et al. 2007, American Wind Energy Association 2010). Direct impacts to prairie grouse from wind energy developments (e.g., collisions) are likely to be low because these species avoid tall structures and areas with human activities (Pruett et al. 2009*a*, *b*; Naugle et al. 2011). However, wind turbines and associated power transmission lines are likely to indirectly affect prairie grouse through habitat fragmentation and displacement. Although no peer-reviewed, published studies estimate the indirect and direct impacts from wind turbines to prairie grouse species, male lek attendance for forest-dwelling black grouse (*Lyrurus tetrix*) was negatively influenced by wind turbines 5 years after development of a wind energy facility in Austria where male lek attendance decreased and collisions with wind energy infrastructure were documented (Zeiler and Grünschachner-Berger 2009). Managers do not know how prairie grouse will respond to this new form of energy development and studies addressing the potential impacts of wind energy development to prairie grouse, including sage-grouse, are lacking (Johnson and Stephens 2011). Given the large overlap between sage-grouse habitats and areas with high wind energy capacity, a better understanding of the relationship between wind energy development and declining sage-grouse populations is necessary (Aldridge et al. 2008, Becker et al. 2009, Garton et al. 2011).

Although the type and magnitude of activities (i.e., timing and amount of anthropogenic traffic, size, and area of development) associated with oil and gas development differ

Received: 15 December 2012; Accepted: 30 December 2013
Published: 10 March 2014

[1]*E-mail: cwlebeau@west-inc.com*

from those related to wind energy development, the demographic responses of sage-grouse populations to wind energy development may be similar to oil and gas development. For example, current sage-grouse declines are at least partially explained by lower annual survival of females (Taylor et al. 2012), and in the case of oil and gas development, impacts on females contribute to population-level declines (Holloran 2005). Negative impacts of oil and gas development on nest initiation and success also contribute to population-level declines (Lyon and Anderson 2003, Holloran 2005, Dzialak et al. 2011). Holloran (2005) found that sage-grouse nests were more successful in areas of lower natural gas well densities compared to that of higher density areas. Nests initiated in close proximity to a natural gas well that existed or were installed the previous year were at greater risk of failing than nests initiated farther from natural gas wells (Dzialak et al. 2011). In addition, nest initiation rates were reduced in areas of greater vehicle traffic associated with gas development (Lyon and Anderson 2003). Similar to nesting, impacts from anthropogenic features also influence brood-rearing. Chick mortality was 1.5 times greater in habitats where oil and gas wells were visible within 1 km from brood-rearing sites in southern Alberta (Aldridge and Boyce 2007). In addition, chicks reared in natural gas fields had lower survival probabilities as yearlings compared to those reared outside of gas fields (Holloran et al. 2010). These examples describe some degree of influence by anthropogenic features on sage-grouse fitness and indicate managers should consider similar impacts to sage-grouse populations from wind energy development.

The purpose of our study was to investigate the effect of wind energy infrastructure and associated habitat features on sage-grouse fitness. Specifically, we investigated sage-grouse nest, brood, and female survival relative to wind energy infrastructure, vegetation characteristics, and topographical features. We hypothesized that sage-grouse nest, brood, and female survival would decrease with proximity to infrastructure, specifically turbines, because similar impacts have been documented for sage-grouse inhabiting areas with oil and gas development (Aldridge and Boyce 2007, Holloran et al. 2010, Doherty et al. 2011, Dzialak et al. 2011, Kirol 2012).

## STUDY AREA

Our study area, Seven Mile Hill (SMH), was located in Carbon County, Wyoming, USA between the towns of Medicine Bow and Hanna (Fig. 1). The study area was positioned north of Elk Mountain and Interstate-80 and south of the Shirley Basin in south-central Wyoming. Land ownership included Bureau of Land Management (BLM; 22.5%), private (69.5%), and State of Wyoming lands (8.0%). The SMH Wind Energy Facility (SWEF) was situated in the northern portion of the study area. Construction of the SWEF facility began in late summer 2008 and the facility became operational by December 2008. The SWEF consisted of 79-General Electric 1.5-Megawatt (MW) turbines capable of producing 118.5 MW of electricity on

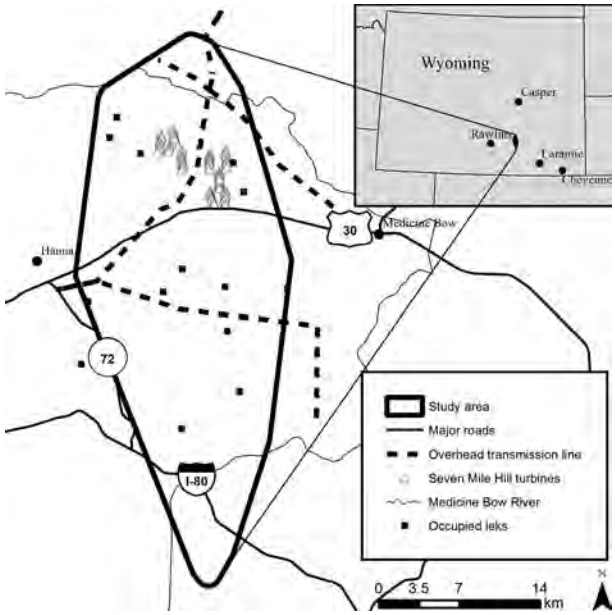



**Figure 1.** Seven Mile Hill study area in Carbon County, Wyoming, USA and occupied greater sage-grouse leks in 2009 and 2010. The Seven Mile Hill Wind Energy facility consisted of 79, 1.5-MW wind turbines.

an annual basis and approximately 29 km of access roads (Fig. 1). The SMH study area contained approximately 50 km of paved roads (Interstate-80, US HWY 30/287, and State HWY 72) and 43 km of overhead transmission lines. Overhead transmission lines and paved roads have existed on the SMH landscape for >10 years. The only anthropogenic features added to the SMH landscape, as a result of constructing the SWEF, were wind turbines and associated access roads (Fig. 1). Fourteen occupied sage-grouse leks were located within SMH, 3 of which occurred within 1.6 km of turbines (Fig. 1). The average peak number of males attending leks within SMH increased from 27 in 2000 to 52 in 2006 before declining to 22 in 2010.

Climate was classified as a semiarid, cold desert with a mean annual precipitation average of 26.7 cm and average temperatures ranging from −2.33° C to 13.61° C (Western Regional Climate Center 2012). Elevations in the study area ranged from 1,737 m to 2,390 m above sea level. Shrub steppe, primarily dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), was the most common cover type in the study area (U.S. Geological Survey [USGS] 2001). Dominant land uses included wind energy development, a surface coal mine near the southwestern edge of the study area, livestock grazing, and hunting.

## METHODS

### Field Methods

We captured 116 female sage-grouse by nighttime spotlighting and use of hoop nets (Giesen et al. 1982, Wakkinen et al. 1992) on roosts surrounding leks during the 2009 and 2010 breeding seasons. We attempted to capture sage-grouse at all accessible active lek sites within 16 km of

the SMH wind turbines proportionately to the number of males attending those leks. We aged, weighed (0.1-g precision), acquired blood samples (year 2009), and fitted each captured grouse with a 22-g necklace-mounted very high frequency radio transmitter with a battery life of 666 days (Advanced Telemetry Systems, Incorporated, model A4000, Isanti, MN). Radio transmitters were equipped with mortality censors that were triggered when transmitters were stationary for 8 hours. We released each radio-marked female at the point of capture and marked the location using a hand-held global positioning system (GPS) unit. We gained approval from the Wyoming Game and Fish Department (Chapter 33 permit 572 issued to Western EcoSystems Technology, Inc.) to capture, handle, and monitor female sage-grouse.

We relocated each radio-marked female 3 times each week during the pre-laying and nesting period (Apr through Jun) and at least once each week for brooding and barren (i.e., females that were not nesting or brood-rearing) females from hatch or nest loss through 31 October. We monitored marked sage-grouse primarily from the ground using hand-held receivers and Yagi antennas. We determined sage-grouse locations by triangulation or homing until visibly observed. In addition, we estimated the triangulation error by placing 6 test collars for each technician throughout the project area and estimated the mean telemetry error between the actual and estimated locations. The mean telemetry error rate was incorporated into our modeling efforts. We employed aerial telemetry to locate missing birds throughout the study period.

During the pre-nesting and nesting seasons (late Apr through 15 Jun), we monitored each radio-marked female sage-grouse from a distance >60 m at least every third day. We assumed females were nesting when movements became localized. We located nests using a progressively smaller concentric circle approach by walking circles around the radio signal using the signal strength as an indication of proximity (Holloran and Anderson 2005). Once a nest location was established, we conducted incubation monitoring on an alternate-day schedule to determine nesting fate. We mapped all nest locations using a hand-held GPS. We considered a nest that successfully hatched (i.e., eggs with detached membranes) ≥1 egg to be a successful nesting attempt (Rotella et al. 2004). We considered nests that failed to successfully hatch ≥1 egg either because of predation or abandonment to be failed nesting attempts. We monitored females that were unsuccessful in their first nesting attempt 3 times per week through 15 June to determine possible re-nesting attempts.

To evaluate brood survival, we located radio-marked females that successfully hatched ≥1 egg each week through 35–37 days post-hatch (Walker 2008). We categorized the brood-rearing period as early (hatch through 14 days post-hatch; Thompson et al. 2006) or late (>14 and ≤35–37 days post-hatch; Walker 2008). We considered females to be successful through the early brood-rearing period if ≥1 chick survived to 14 days post-hatch; we established chick presence during this period either through visual confirmation of a live chick or the brooding female's response to field observers (e.g., chick protective behavior exhibited). We determined fledging success (late brood success) for those females who were successful in early brood-rearing by assessing whether a female was brooding chicks through consecutive nighttime spotlight surveys conducted on days 35–37 post-hatch (Walker 2008); females successful in raising late broods were those we confirmed brooding at least 1 chick during the late brood period. We did not assess brood survival among individuals (i.e., marked chicks), but derived survival from flush and nighttime spotlighting of unmarked chicks and in some instances mixed broods. Brood amalgamation may have occurred, but we were concerned with the overall ability of a female to successfully rear at least 1 chick so we did not account for brood mixing in this analysis. We treated instances where a marked female could not be associated with a chick as brood failures.

### Landscape Covariates

We developed a suite of covariates to estimate the hazard of nest, brood, and female survival. Anthropogenic features included major roads, transmission lines, and wind turbines (see Fig. 1). We included US HWY 30/287, Wyoming State Highway 72, and Interstate 80 as major roads. We digitized major roads and overhead transmission lines (230 kV wooden H-frame) using aerial photography imagery within ArcMap 10 (Environmental Systems Research Institute, Redlands, CA). We obtained turbine locations from PacifiCorp Energy (Salt Lake City, UT), the operators of the SWEF. Vegetation layers used in the analysis were developed by Homer et al. (2012) and derived using remote-sensed products and a combination of methods to integrate 2.4 m QuickBird, 30-m Landsat TM, and 56-m AWiFS (Advanced Wide Field Sensor) imagery from 2006 to 2007 into the characterization of vegetation components. We considered 4 primary components (percent bare ground, percent herbaceous cover, percent litter, and percent shrub cover) and 4 secondary components (3 types of shrub cover—percent sagebrush [*Artemisia* spp.], percent big sagebrush [*A. tridentata* spp.], and percent Wyoming big sagebrush—and shrub height; Homer et al. 2009, 2012; Table 1). We included the standard deviation of shrub height, total shrub cover, and total sagebrush cover in our modeling. We calculated landscape features, including elevation, slope, and rugged, from a 10-m National Elevation Dataset (USGS, EROS Data Center, Sioux Falls, SD). Rugged captured the variability in slope and aspect into a single measure ranging from 0 (no terrain variation) to 1 (complete terrain variation; Sappington et al. 2007; Table 1).

### Survival Analyses

We used Cox proportional hazards models (Cox 1972) to estimate sage-grouse nest survival. We used the Andersen–Gill formulation of the Cox proportional hazards model (Therneau and Grambsch 2000) to estimate brood and female survival (Anderson and Gill 1982). The Anderson–Gill formulation of the Cox model accommodates multiple monitoring intervals by incorporating changes in habitat characteristics at each relocation that represent changes in

**Table 1.** Explanatory anthropogenic and environmental covariates used in modeling sage-grouse nest, brood, and female survival at the Seven Mile Hill study area, Carbon County Wyoming, USA, 2009 and 2010.

| Covariates | Variable description |
|---|---|
| Anthropogenic infrastructure | |
| Roads | Distance to nearest major road [WYO HWY 72, US HWY 287/30, and I-80 (km)] |
| Tline | Distance to nearest overhead transmission line (km) |
| Turbine | Distance to nearest turbine (km) |
| Environmental | |
| Bare ground[a] | Percent bare ground |
| Big sagebrush[a] | Percent big sagebrush (*Artemisia tridentata* spp.) |
| Elevation | Altitude above sea level (m) |
| Herbaceous[a] | Percent herbaceous cover |
| Litter[a] | Percent litter |
| Sagebrush[a,b] | Percent sagebrush (*Artemisia* spp.) |
| Shrub[a,b] | Percent shrub cover |
| Shrub height[a,b] | Shrub height (0–253 cm) |
| Slope | Degrees 0–90 |
| Rugged | Variability in slope and aspect (0–1; 1 = complete terrain variation; Sappington et al. 2007) |
| Wyoming big sagebrush[a] | Percent Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) |

[a] Vegetation covariates obtained from Homer et al. (2012).
[b] SD is the standard deviation of these shrub covariates, which we also included in the analysis.

exposure during the brood-rearing and female survival period (Therneau and Grambsch 2000, Johnson et al. 2004).

We assessed nest survival for a 26-day incubation period during the 2009 and 2010 nesting seasons (incubation period lasts 25–29 days; Schroeder et al. 1999). We combined nests observed across the study area into 1 sample to model survival relative to wind energy development. Re-nests can only result from a failed nesting attempt and may not be independent of first nests; thus, we excluded re-nests from analyses. Events or failures occurred when the sage-grouse abandoned its nest or its nest was depredated. We did not include abandoned nests thought to be caused by field observers in the survival analysis because of the potential bias associated with those nests. We estimated nest fate date using the last known monitoring interval as well as the condition of the nest to estimate the event date as well as the type of predator (mammalian or avian). We censored nests that were successful through the 26-day period (Nur et al. 2004). We used Cox proportional hazards to estimate the effects of wind energy infrastructure on nest survival (Nur et al. 2004, Aldridge and Boyce 2007, Liebezeit et al. 2009).

We combined early and late brood-rearing monitoring from both years for modeling survival of broods (Aldridge and Boyce 2007). To determine brood survival, we assessed the presence of chicks with hens at least 2 times during the first 14 days of the brood-rearing period and 1 final time at the end of the brood-rearing period. We used 5 weekly monitoring intervals during the brooding period. The first monitoring interval began directly after a successful hatched nest and monitoring ended on the fifth interval 35–37 days post-hatch. Events or failures occurred when we did not observe chicks or the female did not elicit behaviors indicating she had chicks during any 1 of the checks. The cause of brood failure could not be assessed because individual chicks were not marked. We defined the interval containing the event to be the interval between the last monitoring visit where chick presence was confirmed and the first visit where chicks were absent. Because of our revisit schedule, events could have occurred during weeks 1, 2, and 5 when we assessed survival. The exact week of the event could not be determined if chicks were absent during week 5 (i.e., brood could have failed during weeks 3, 4, or 5). By assigning the event to week 5 and not week 3, reported overall brood survival rates may be overestimated by at most 10%; however, the relative difference in survival between broods as compared to covariate values is unbiased. We censored broods that were successful and survived the entire monitoring period to week 5 (Nur et al. 2004). We averaged covariates associated with intervals containing 2 or more relocations of the female.

Lastly, we modeled weekly female sage-grouse survival from time of capture to 31 October during both years. We assessed weekly survival for all monitored sage-grouse. Events or mortalities occurred when we confirmed mortality via telemetry. We evaluated the condition of the carcass in an attempt to determine cause of death. We estimated date of mortality by the condition of the carcass and last known monitoring interval. For example, when we discovered a mortality, we reviewed the most recent location where the individual was determined to be alive and either selected the date that was the mid-point between the last 2 locations (i.e., the last alive and dead intervals) or we estimated the date of mortality by assessing the condition of the carcass. We averaged covariates corresponding to individuals that recorded multiple locations within a specified interval.

## Model Development

We included an indicator variable for age (adult = 1, yearling = 0) and year (2009 = 1, 2010 = 0) to determine if age or year influenced survival. We calculated average values of each environmental feature at 3 different scales defined by a circle with the radii corresponding to the mean telemetry error rate (0.30 km), the median distance between consecutive year's nests from 2009 to 2010 (0.46 km), and the median distance traveled by brooding females between

monitoring intervals during the brood-rearing period (1.0 km).

We used a forward model selection procedure to identify the effects of wind energy infrastructure on nest, brood, and female survival. We allowed each covariate to compete with each other in a forward selection procedure but did not allow 2 correlated variables ($r \geq |0.60|$) to be included in any 1 model to avoid collinearity. We performed model building using forward variable selection via improvements in adjusted Akaike's Information Criterion for small sample sizes ($AIC_c$; Burnham and Anderson 2002) using R language for statistical computing (R Development Core Team 2012). For example, the covariate selected first during the model building process for a survival estimate resulted in the lowest $AIC_c$ score among other univariate models. We then added remaining covariates to the first selected covariate and reevaluated the model via $AIC_c$ to see if the additional covariate further reduced the $AIC_c$ score. If the model $AIC_c$ was further reduced, then the model building process continued looking forward (adding covariates) until the $AIC_c$ value could not be further reduced.

We calculated hazards ratios [exp(β)] and 90% hazard ratio confidence intervals to interpret the magnitude and influence of habitat and anthropogenic variables on survival of an individual nest, brood, or female. We considered hazards ratios that included 1 within their 90% confidence interval to be insignificant (alpha level = 0.10). We used survival curves to illustrate the varying degree of risk as a function of the top model covariates (Therneau and Grambsch 2000, Johnson et al. 2004). We used Schoenfeld residuals (Schoenfeld 1982) to assess model fit (Therneau et al. 1990, Grambsch and Therneau 1994, Kleinbaum and Klein 2005). We plotted the ranked Schoenfeld residuals for each covariate and for the top model as a whole against time to inspect the distribution of the residuals (see Figs. S1, S2, and S3, available online at www.onlinelibrary.wiley.com). Lastly, using the top hazard models, we estimated the relative risk of mortality at a resolution (100-m grid cells) that was meaningful to managers and comparable to the scale of habitat layers used in the analysis within a minimum convex polygon around all locations observed during each survival period (Johnson et al. 2004). We used these estimates to visually depict the relative risk of mortality across the study area.

# RESULTS

### Nest Survival

We located 50 nests in 2009 and 45 nests in 2010. We observed 2 re-nests in 2009 and 5 re-nests in 2010. We estimated nesting propensity, apparent nest success, and nest survival for all first nesting attempts ($n = 48$ [2009] and $n = 40$ [2010]). Nesting propensity, or the percentage of females observed initiating a nesting attempt, was 64.0% in 2009 ($n = 75$ females; 90% CI: 53.9–73.2%) and 48.8% in 2010 ($n = 82$ females; 90% CI: 39.2–58.4%). Nest hatch dates ranged from 26 May to 28 June (mean = 1 Jun) for all assumed first nesting attempts and from 29 June to 2 July (mean = 30 Jun) for all second nesting attempts. Two of the 7 observed re-nests were successful. Apparent nest success (fraction of the found first nesting attempts that successfully hatched ≥1 egg) was similar in 2009 (39.6%; $n = 19$; 90% CI: 27.7–52.5%) and 2010 (37.5%; $n = 15$; 90% CI: 24.7–51.7%). Although cause of death could not be determined for all nest failures, we determined 14 (14.7%) were killed by avian predators and 34 (35.8%) were killed by mammalian predators. We documented 16 first attempt nests within 1.6 km of wind turbines at SMH; 4 (25.0%) of these nests were successful but none of the 5 nests closest to turbines were successful.

We used 88 sage-grouse nests in Cox proportional hazards modeling (we removed 7 re-nests from the survival modeling). We estimated the nest survival rate during the 26-day incubation period as 39.7% (90% CI: 31.7–49.7%). The top model ($w_i = 0.51$) relating environmental and anthropogenic features to sage-grouse nest survival included standard deviation of shrub height (cm) within 0.30 km of a nest, distance (km) to nearest turbine, and distance to nearest overhead transmission line (Table 2).

The risk of a nest failing decreased by 17.3% for every 1 cm increase in the standard deviation of shrub height within 0.30 km of a nest (90% CI: 8.7–25.1%; Table 3). The risk of a nest failing increased by 12.4% with every 1.0 km increase in the distance to nearest overhead transmission line (90% CI: 0.3–25.9%; Table 3). Lastly, the risk of a nest failing decreased by 7.1% with every 1.0 km increase in distance from a turbine (90% CI: 2.7–11.3%; Table 3, Fig. 2). Spatially, habitats closer to turbines had higher relative risk of a nest failing than habitats farther from turbines (Fig. 3). Based on examination of the plotted Schoenfeld residuals, we found no evidence of non-proportional hazards for any of the 3 covariates included in the top model, suggesting that nest failures were independent.

### Brood Survival

We monitored 31 females with broods during the brood-rearing period ($n = 20$ in 2009 and $n = 11$ in 2010). Early brood-rearing (hatch through 2 weeks post-hatch) success was relatively high during both study years but was greatest in 2009 (95.0%; 90% CI: 78.4–99.7%) compared to 72.7% (90% CI: 43.6–92.1%) in 2010; however, the difference in the means was not statistically different. Of the successful early brood females, 11 broods were successful through the late brood-rearing period (35–37 days post-hatch) in 2009 and 8 were successful in 2010. Apparent late brood-rearing success (fraction of females with broods successfully raising ≥1 chick 35–37 days post-hatch) was 18.9% lower in 2009 than in 2010 but was not statistically different (2009 = 61.1%, 90% CI: 39.4–79.5%; 2010 = 80.0%, 90% CI: 49.0–95.6%).

We used 131 locations, 5 monitoring intervals, and 31 broods to model brood survival relative to the landscape covariates. We censored 2 broods and did not included them in modeling, 1 because the brooding female was killed immediately following hatch and 1 because the female could not be found. Twelve broods failed during the brood-rearing period (survival = 83.5%; 90% CI: 69.8–99.8%). The top model ($w_i = 0.92$) relating environmental and anthropogenic

**Table 2.** Model fit statistics for greater sage-grouse nest, brood, and female survival at the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010. Competing models are listed according to the model best fitting the data and ranked by ($\Delta AIC_c$), the difference between the model with the lowest Akaike's Information Criterion for small samples ($AIC_c$) and the $AIC_c$ for the current model. The value of the maximized log-likelihood function (log [L]), the number of estimated parameters ($K$), and Akaike's weights ($w_i$) for each model are also presented. Competing models were limited to models with improved $AIC_c$ scores.

| Model[a] | log[L] | $K$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|---|
| Nest survival | | | | | |
| Shrub height SD, turbine, tline | −214.716 | 3 | 435.696 | 0.000 | 0.513 |
| Shrub height SD, turbine | −216.087 | 2 | 436.304 | 0.608 | 0.378 |
| Shrub height SD | −218.372 | 1 | 438.786 | 3.090 | 0.109 |
| Null | −220.583 | | 441.167 | 5.471 | 0.032 |
| Brood survival | | | | | |
| Turbine, rugged, shrub | −30.053 | 3 | 66.384 | 0.000 | 0.917 |
| Turbine, rugged | −33.670 | 2 | 71.468 | 5.085 | 0.072 |
| Turbine | −36.610 | 1 | 75.263 | 8.879 | 0.011 |
| Null | −38.300 | | 76.500 | 10.116 | 0.006 |
| Female survival | | | | | |
| Roads, tline | −187.313 | 2 | 378.750 | 0.000 | 0.395 |
| Roads | −188.560 | 1 | 379.167 | 0.417 | 0.320 |
| Null | −189.707 | | 379.400 | 0.650 | 0.285 |

[a] Shrub height SD is the standard deviation of shrub height within 0.30-km buffer, rugged within 0.46-km buffer, and shrub within 1-km buffer. Tline represents the distance to nearest overhead transmission line.

features to sage-grouse brood survival included distance to nearest turbine (km), rugged (scale = 0.46 km), and percent shrub cover within 1.0 km of a brood location (Table 2).

The relative risk of a brood failing increased approximately 5 fold with every 1-unit increase in rugged within 0.46 km of a brood location (90% CI: 2.1–11.3; Table 3). The risk of a brood failing increased approximately 3 fold with every 1.0% increase in percent shrub cover within 1.0 km of a brood location (90% CI: 1.5–6.2; Table 3). Lastly, the risk of a brood failing decreased by 38.1% with every 1.0 km increase in distance from nearest turbine (90% CI: 18.6–52.9%; Table 3, Figs. 2 and 3). Based on examination of the plotted Schoenfeld residuals, we found no evidence of non-proportional hazards for any of the 3 covariates included in the top model, suggesting that brood failures were independent.

## Female Survival

During our study, 45 of 116 (38.8%) radio-marked female sage-grouse died. Similar to nest failures, we could not determine cause of death for all mortalities. Thirteen sage-grouse (28.9%) were killed by avian predators and 16 (35.6%) were killed by mammalian predators. In 2009, we submitted 3 dead radio-collared females that did not exhibit any signs of trauma to the Wyoming State Veterinary Laboratory in Laramie, Wyoming to be examined for the presence of West Nile virus. Two of the 3 (4.4% of all mortalities) female sage-grouse tested positive for West Nile virus.

We used 1,417 locations, 23 monitoring intervals, and 116 female sage-grouse to model weekly female sage-grouse survival. The estimated female survival rate during the summer period was 50.0% (90% CI: 41.0–61.1%). We censored 8 events because they occurred within 2 weeks of capture and may have been related to the capture event. The univariate modeling estimating differences in female survival indicated that capture location (i.e., lek of capture) did not influence female survival (hazard ratio = 0.84; 90% CI: 0.49–1.43). In addition, the age of each female (adult or yearling) did not influence female survival (hazard ratio = 1.3; 90% CI: 0.75–2.22). The set of competing models (i.e., models within 4 $AIC_c$ points) included the null model (Table 2), suggesting none of the covariates we considered explained the variation in female survival within our study. Based on examination of the plotted Schoenfeld residuals, we found no evidence of non-proportional hazards for the 2 covariates included in the top model.

**Table 3.** Relative risks of sage-grouse nests and broods for each covariate or risk factor included in the top model for the Seven Mile Hill study area in Carbon County, Wyoming, USA, 2009 and 2010.

| | | | | | Hazard ratio 90% CI | |
|---|---|---|---|---|---|---|
| Covariate[a] | Scale (km) | Estimate | SE | Hazard ratio | Lower | Upper |
| Nest survival | | | | | | |
| Shrub height SD | 0.30 | −0.190 | 0.060 | 0.827 | 0.749 | 0.913 |
| Turbine (km) | | −0.074 | 0.028 | 0.929 | 0.887 | 0.973 |
| Tline (km) | | 0.117 | 0.069 | 1.124 | 1.003 | 1.259 |
| Brood survival | | | | | | |
| Turbine (km) | | −0.479 | 0.167 | 0.619 | 0.471 | 0.814 |
| Rugged | 0.46 | 1.576 | 0.517 | 4.834 | 2.066 | 11.31 |
| Shrub | 1.00 | 1.108 | 0.431 | 3.028 | 1.490 | 6.155 |

[a] Tline represents the distance to nearest overhead transmission line.

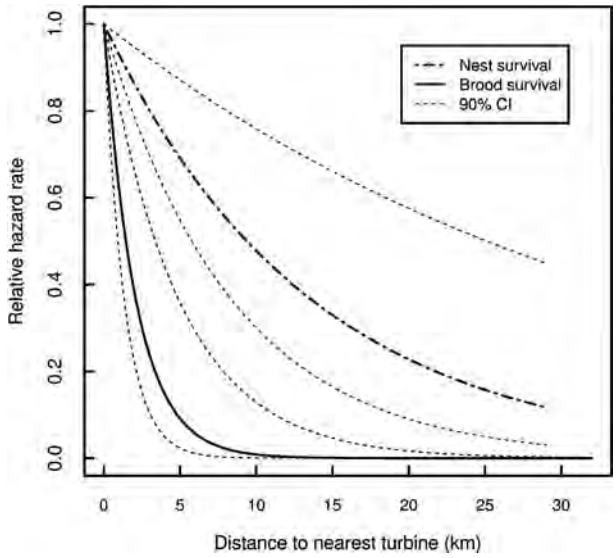



**Figure 2.** Relative hazard rate of sage-grouse nest and brood survival adjusted for the distance to nearest turbine at the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010. Dotted lines indicate the lower and upper 90% confidence limits.

## DISCUSSION

Our study is the first to estimate the short-term impacts of wind energy development on sage-grouse fitness parameters. The survival models we developed detected a greater relative probability of nest and brood failure in habitats within close proximity to turbines. However, the covariates used to model female survival did not detect any variability among individuals, indicating none of the landscape features we examined affected female survival, including distance to turbine. In addition to distance to nearest turbine, the relative risk of a nest failing within the study area increased in habitats with a lower variability of shrub height and decreased in habitats closer to transmission lines. However, the relationship between nest survival and distance to transmission line was not substantial because of the large 90% confidence intervals. Lastly, the risk of a brood failing increased in habitats with higher rugged and percent shrub cover.

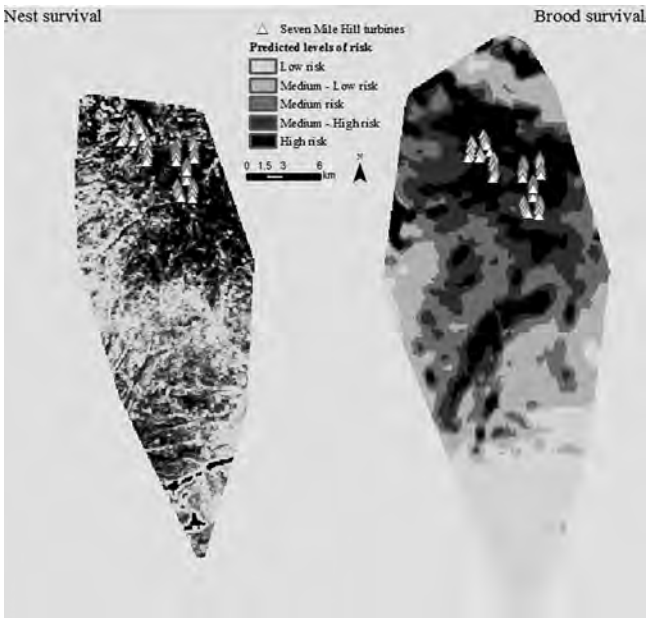



**Figure 3.** Spatial variation in the predicted relative risk of sage-grouse brood failure and nest failure (low to high) within the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010.

A synthesis of 50 sage-grouse demographic studies determined female survival was the most important fitness parameter that influenced population growth rate and concluded that future management of sage-grouse populations should focus on increasing female survival (Taylor et al. 2012). We did not detect any variability in female survival related to the distance to turbines, which is counter to research conducted in natural gas fields for sage-grouse and lesser prairie-chickens (Hagen 2003, Holloran 2005). At wind energy facilities, each turbine is visited on average 4 times per year for operation and maintenance purposes, whereas approximately 1,825 vehicle trips per year occurred on average at a producing natural gas well (Sawyer et al. 2009, BLM 2012). Reduced human activity within the wind development compared to oil and gas development may disturb sage-grouse less, thus having a smaller effect on female survival (Remington and Braun 1991, Holloran 2005). For example, meso-carnivore mammals and corvids, primary sage-grouse nest predators (Hagen 2011), may be attracted to wind energy developments because of subsidized food resources from deaths of birds by turbines, combined with low levels of human activity, whereas predators that prey on adults (e.g., golden eagles [*Aquila chrysaetos*]) may not. Alternatively, the inability of our models to detect variability in female survival within the SMH study area could be related to the omission of a covariate important for survival from the models. Disease could influence survival rate; however, West Nile Virus accounted for only 4.4% of all mortalities, thus appearing to be isolated incidents that would not affect the overall survival rate within the study area.

We used the best available habitat layers in our nest and brood survival analysis but are aware that some habitat features influential to nest and brood success were omitted. Numerous studies have established the importance of herbaceous understory in sagebrush-dominated habitats for sage-grouse nest and brood success (Connelly et al. 2011). The vegetation covariate layers we used from Homer et al. (2012) did not include some habitat features known to influence nest and brood success (e.g., residual grass cover and height, and forb cover and diversity [see Connelly et al. 2011]). Therefore, we cannot rule out that our nest and brood survival results reflect higher inherent quality nesting and brood-rearing habitats farther from wind turbines. In addition, small brood sample sizes reduced our power to detect variability in brood survival in our study area. However, because of the biology of sage-grouse, our sample size was similar to other brood survival studies (e.g., 35 [Aldridge and Boyce 2007], 33 [Kirol 2012], and 21 [Dahlgren et al. 2010]).

Similar to our results, Kirol (2012) identified an increased risk of nest failure in habitats with low standard deviation of shrub height within habitats characteristic of oil and gas development. However, this may not be due to the influence of development type but rather the ecology of sage-grouse nest site selection. For example, increased variation in shrub height may provide adequate nesting habitat where nests are located in areas of higher shrub heights but are surrounded by habitat that contains lower shrub heights with increased herbaceous cover for foraging. Further development of finer-scaled, site-specific GIS layers may provide a more detailed summary of the influence of standard deviation of shrub height on nest survival.

The lack of other studies investigating impacts from wind energy development to sage-grouse survival limits our ability to make inferences about the cumulative impacts of wind energy development on sage-grouse survival, but we were able to describe some of the short-term impacts that wind energy developments may have on sage-grouse populations. Although available GIS data may have produced some uncertainty in the interpretation of our results, our results demonstrate that wind energy development has short-term implications to sage-grouse populations during nesting and brood-rearing. Our findings also point to the need for further research to identify potential mechanisms that may lead to reduce demographic fitness parameters of sage-grouse in areas near wind turbines. The potential reason for decreased nest and brood survival within habitats in close proximity to turbines in our study is unknown but is likely attributable to increased predation (Coates and Delehany 2010). However, the lack of pre-development data and concurrent predator surveys limit our ability to speculate as to the mechanism (e.g., edge effects or limitation of predatory defense mechanisms) driving predator-prey interactions in the wind development area.

## MANAGEMENT IMPLICATIONS

Future wind energy project placement should consider the increased levels of risk to sage-grouse nests and broods within habitats of close proximity to wind turbines. Current United States Fish and Wildlife Service (USFWS) Land-Based Wind Energy Guidelines do not have specific prairie grouse avoidance measures for wind energy developers but do suggest impacts will be similar to those from other anthropogenic structures (USFWS 2012). Guidelines specific to Wyoming suggest wind energy development should not occur within 0.40 km of the perimeter of occupied leks outside of sage-grouse core areas and no development should occur within sage-grouse core areas (Wyoming Game and Fish Department 2010). We did not determine actual thresholds, but placing wind turbines at least 5 km from nesting and brood-rearing habitats should reduce negative influences from wind energy infrastructure in the short-term. These results indicate the current guidelines may be inadequate for future wind energy developments outside of Wyoming sage-grouse core areas. Because most mortalities and failures were attributable to predation, we are confident that decreased probabilities of survival were related to increased predation risk; but, identifying the direct source of risk was difficult (e.g., increased predator numbers, ecological trap habitats, subsidized predators, compromised defense mechanisms). We recommend that future research consider predator-prey mechanisms by estimating avian and mammal predator density to better understand the impacts of wind energy development on sage-grouse fitness parameters to develop sustainable mitigation measures. We also recommend that future studies investigating fitness consequences to sage-grouse from energy development consider habitat covariates not currently available in GIS including residual grass cover and height and forb cover and diversity.

## ACKNOWLEDGMENTS

We thank EDP Renewables North America (formerly Horizon Wind Energy), Iberdrola Renewables, Shirley Basin/Bates Hole Local Sage-grouse Working Group, United States Department of Energy, University of Wyoming School of Energy Resources, and the Margaret and Sam Kelly Ornithological Research Fund for providing funding support. We thank PacifiCorp Energy and Hi-Allen Ranch, LLC for allowing us access to the SMH study area. We appreciate assistance with data analyses provided by T. McDonald, R. Nielson, and K. Gerow. B. Collier and 2 anonymous reviewers provided comments that markedly improved our paper.

## LITERATURE CITED

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. Diversity and Distributions 14:983–994.

American Wind Energy Association. 2010. U.S. projects database. <http://www.awea.org/la_usprojects.cfm>. Accessed 1 Feb 2011.

Anderson, P. K., and R. D. Gill. 1982. Cox's regression model for counting processes: a large sample study. The Annals of Statistics 10:1100–1120.

Becker, J. M., J. D. Tagestad, C. A. Duberstein, and J. L. Downs. 2009. Sage-grouse and wind energy: biology, habits, and potential effects from development. PNNL-18567. Pacific Northwest National Laboratory, Richland, Washington, USA. <http://www.pnl.gov/main/publications/external/technical_reports/PNNL-18567.pdf>. Accessed 1 Dec 2012.

Bureau of Land Management [BLM]. 2012. Proposed plan amendment & final environmental impact statement/final environmental impact report for the Ocotillo Wind Energy Facility. El Centro Field Office, El Centro, California, USA. <http://www.blm.gov/ca/st/en/fo/elcentro/nepa/ocotillo_express_wind.html>. Accessed 14 Dec 2012.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Coates, P. S., and D. J. Delehany. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. Journal of Wildlife Management 74:240–248.

Connelly, J. W., E. T. Rinkes, and C. E. Braun. 2011. Characteristics of greater sage-grouse habitats: a landscape species at micro- and macro-scales. Pages 69–83. *in* S. T. Knick, and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38. University of California Press, Berkeley, California, USA.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society Series B-Statistical Methodology 34:187–220.

Dahlgren, D. K., T. A. Messmer, and D. N. Koons. 2010. Achieving better estimates of greater sage-grouse chick survival in Utah. Journal of Wildlife Management 74:1286–1294.

Doherty, K. E., D. E. Naugle, H. Copeland, A. Pocewiz, and J. Kiesecke. 2011. Energy development and conservation tradeoffs: systematic planning for sage-grouse in their eastern range. Pages 505–517. in S. T. Knick, and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38. University of California Press, Berkeley, California, USA.

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, J. P. Mudd, J. B. Winstead, and L. D. Hayden-Wing. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. PLoS ONE 6:e26273.

Garton, E. O., J. W. Connelly, J. S. Horne, C. A. Hagen, A. Moser, and M. A. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Pages 293–381. *in* S. T. Knick, and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38 University of California Press, Berkeley, California, USA.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Grambsch, P. M., and T. M. Therneau. 1994. Proportional hazards test and diagnostics based on weighted residuals. Biometrika 81:515–526.

Hagen, C. A. 2003. A demographic analysis of lesser prairie-chicken populations in southwestern Kansas: survival, population viability, and habitat use. Dissertation, Kansas State University, Manhattan, USA.

Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effect. Pages 95–100. *in* S. T. Knick, and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38 University of California Press, Berkeley, California, USA.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Homer, C. G., C. L. Aldridge, D. K. Meyer, M. J. Coan, and Z. H. Bowen. 2009. Multiscale sagebrush rangeland habitat modeling in southwest Wyoming. U.S. Geological Survey, Washington, D.C., USA.

Homer, C. G., C. L. Aldridge, D. K. Meyer, and S. J. Schell. 2012. Multi-scale remote sensing sagebrush characterization with regression trees over Wyoming, USA: laying a foundation for monitoring. International Journal of Applied Earth Observation and Geoinformation 14:233–244.

Johnson, C. J., M. S. Boyce, C. C. Schwartz, and M. A. Haroldson. 2004. Modeling survival: application of the Andersen-Gill Model to Yellowstone grizzly bears. Journal of Wildlife Management 68:966–978.

Johnson, G. D., and S. E. Stephens 2011. Windpower and biofuels: a green dilemma for wildlife conservation. Pages 131–157. *in* D. E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

Kirol, C. P. 2012. Quantifying habitat importance for greater sage-grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. Thesis, University of Wyoming, Laramie, USA.

Kleinbaum, D. G., and M. Klein. 2005. Survival analysis, a self-learning text. Second edition. Springer Science + Business Media, Inc., New York, New York, USA.

Kuvlesky, W. P., L. A. Brennan, M. L. Morrison, K. K. Boydston, B. M. Ballard, and F. C. Bryant. 2007. Wind energy development and wildlife challenges and opportunities. Journal of Wildlife Management 71:2487–2498.

Liebezeit, J. R., S. J. Kendall, S. Brown, C. B. Johnson, P. Martin, T. L. McDonald, D. C. Payer, C. L. Rea, A. Streever, A. M. Wildman, and S. Zack. 2009. Influence of human development and predators on nest survival of tundra birds, Arctic Coastal Plain, Alaska. Ecological Applications 19:1628–1644.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486–491.

Naugle, K., E. Doherty, B. L. Walker, M. J. Holloran, and H. E. Copeland, 2011. Energy development and greater sage-grouse. Pages 489–505. *in* S. T. Knick, and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38 University of California Press, Berkeley, California, USA.

Nur, N., A. L. Holmes, and G. R. Geupel. 2004. Use of survival time analysis to analyze nesting success in birds: an example using loggerhead shrikes. Condor 106:457–471.

Pruett, C. L., M. A. Patten, and D. H. Wolfe. 2009*a*. It's not easy being green: wind energy and a declining grassland bird. Bioscience 59:257–262.

Pruett, C. L., M. A. Patten, and D. H. Wolfe. 2009*b*. Avoidance behavior by prairie grouse: implications for development of wind energy. Conservation Biology 23:1253–1259.

Remington, T. E., and C. E. Braun. 1991. How surface coal mining affects sage grouse, North Park, Colorado. Proceedings, issues and technology in management of impacted western wildlife. Thorne Ecological Institute 5:128–132.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187–205.

Sappington, M. J., K. M. Longshore, and D. B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71:1419–1426.

Sawyer, H., M. J. Kauffman, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052–1061.

Schoenfeld, D. 1982. Residuals for the proportional hazards regression model. Biometrika 69:239–241.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Pages 1–28. *in* A. Poole, and F. Gill, editors. The birds of North America. The Birds of North America Inc., Philadelphia, Pennsylvania, USA.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336–347.

Therneau, T. M., and P. M. Grambsch 2000. Modeling survival data: extending the Cox model. Springer-Verlag, New York, New York, USA.

Therneau, T. M., P. M. Grambsch, and T. R. Fleming. 1990. Martingale-based residuals for survival models. Biometrika 77:147–160.

Thompson, K. M., M. J. Holloran, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2006. Early brood-rearing habitat use and productivity of greater sage-grouse in Wyoming. Western North American Naturalist 66:332–342.

U.S. Fish and Wildlife Service [USFWS]. 2012. Final land-based wind energy guidelines. U.S. Fish and Wildlife Service, Arlington, Virginia, USA.

U.S. Geological Survey [USGS]. 2001. Land use/land cover national land cover database. USGS Headquarters, USGS National Center, Reston, Virginia, USA.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

Walker, B. L. 2008. Greater sage-grouse response to coal-bed natural gas development and West Nile virus in the Powder River Basin, Montana and Wyoming, USA. Dissertation, University of Montana, Missoula, USA.

Western Regional Climate Center. 2012. Medicine Bow, Wyoming (486120). <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wy6120>. Accessed 1 Feb 2012.

Wyoming Game and Fish Department. 2010. Wildlife protection recommendations for wind energy development in Wyoming. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

Zeiler, H. P., and V. Grünschachner-Berger. 2009. Impact of wind power plants on black grouse, *Lyrurus tetrix* in Alpine regions. Folia Zoologica 58:173–182.

*Associate Editor: Bret Collier.*

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

USGS
science for a changing world

# Conservation Buffer Distance Estimates for Greater Sage-Grouse—A Review

By Daniel J. Manier, Zachary H. Bowen, Matthew L. Brooks, Michael L. Casazza, Peter S. Coates, Patricia A. Deibert, Steven E. Hanser, and Douglas H. Johnson



Open-File Report 2014–1239

U.S. Department of the Interior
U.S. Geological Survey

U.S. Department of the Interior
SALLY JEWEL, Secretary

U.S. Geological Survey
Suzette M. Kimball, Acting Director

U.S. Geological Survey, Reston, Virginia: 2014

For more information on the USGS—the Federal source for science about the Earth, its natural and living resources, natural hazards, and the environment—visit *http://www.usgs.gov* or call 1–888–ASK–USGS

For an overview of USGS information products, including maps, imagery, and publications, visit *http://www.usgs.gov/pubprod*

To order this and other USGS information products, visit *http://store.usgs.gov*

Suggested citation:
Manier, D.J., Bowen, Z.H., Brooks, M.L., Casazza, M.L., Coates, P.S., Deibert, P.A., Hanser, S.E., and Johnson, D.H., 2014, Conservation buffer distance estimates for Greater Sage-Grouse—A review: U.S. Geological Survey Open-File Report 2014–1239, 14 p., *http://dx.doi.org/10.3133/ofr20141239*.

ISSN 2331-1258 (online)

Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Although this report is in the public domain, permission must be secured from the individual copyright owners to reproduce any copyrighted material contained within this report.

# Contents

Introduction ..... 1
Analytical Realities and Additional Background ..... 2
Surface Disturbance ..... 3
Linear Features ..... 5
Energy Development ..... 7
Tall Structures ..... 8
Low Structures ..... 9
Activities (Without Habitat Loss) ..... 9
References Cited ..... 10

## Table

Table 1. Lek buffer-distance estimates for six categories of anthropogenic land use and activity ..... 14

# Conversion Factors

## Inch/Pound to SI

| Multiply | By | To obtain |
|---|---|---|
| | Length | |
| foot (ft) | 0.3048 | meter (m) |
| mile (mi) | 1.609 | kilometer (km) |
| yard (yd) | 0.9144 | meter (m) |
| | Area | |
| acre | 4,047 | square meter ($m^2$) |
| acre | 0.4047 | hectare (ha) |
| acre | 0.004047 | square kilometer ($km^2$) |
| section (640 acres or 1 square mile) | 259.0 | square hectometer ($hm^2$) |
| square mile ($mi^2$) | 259.0 | hectare (ha) |
| square mile ($mi^2$) | 2.590 | square kilometer ($km^2$) |

## SI to Inch/Pound

| Multiply | By | To obtain |
|---|---|---|
| | Length | |
| meter (m) | 3.281 | foot (ft) |
| kilometer (km) | 0.6214 | mile (mi) |
| meter (m) | 1.094 | yard (yd) |
| | Area | |
| square meter ($m^2$) | 0.0002471 | acre |
| hectare (ha) | 2.471 | acre |
| square kilometer ($km^2$) | 247.1 | acre |
| square hectometer ($hm^2$) | 0.003861 | section (640 acres or 1 square mile) |
| hectare (ha) | 0.003861 | square mile ($mi^2$) |
| square kilometer ($km^2$) | 0.3861 | square mile ($mi^2$) |

# Conservation Buffer Distance Estimates for Greater Sage-Grouse—A Review

By Daniel J. Manier, Zachary H. Bowen, Matthew L. Brooks, Michael L. Casazza, Peter S. Coates, Patricia A. Deibert, Steven E. Hanser, and Douglas H. Johnson

## Introduction

This report was prepared at the request of the U.S. Department of the Interior and is a compilation and summary of published scientific studies that evaluate the influence of anthropogenic activities and infrastructure on Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) populations. The purpose of this report is to provide a convenient reference for land managers and others who are working to develop biologically relevant and socioeconomically practical buffer distances around sage-grouse habitats. The framework for this summary includes (1) addressing the potential effects of anthropogenic land use and disturbances on sage-grouse populations, (2) providing ecologically based interpretations of evidence from the scientific literature, and (3) informing implementation of conservation buffers around sage-grouse communal breeding locations—known as leks.

We do not make specific management recommendations but instead provide summarized information, citations, and interpretation of findings available in scientific literature. We also recognize that because of variation in populations, habitats, development patterns, social context, and other factors, for a particular disturbance type, there is no single distance that is an appropriate buffer for all populations and habitats across the sage-grouse range. Thus, we report values for distances upon which protective, conservation buffers might be based, in conjunction with other considerations (table 1). We present this information for six categories of land use or disturbance typically found in land-use plans which are representative of the level of definition available in the scientific literature: surface disturbance (multiple causes; immediate and cumulative influences); linear features (roads); energy development (oil, gas, wind, and solar); tall structures (electrical, communication, and meteorological); low structures (fences and buildings); and activities (noise and related disruptions). Minimum and maximum distances for observed effects found in the scientific literature, as well as a distance range for possible conservation buffers based on interpretation of multiple sources, expert knowledge of the authors regarding affected areas, and the distribution of birds around leks are provided for each of the six categories (table 1). These interpreted values for buffer distances are an attempt to balance the extent of protected areas with multiple land-use requirements using estimates of the distribution of sage-grouse habitat. Conservation efforts may then focus on the overlap between potential effect zone and important habitats. We provide a brief discussion of some of the most relevant literature for each category. References associated with the minimum and maximum values in table 1 are identified in the References Cited section with corresponding symbols.

Distances in this report reflect radii around lek locations because these locations are typically (although not universally) known, and

management plans often refer to these locations. Lek sites are most representative of breeding habitats, but their locations are focal points within populations, and as such, protective buffers around lek sites can offer a useful solution for identifying and conserving seasonal habitats required by sage-grouse *throughout* their life cycle. However, knowledge of local and regional patterns of seasonal habitat use may improve conservation of those important areas, especially regarding the distribution and utilization of nonbreeding season habitats (which may be underrepresented in lek-based designations).

## Analytical Realities and Additional Background

Understanding the effects of multiple human land uses on sage-grouse and their habitats is complicated by the combination of environmental, ecological, and socioeconomic conditions across the species range, which includes parts of 11 U.S. States and 2 Canadian Provinces in western North America. Responses of individual birds and populations, coupled with variability in land-use patterns and habitat conditions, add variation in research results. This variability presents a challenge for land managers and planners seeking to use research results to guide management and plan for sage-grouse conservation measures.

Variability between sage-grouse populations and their responses to different types of infrastructure can be substantial across the species' range. Our interpretations attempt to encompass variability in populations (for example, migratory versus nonmigratory) and rangewide response patterns of sage-grouse to various human activities. Logical and scientifically justifiable departures from the "typical response," based on local data and other factors, may be warranted when implementing buffer protections or density limits in parts of the species' range.

Natural movement behaviors of sage-grouse have been documented by multiple studies that provide direct evidence of inter- and intraseasonal movements from a few kilometers (km) (nonmigratory populations; Berry and Eng, 1985; Connelly and others, 2004) to 20–30 km or more (Connelly and others, 2004; Fedy and others, 2012; Tack and others, 2012). An influential, telemetry-based, tracking project in central Montana indicated more than 90 percent of *breeding season* movements by male grouse were within 1.3 km (0.8 mi) of a lek and 76 percent were within 1 km of a lek (0.6 mi; Wallestad and Schladweiler, 1974). The 1-km (0.6-mi) buffer used in many management efforts was based upon this research. More recent analyses have indicated that 90–95 percent of habitat use at the population level was focused within approximately 8 km (5 miles [mi]) of several California and Nevada lek sites (Coates and others, 2013), and 95 percent of all nests were located within approximately 5 km (3.1 mi) of leks. Holloran and Anderson (2005) found that 64 percent of nests in Wyoming occurred within 5 km (3.1 mi) of leks, suggesting considerable protection of sage-grouse within these proximate habitats. In contrast, home ranges as large as 2,975 $km^2$ (1,149 $mi^2$) have been documented (Connelly and others, 2000, 2004) in some portions of the species' range. These larger distances suggest that for some populations, the minimum distance inferred here (5 km [3.1 mi]) from leks may be insufficient to protect nesting and other seasonal habitats. Based on the collective information reviewed for this study, conservation practices that address habitats falling within the interpreted distances may be expected to protect as much as 75 percent (Doherty and others, 2010) to 95 percent (Coates and others, 2013) of local population's habitat utilization.

Habitat condition, composition, structure, and distribution are important potential modifiers of the effect of human infrastructure and activities on sage-grouse

populations (Dinkins and others, 2014; Walters and others, 2014). The distribution of sagebrush (*Artemisia* spp.) is a well-known biological and statistical predictor of sage-grouse response to their environment (for example, Connelly and others, 2004; Aldridge and Boyce, 2007; Hagen and others, 2007; National Technical Team, Sage Grouse, 2011; Wisdom and others, 2011; Kirol and others, 2012; Beck and others, 2014; Smith and others, 2014). Differences among sagebrush communities within a population range may also affect the impact of infrastructure. For example, primary productivity of sites is typically greater in mountain big sagebrush (*A. tridendata* ssp. *vaseyana*) communities than Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*) communities (Davies and Bates, 2010).

Sage-grouse depend on sagebrush, so buffer protections may be most effective when focused on avoidance of disturbance to sagebrush that provides the keystone to sage-grouse habitat. Important sage-grouse habitats include those with >40 percent sagebrush landcover (within 5 km [3.1 mi] radial assessment area; Knick and others, 2013), sagebrush patch sizes greater than 1 $km^2$ (0.4 $mi^2$) (Aldridge and Boyce, 2007), and plot-level composition of approximately 10–30 percent sagebrush cover and >15 percent grasses and forbs (Connelly and others, 2004; Stiver and others, 2006). Avoidance of activities that increase distance between sagebrush patches or that impose barriers to dispersal could also help maintain populations (Wisdom and others, 2011; Knick and Hanser, 2011).

Various protection measures have been developed and implemented, including complete closure of important habitats, distance buffers that restrict disturbing activities within designated distances, and development-disturbance density limits within habitats (for examples see, "Policy and Rules for Development" at *http://utahcbcp.org/htm/tall-structure-info*). Timing restrictions have also commonly been employed at lek sites, primarily to reduce disturbance to breeding sage-grouse. Although specific details and implementation of these different approaches have varied, each approach has the ability (alone or in concert with others) to protect important habitats, sustain populations, and support multiple-use demands for public lands. As such, local and regional differences in design and implementation of conservation plans should be assessed with explicit attention to the details and cumulative impact of a suite of actions, including but not limited to the buffer distances, which are the focus of this report.

## Surface Disturbance

Surface disturbance represents a combination of human activities that alter or remove the natural vegetation community on a site. Isolating the potential effects of human land-use patterns on sage-grouse is challenging because causal factors are frequently interrelated and interactive (for example roads and distribution lines or roads and well pads) making a general discussion of "development effects" necessary. In cases where better discrimination is available, those specific types of surface disturbances are addressed in the following sections. The values in this section reflect a nondiscriminatory understanding of the independent and interactive and cumulative effects of activities that remove sagebrush cover and other natural vegetation, and often include continual and (or) intermittent activities, such as running motors and pumps, vehicle visits, and equipment servicing. The collective influence of human activity on the landscape, often referred to as the human footprint (Leu and others, 2008), has been associated with negative trends in sage-grouse lek counts (Johnson and others, 2011) and population persistence (Aldridge and others, 2008; Wisdom and others, 2011). A multiscale assessment of factors associated with lek abandonment between 1965 and 2007 found that the level of the human footprint within 5 km (3.1 mi) of the lek was negatively associated

with lek persistence (Knick and Hanser, 2011). Agricultural activities, including tilling, seeding, and other highly managed activities, are a component of the human footprint and clearly fall into the category of surface disturbance (removal of native vegetation); however, agriculture is a special case because, although agriculture occupies large areas with transformed conditions, these lands are typically privately owned and the habitat value of agricultural areas is not zero because these lands can provide cover and forage for some populations in some seasons (Fischer and others, 1996). For example, sage-grouse have been known to use agricultural lands in late summer and early spring (Fischer and others, 1996). Though we found no direct evidence for spacing recommendations between agricultural lands and leks or other sage-grouse habitat, the conversion of sagebrush to agriculture within a landscape has been shown to lead to decreased abundance of sage-grouse in many portions of their range (Swenson and others, 1987; Smith and others, 2005; Aldridge and Boyce, 2007; Aldridge and others, 2008). A potential mechanism for this decrease in abundances, besides the direct loss of habitat, is the association of generalist predators (Common Raven [*Corvus corax*] and Black-billed Magpie [*Pica hudsonia*]) with agricultural infrastructure (Vander Haegen and others, 2002) and subsequent predation on sage-grouse (Connelly and others, 2004; Coates and Delehanty, 2010).

Estimated distance effects were translated to a 5- to 8-km (3.1- to 5-mi) radius around each lek to describe a possible conservation buffer area (interpreted range) based on interpretation of two principal factors: the potential effect area and the potential distribution of habitat use within affected areas. The need for protection of populations that are not well understood requires some generalization, and this distance range is proposed because research suggests that a majority of sage-grouse distributions and movements (within and between seasons) occur within this range (for example, Berry and Eng, 1985; Lyon and Anderson, 2003; Holloran and Anderson, 2005; Walker and others, 2007; Aldridge and others, 2008; Knick and others, 2011; Naugle and others, 2011; Coates and others, 2013). Importantly, due to variability among individuals and populations, some individuals in most populations (migratory and nonmigratory) may move greater distances than those included in the buffer, but specific protections cannot, practically, be determined for all individuals and all behavioral patterns. Although leks are generally recognized as the center of breeding and nesting habitats, recent utilization distribution analyses have helped to refine understanding of sage-grouse habitat-use patterns throughout the year. Based on this approach, Coates and others (2013) suggested that an 8-km (5-mi) protection area centered on an active lek location should encompass the seasonal movements and habitat use of 90–95 percent of sage-grouse associated with the lek. Longer distance movements are not always explicitly protected in this context, and habitats associated with previously unidentified leks may not be protected. However, final settling locations for more mobile individuals may be associated with quality habitats protected by buffers around adjacent lek sites. Furthermore, buffer distances beyond 8 km (5 mi) result in a decreasing benefit (cost-benefit trade-off) of increasing protection in areas that are less commonly used by sage-grouse. Without population-specific information regarding the location of habitats and movement of birds, which may be utilized when available (for an example see, Colorado Greater Sage-grouse Steering Committee, 2008), this generalized protection area (circular buffer around active leks with radius of 8 km [5mi]) offers a practical tool for determining important habitat areas. (Note: the Colorado Plan [Colorado Greater Sage-grouse Steering Committee, 2008] recommended a 6.4-km [4-mi] circular buffer, which may be well suited for those populations and falls within the range identified here.)

Importantly, similar results and interpretations to those derived from California and Nevada populations (Coates and others, 2013) were attained from the eastern portion of sage-grouse range; namely, Holloran and Anderson (2005) reported 64 percent of monitored nests fell within 5 km (3.1 mi) of a lek, and response to industrial development (decreased nesting rates and success rates) was observable to distances between 5 and 10 km (3.1–6.2 mi) from a lek suggesting that similar buffer distances are as relevant in Wyoming as in the Great Basin. In Utah, approximately 90 percent of nests (not all movements) were located within 5 km (3 mi) of a lek and threshold distance increased with greater contiguity of habitats. The smallest effect distance (3.2 km [2 mi] from a lek) described by Naugle and others (2011) was previously described and tested in field research by Holloran and Anderson (2005) and Walker and others (2007); these studies were designed to evaluate the effectiveness of existing stipulations. However, recent evaluation of different effect areas (Gregory and Beck, 2014) suggested significant immediate effects on lek attendance with one well pad within 2 km (1.2 mi) of a lek and time-lagged effects due to industrial development within 10 km (6.2 mi) of a lek indicating a habitat within the 8 km (5 mi) identified here may still experience an influence of development on some landscapes. Although considerable protections would be afforded by using a greater buffer distance from leks, research has indicated population effects are variable, and the cumulative effect of development may extend across the landscape many kilometers (>10 km [6 mi]) beyond the immediately affected areas. Diminishing gain analysis (Coates and others, 2013) suggested that sustained gains from habitat protection (based on percent of *highly used areas* protected versus *total* area protected) diminished after 8 km (5 mi)(radius) from leks, which helped to establish a ceiling on interpretations for habitat buffers seeking to maximize conservation benefits and minimize impacts on land uses.

## Linear Features

Roads, especially active roads such as collectors, major haul, and service roads, as well as county, State, and Federal highways, create many of the same “aversion” factors described previously that are related to traffic noise on roadways and interactions with infrastructure associated with corridors (such as fences, poles, and towers). One potential mechanism behind road-aversion behavior by sage-grouse could be the intermittent noise produced by passing traffic. Blickley and others (2012) discovered that noise-disturbance simulations that mimicked intermittent sources (road noise), or separately, drilling noises (continuous), generated a significant reduction in lek attendance of sage-grouse (73-percent reduction with road noise, 29 percent with drilling noise).

Most planning related to linear features applies to new construction, that is, avoidance of placing new roads or transmission lines in important habitats, but existing roads might also be addressed by considering seasonal closures, or removal, of roads within protective buffer areas. Fragmentation of habitats related to the network of roads and other linear features (potential for cumulative effects) may have negative effects on sage-grouse populations by reducing and fragmenting sagebrush habitat. When compared to extirpated leks, occupied leks have twice the cover of sagebrush (46 percent versus 24 percent) and ten times larger average sagebrush patches (4,173 hectares [ha] [10,310 acres] versus 481 ha [1,190 acres]) (Wisdom and others, 2011). However, it is important to recognize that previous assessments of relations between sage-grouse distributions and roads include a combination of positive and negative relations (Johnson and others, 2011), and local effects may be restricted to visible (or audible) range. Correlations between the distribution of roads with the distribution of quality sagebrush habitats (due to moderate topographic relief), interactions between influence of roads and

infrastructure with topography and habitat conditions (visibility and audibility), and differences in traffic volumes may all contribute to population effects on sage-grouse; not all roads have the same effect (Carpenter and others, 2010; Dinkins and others, 2014). Because roads and other linear features can have different effects on sage-grouse behavior, regional models of distributions and population dynamics have attempted to capture some differences; for example, roads closer to lek locations and other seasonal habitats may have greater effects than those occurring farther from important habitats (Hanser and others, 2011). Effects of pipelines and powerline corridors were tested but were not found to have clear, rangewide effects on lek trends (Johnson and others, 2011). However, it has become evident that interactions and co-location of linear features (for example, power distribution lines along roads and railroads) can make separation of effects difficult (Walters and others, 2014); power lines are addressed in a following section (Tall Structures).

Because of general concerns about habitat fragmentation and loss due to transportation networks, rangewide assessment of the effects of distributed human features, including road proximity (distance) and density, on trends in sage-grouse populations (based on lek counts), were conducted (Johnson and others, 2011). Incremental effects of accumulating length of roads in proximity to leks were apparent rangewide, although limited to major roads (State and Federal highways and interstates). This effect was demonstrated by decreasing lek counts when there were more than 5 km (3.1 mi) of Federal or State highway within 5 km (3.1 mi) of leks and when more than 20 km (12.4 mi) of highway occurs within an 18-km (11.2-mi) window (Johnson and others, 2011). Regional assessments (sage-grouse management zones, MZs; see Stiver and others, 2006) indicated downward trends in northern Great Basin (MZ4 and a portion of MZ5) populations when road density within 5-km (3.1-mi) radius of lek exceeded 30 km (18.6 mi). In Great Plains populations (MZ1), lek trends declined within a 10 km (6.2 mi) radius of a major road. It is important to note that many of the regional assessments did not indicate decreasing lek trends associated with the various size-classes of roads that were assessed (Johnson and others, 2011). In separate analyses in Wyoming, probability of sage-grouse habitat use (based on pellet-count surveys) declined around major roads (State and Federal highways and interstates) when assessed using a 1-km (0.6-mi) exponential decay function ($\exp^{(\text{distance}/-1\text{km})}$; Hanser and others, 2011). Assessment of lek trends in proximity to a large, interstate highway (I-80) indicated that all formerly recorded lek sites within 2 km (1.25 mi) of the highway were unoccupied, and leks within 7.5 km (4.7 mi) of the highway had declining attendance (Connelly and others, 2004).

Radio-telemetry (Very High Frequency, VHF) studies are often used to help track and document animal movements and habitat use, and some have reflected affinity of sage-grouse to roads (for example, Carpenter and others, 2010; Dinkens and others, 2014). However, this pattern may be due to search patterns employed by road-bound investigators (Fedy and others, 2014) or the distribution of roads across quality habitats in flat and lower elevation terrain (Carpenter and others, 2010; Dinkins and others, 2014) as opposed to selection of roads as preferred habitats. Seasonal, Statewide habitat models in Wyoming indicated a difference in seasonal sensitivity to density of paved roads, suggesting a decaying effects function approaching zero as distance approaches 3.2 km (2 mi) of leks (negative exponential) during the nesting and summer seasons, and a decay function approaching zero as distance approaches 1.5 km (0.9 mi) of leks during winter (Fedy and others, 2014). However, Dinkins and others (2014) found decreased risk of death for hens with *increasing* road density, but they also noted that the co-location of road

distribution and quality habitat may have influenced this result. Although noise has been clearly demonstrated to influence sage-grouse (Blickley and others, 2012), the influence of individual roads or networks of roads on sage-grouse habitat use and demographic parameters remains a research need. This is a good example of the challenge associated with making clear interpretations of the effect area (and therefore, a definitive buffer distance) for these types of infrastructure.

## Energy Development

Research and applications addressing surface disturbances in sagebrush ecosystems have been commonly conducted in relation to energy development activities. Lands affected by these activities have been the focus of many studies investigating the effects of anthropogenic activities on sage-grouse behavior and population dynamics, so the previous section (Surface Disturbance) contains much of the information relevant here.

Direct impacts of energy development on sage-grouse habitats and populations, such as loss of sagebrush canopy or nest failure, have been estimated to occur within a 1.2-ha (3-acre) area of leks (radius: 62 m [68 yards]); indirect influences, such as habitat degradation or utilization displacement, have been estimated to extend out to 19 km (11.8 mi) from leks (Naugle and others, 2011). Regional analyses of well-density and distance effects (Johnson and others, 2011) suggested negative trends in populations (lek counts) when distance was less than 4 km (2.5 mi) to the nearest producing well; whereas density effects were evident rangewide based on decreasing population trends when greater than eight active wells occurred within 5 km (3.1 mi) of leks, or when more than 200 active wells occurred within 18 km (11 mi)of leks. In Wyoming, significant negative relations between use of seasonal habitats and well densities have been demonstrated. Fedy and others (2014) found a significant negative relation between well density and probability of sage-grouse habitat selection during nesting (3.2-km [2-mi] radius) and winter (6.44-km [4-mi] radius) seasons. In the Powder River Basin, wintering sage-grouse were negatively associated with increasing coalbed natural gas well densities within a 2-km × 2-km (1.24-mi × 1.24-mi) window (Doherty and others 2008). Also, Gregory and Beck (2014) documented lek attendance decline when energy development averaged 0.7 well pads/km$^2$ (1.81 well pads/mi$^2$; using a 10-km × 10-km [6.2-mi × 6.2-mi] assessment window) across multiple populations and different development patterns.

A key consideration, besides the impacts of the development footprint on habitat condition and predation potential, is the effect of intermittent noise on behavior (avoidance) as evident from work by Blickley and others (2012) who found decreased lek activity due to mimicked drilling and road noise produced at close range (volume level equivalent to a road or well 400 m [1300 ft] away). A precise distance for noise effects has not been determined, but this value likely varies depending on the source (equipment, vehicles) and the terrain.

Less information is available about the effects of renewable energy development, such as wind-turbine arrays, on sage-grouse. LeBeau and others (2014) monitored effects during breeding season (95 nests and 31 broods) and found a linear decline of 7.1 percent in nest failure and 38 percent in brood failure with each 1-km (0.6-mi) increase in distance from wind energy infrastructure (less effect with greater distance). Changes in mortality were not attributed to direct collisions but to increased predation. It is notable that one study on prairie chickens (a related galliform, *Tympanuchus cupido*) found *increased* nest success rates adjacent to recent wind-energy facilities (Winder and others, 2014).

Suggestions that sage-grouse instinctively avoid wind turbines (tall

structures) to avoid predators are debated because of the difficulty in directly connecting predation risk to infrastructure, which often includes a combination of features (Walters and others, 2014). A further discussion of this topic is contained in the Tall Structures section below. It is notable that use of wind turbines as perches has not been documented.

## Tall Structures

It is important to recognize that the effect of tall structures remains debated, and this category contains a wide array of infrastructure including poles that support lights, telephone and electrical distribution, communication towers, meteorological towers, and high-tension transmission towers. Determining effects of these structures has remained difficult due to limited research and confounding effects (for example, towers and transmission lines are typically associated with other development infrastructure; Messmer and others, 2013; Walters and others, 2014). Lacking precise information regarding the influence of tall structures on the foraging behavior of corvids and raptors, management plans have adopted similar buffer distances to other infrastructure, for example a 1-km (0.6-mi) buffer of avoidance around lek sites. The general assumption is that these structures offer opportunities for increased predator use and thereby generate aversion behaviors among prey species (that is, sage-grouse); however, other effects, such as electro-magnetic radiation, have not been eliminated, and effects on predation rates have not been confirmed (Messmer and others, 2013). Habitat alteration, akin to other linear features (see previous section), may also be considered an important component of interactions between powerline corridors and sage-grouse populations. The 1-km (0.6-mi) buffer indicated here (table 1) was based upon Wallestad and Schladweiler (1974) who observed that more than 90 percent of breeding season movements by male grouse were within 1.3 km (0.8 mi) of a lek (76 percent of movements occurred within 1 km [0.6 mi]). Subsequently, Connelly and others (2000, p. 977) suggested, "avoid building powerlines and other tall structures that provide perch sites for raptors within 3 km of seasonal habitats... lines should be buried or posts modified to prevent use as perches..." Recent research has added important information to previous speculations and estimations, specifying concentrated foraging behaviors by common ravens (a common predator of sage-grouse nests) at 2.2 km (1.4 mi) from electrical transmission towers with the observed foraging area extending out to 11 km (6.8 mi; Coates, and others, 2014a). According to estimates, the greatest potential impact on sage-grouse nests occurs within 570 m (0.35 mi) of structures (Howe and others, 2014). Negative trends in lek counts were associated with increasing number of communication towers within 18km of leks range wide (Johnson and others 2011). Johnson and others (2011) also documented negative trends in lek counts for Great Plains populations within 20 km (12.4 mi) of a power transmission line or when the linear density of powerlines within 5 km (3.1 mi) of leks was greater than 10 km (6.2 mi)—notably, affected areas may be greater in these habitats (compared to other intermountain communities) because visibility is often greater in gentle terrain.

Although considerable attention has been paid to the influence of tall structures (both anthropogenic and trees) on the quality of sage-grouse habitat (for example, Connelly and others, 2000; Connelly and others, 2004; Stiver and others, 2006; National Technical Team, Sage-Grouse, 2011; Manier and others, 2013), solid evidence that sage-grouse instinctively avoid tall structures to avoid predators remains debated because of the difficulty in connecting predation risk to various combinations of infrastructure (Walters and others, 2014). However some evidence exists; in Wyoming the risk of death for sage-grouse hens was greater near potential raptor perches (Dinkins and

others, 2014), and in Idaho common raven abundance was greater near energy infrastructure (2.2 km [1.4 mi]; Coates and others 2014a,b). Coates and others (2014b) found different effects of infrastructure on three species of raptor (*Buteo* spp.) and common ravens, with clear increases in raven abundance with infrastructure but less consistent results with raptors. Also, in Wyoming, common raven habitat use was greatest within 3 km (1.8 mi) of human activity centers, and raven occupancy was correlated with nest failure (Bui and others, 2010). These studies suggest a potential increase in predators of sage-grouse, in particular ravens, which may influence predation pressure more than raptors.

## Low Structures

Collisions of flying sage-grouse with fences have been associated with mortality (Beck and others, 2006; Stevens and others, 2012a,b). Incidents were focused within 1.6–3.2 km (1–2 mi) of leks on flat to rolling terrain and fences with wide spacing of poles and (or) less visible 't-posts' (as opposed to wooden posts) (Stevens and others 2012a,b). Importantly, the effect of fences was apparently less in rougher terrain, presumably due to differences in flight behaviors in the birds. Marking fences helps flying grouse avoid these collisions; therefore, marking or removal of fences within 2 km (1.2 mi) of leks on flat or rolling terrain can reduce sage-grouse mortality associated with collisions. In a review of previous research, including theses and reports, Connelly and others (2004, p. 4–2) described findings of Rogers (1964) who stated that only 5 percent of leks were found within 200 m (656 ft) of a building, which suggests structures, even without regular activity and (or) noise, may have produced aversion behavior in historic sage-grouse populations. Recent research provides evidence that ravens forage at distances as far as 5.1 km (xx mi) from buildings in sagebrush environments (Coates and others, 2014a) suggesting that a wide distribution of infrastructure that can supply nesting or resting sites for ravens could have negative effects on sage-grouse populations.

## Activities (Without Habitat Loss)

Tests using recorded noises and wild sage-grouse populations (Blickley and others, 2012) suggest that loud noises transmitted at decibels (70 dB at 0 m; 40 dB at 100 m [328 ft]) to approximate a noise source 400 m (1300 ft) from leks caused decreased activity on leks. Though they did not test the range of potential noise volumes or activities (different noises) associated with recreation or other (nonindustrial) activities, this research is our best evidence of the effect of noise (independent from infrastructure) on sage-grouse behavior. The upper limit (4.8 km [3 mi]) is the value being used by the State of Nevada for reducing noise effects on sage-grouse due to locations of geothermal energy facilities (Nevada Governor's Sage-Grouse Conservation Team, 2010). Better understanding of the type, frequency, and volume of noise effects on sage-grouse behavior will enhance our ability to define effect areas.

## References Cited

Symbols in this section refer to citations in Table 1.


Aldridge, C.L., and Boyce, M.S., 2007, Linking occurrence and fitness to persistence—Habitat-based approach for endangered Greater Sage-Grouse: Ecological Applications, v. 17, p. 508–526.

Aldridge, C.L., Nielsen, S.E., Beyer, H.L., Boyce, M.S., Connelly, J.W., Knick, S.T., and Schroeder, M.A., 2008, Range-wide patterns of Greater Sage-Grouse persistence: Diversity and Distributions, v. 14, p. 983–94.

Beck, J.L., Booth, D.T., and Kennedy, C.L., 2014, Assessing Greater Sage-Grouse breeding habitat with aerial and ground imagery: Rangeland Ecology and Management, v. 67, p. 328–332.

Beck, J.L., Reese, K.P., Connelly, J.W., and Lucia, M.B., 2006, Movements and survival of juvenile Greater Sage-Grouse in southeastern Idaho: Wildlife Society Bulletin v. 34, p. 1070–1078.

Berry, J.D., and Eng, R.L., 1985, Interseasonal movements and fidelity to seasonal use areas by female sage-grouse: Journal of Wildlife Management, v. 49, p. 237–40.

‡ Blickley, J.L., Blackwood, D., Patricelli, G.L., 2012, Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks: Conservation Biology, v. 26, p. 461–471.

Bui, T.V.D., Marzluff, J.M., Bedrosian, B., 2010, Common raven activity in relation to land use in western Wyoming: implications for greater-sage grouse reproductive success: Condor, v. 112, p. 65–78.

Carpenter, J., Aldridge, C.L., and Boyce, M.S., 2010, Sage-grouse habitat selection during winter in Alberta: Journal of Wildlife Management, v. 74, p. 1806–1814.

Coates, P.S. and Delehanty, D.J., 2010, Nest predation of Greater Sage-Grouse in relation to microhabitat factors and predators: Journal of Wildlife Management, v. 74, p. 240–248.

Coates, P.S., Casazza, M.L., Blomberg, E.J., Gardner, S.C., Espinosa, S.P., Yee, J.L., Wiechman, L., and Halstead. B.J., 2013, Evaluating Greater Sage-Grouse seasonal space use relative to leks: Implications for surface use designations in sagebrush ecosystems: Journal of Wildlife Management, v. 77, p. 1598–1609.

Coates, P.S., Howe, K.B., Casazza M.L., and Delehanty, D.J., 2014a, Common raven occurrence in relation to energy transmission line corridors transiting human-altered sagebrush steppe: Journal of Arid Environments, v. 111, p.68–78.

Coates, P.S., Howe, K.B., Casazza, M.L., and Delehanty D.J., 2014b, Landscape alterations influence differential habitat use of nesting buteos and ravens within sagebrush ecosystem: Implications for transmission line development: Condor, v. 116, p. 341–356.

Connelly, J. W., Schroeder, M. A., Sands, A. R., and Braun, C. E., 2000, Guidelines to manage sage grouse populations and their habitats: Wildlife Society Bulletin, v. 28, p. 967–985.

§ Connelly, J. W., Knick, S.T., Schroeder, M. A. and Stiver, S. J., 2004, Conservation assessment of greater sage-grouse and sagebrush habitats: Western Association of Fish and Wildlife Agencies (WAFWA), 600 p.

Colorado Greater Sage-grouse Steering Committee, 2008, Colorado Greater Sage-Grouse Conservation Plan. Colorado Division of Wildlife, Denver, Colorado, USA.

Davies, K.W. and Bates, J.D., 2010, Vegetation Characteristics of Mountain and Wyoming Big Sagebrush Plant Communities in the

Northern Great Basin: Rangeland Ecology and Management, v. 63, p. 461–466.

Dinkins, J.B., Conover, M.R. Kirol, C.P. Beck, J. L. and Frey S.N,. 2014, Greater sage-grouse hen survival: effects of raptors, anthropogenic and landscape features, and hen behavior: Canadian Journal of Zoology, v. 92, p. 319–330.

Doherty, K.E., Naugle, D.E., Walker, B.L., and Graham J.M., 2008, Greater Sage-Grouse Winter Habitat Selection and Energy Development: Journal of Wildlife Management, v. 72, p. 187–95.

Doherty, K.E., Naugle, D.E., and Walker B.L., 2010, Greater Sage-Grouse nesting habitat: the importance of managing at multiple scales: Journal of Wildlife Management, v. 74, p. 1544–1553.

Fedy, B.C., Aldridge, C.L., Doherty, K.E., O'Donnell, M., Beck, J.L., Bedrosian, B., Holloran, M.J., Johnson, G. D., Kaczor, N.W., Kirol, C.P., Mandich, C.A., Marshall, D., McKee, G., Olson, C., Swanson, C.C. and Walker, B.L., 2012, Interseasonal Movements of Greater Sage-Grouse, Migratory Behavior, and an Assessment of the Core Regions Concept in Wyoming: Journal of Wildlife Management, v. 76, p. 1062–1071.

Fedy, B.C., Doherty, K.E., Aldridge, C.L., O'Donnell, M., Beck, J.L., Bedrosian, B., Gummer, D., Holloran, M.J., Johnson, G.D., Kaczor, N.W., Kirol, C.P., Mandich, D.A., Marshall, D., McKee, G., Olson, C., Pratt, A.C., Swanson, C.C.,Walker, B.L., 2014, Habitat prioritization across large landscapes, multiple seasons, and novel areas: An example using Greater Sage-Grouse in Wyoming: Wildlife Monographs, v. 190, p. 1–39.

Fischer, R.A., Reese, K.P., and Connelly, J.W., 1996, Influence of vegetal moisture content and nest fate on timing of female sage grouse migration: Condor, v. 98, p.868–872.

Gregory, A.J., and Beck, J.L., 2014, Spatial heterogeneity in response of male greater sage-grouse lek attendance to energy development: PLoS ONE, v. 9, e97132.

Hagen, C.A., Connelly, J.W., Schroeder, M.A., 2007, A meta-analysis of greater sage-grouse Centrocercus urophasianus nesting and brood-rearing habitats: Wildlife Biology, v. 13, p. 42–50

Hanser, S.E., Aldridge, C.L., Leu, M., Rowland, M.M., Nielsen, S.E., and Knick S.T., 2011, Greater Sage-Grouse: General Use and Roost Site Occurrence with Pellet Counts as a Measure of Relative Abundance, p. 112–140 *in* S. E. Hanser, M. Leu, S. T. Knick, and C. L. Aldridge, eds., Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins: Allen Press, Lawrence, KS.

* Holloran, M.J., and Anderson. S.H., 2005, Spatial Distribution of Greater Sage-Grouse Nests in Relatively Contiguous Sagebrush Habitats: Condor, v. 107, p. 742–52.

° Howe, K.B., Coates, P.S., and Delehanty, D.J., 2014, Selection of anthropogenic features and vegetation characteristics by nesting Common Ravens in the sagebrush ecosystem: Condor, v. 116, p. 25–49.

◊ Johnson, D. H., Holloran, M. J. Connelly, J. W. Hanser, S. E. Amundson, C. L. andKnick S. T., 2011, Influences of Environmental and Anthropogenic Features on Greater Sage-Grouse Populations, 1997–2007, Chapter 17 *In* S. T. Knick and J. W. Connelly, eds., Greater Sage-Grouse: Ecology of a Landscape Species and Its Habitats, Studies in Avian Biology No. 38: University of California Press: Berkeley, CA, p. 407–450.

Kirol, C.P., Beck, J.L., Dinkins, J.B., and Conover, M.R., 2012, Microhabitat selection for nesting and brood-rearing by the Greater Sage-Grouse in xeric big sagebrush: Condor, v. 114, p.75–89.

Knick, S.T., 2011, Historical development, principal federal legislation, and current management of sagebrush habitats: implications for conservation. *in* S. T. Knick and J. W. Connelly, eds. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology No. 38, University of California Press, Berkeley, CA. p. 13–31.

Knick, S.T., and Hanser, S.E., 2011, Connecting pattern and process in Greater Sage-Grouse populations and sagebrush landscapes, *in* S. T. Knick and J. W. Connelly, eds., Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology No. 38: University of California Press, Berkeley, CA. p. 383–405.

Knick, S.T., Hanser, S.E., and Preston, K.L,. 2013, Modeling ecological minimum requirements for distribution of greater sage-grouse leks: implications for population connectivity across their western range, U.S.A.: Ecology and Evolution, v. 3, p.1539–1551.

Knick, S.T., Hanser, S.E. Miller, R.F., Pyke, D.A., Wisdom, M.J., Finn, S. P., Rinkes, E.T. and Henny C.J., 2011, Ecological Influence and Pathways of Land Use in Sagebrush, *In* S. T. Knick and J. W. Connelly, eds., Greater Sage-Grouse: Ecology of a Landscape Species and Its Habitats, Studies in Avian Biology No.38: University of California Press: Berkeley, CA, p. 203–252.

LeBeau, C.W., Beck, J.L., Johnson G.D. and Holloran, M.J., 2014, Short-term impacts of wind energy development on Greater Sage-Grouse fitness: Journal of Wildlife Management, v. 78, p. 522–530.

Leu, M., Hanser, S.E., and Knick S.T., 2008, The human footprint in the West: a large-scale analysis of anthropogenic impacts, Ecological Applications, v. 18, p. 119–1139.

Lyon, A.G., and Anderson S.H,. 2003, Potential Gas Development Impacts on Sage Grouse Nest Initiation and Movement. Wildlife Society Bulletin, v. 31, p. 486–91.

Manier, D.J., Wood, D.J.A., Bowen, Z.H., Donovan, R.M., Holloran, M.J., Juliusson, L.M., Mayne, K.S., Oyler-McCance, S.J., Quamen, F.R., Saher, D.J., and Titolo, A.J., 2013, Summary of science, activities, programs, and policies that influence the rangewide conservation of Greater Sage-Grouse (*Centrocercus urophasianus*): U.S. Geological Survey Open–File Report 2013–1098, 331 p.

Messmer, T.A., Hasenyager, R. Burruss, J. and Liguori S., 2013, Stakeholder contemporary knowledge needs regarding the potential effects of tall structures on sage-grouse. Human-Wildlife Interactions, v. 7, p. 273–298.

National Technical Team, Sage-Grouse, 2011, A report on national Greater Sage-Grouse conservation measures. Bureau of Land Management: Technical Report. Washington, D.C. and Denver, Colorado. 74p.

ǂ Naugle, D. E., Doherty, K.E. Walker, B.L. Holloran, M.J. and Copeland H.E., 2011, Energy Development and Greater Sage-Grouse. In Greater Sage-Grouse: Ecology of a Landscape Species and Its Habitats, edited by S.T. Knick and Connelly J.W. Studies in Avian Biology No. 38, University of California Press: Berkeley, CA, p. 489–504.

ψ Nevada Governor's Sage-Grouse Conservation Team, 2010, Nevada energy and infrastructure development standards to conserve Greater Sage-Grouse populations and their habitats. State of Nevada, Reno, 58 p.

Rogers, G.E., 1964, Sage-grouse investigations in Colorado. Colorado Game and Fish Department, Technical Publication No. 16, Fort Collins, Colo.

Smith, J.T., Flake, L.D., Higgins, K F., Kobriger, G.D., and Homer C.G., 2005,

Evaluating lek occupancy of Greater Sage-Grouse in relation to landscape cultivation in the Dakotas: Western North American Naturalist, v. 65, p. 310–320.

Smith, K.T., Kirol, C.P., Beck, J.L, .and Blomquist, F.C., 2014, Prioritizing winter habitat quality for greater sage-grouse in a landscape influenced by energy development: Ecosphere, vol. 5, article 15

Stevens, B.S., Reese, K.P. Connelly, J.W., and Musil D.D., 2012a, Greater sage-grouse and fences: Does marking reduce collisions? Wildlife Society Bulletin, v. 36, p. 297–303.

« Stevens, B.S., Connelly, J.W. and Reese K.P., 2012b, Multi-scale assessment of greater sage-grouse fence collision as a function of site and broad scale factors.: Journal of Wildlife Management, v. 76, p. 1370–1380.

Stiver, S.J., Apa, A.D., Bohne, J.R., Bunnell, S.D., Deibert, P.A., Gardner, S.C., Hilliard, M.A., McCarthy C.W., and Schroeder M.A., 2006, Greater Sage-grouse Comprehensive Conservation Strategy. Western Association of Fish and Wildlife Agencies. WAFWA Report, Cheyenne, Wyoming. Available online: *http://www.wafwa.org/documents/pdf/GreaterSage-grouseConservationStrategy2006.pdf*

Swenson, J. E., Simmons, C.A. and Eustace C.D., 1987, Decrease of Sage Grouse Centrocercus urophasianus after ploughing of sagebrush steppe: Biological Conservation, v. 41, p. 125–132.

Tack, J.D., Naugle D.E., Carlson J.C. and Fargey P.J., 2012,. Greater sage-grouse (Centrocercus urophasianus) migration links the USA and Canada: a biological basis for international prairie conservation: Oryx, vol. 46, p. 64–68.

Vander Haegen, W.M., Schroeder M.A. and DeGraaf R.M.. 2002. Predation on real and artificial nests in shrub steppe landscapes fragmented by agriculture: Condor, v. 104, p. 496–506.

* Walker, B. L., Naugle, D. E. and Doherty K. E.. 2007. Greater Sage-Grouse population response to energy development and habitat loss: Journal of Wildlife Management, v. 71, p. 2644–2654.

° Wallestad, R. O., and Schladweiler, P, 1974. Breeding season movements and habitat selection of male sage grouse: Journal of Wildlife Management, v.38, p. 634–637.

Walters, K., Kosciuch K., and Jones, J., 2014, Can the effect of tall structures on birds be isolated from other aspects of development: Wildlife Society Bulletin, vol. 38, p. 250–256.

Winder, V.L., McNew, L.B., Gregory, A.J., Hunt, L.M., Wisely, S.M., and Sandercock, B.K., 2014, Effects of wind energy development on survival of female greater prairie- chickens: Journal of Applied Ecology, v. 51, p. 395–405.

Wisdom, M. J., Meinke, C. W. Knick, S. T. and Schroeder, M. A., 2011, Factors associated with extirpation of sage-grouse. *In* Knick, S. T. and Connelly, J. W., eds. Greater Sage-Grouse: ecology of a landscape species and its habitats. Studies in Avian Biology No. 38, University of California Press: Berkeley, California, p. 451–472**.**

ISSN 2331-1258 (online)
*http://dx.doi.org/10.3133/ofr20141239*

Table 1. Lek buffer-distance estimates for six categories of anthropogenic land use and activity. Literature minimum and maximum values are distances for observed effects found in the scientific literature. Interpreted ranges indicate potential conservation buffer distances based on multiple sources. [Citations for literature minimum and maximum values are denoted using corresponding symbols in the References Cited section.]

| Category | Literature minimum | Interpreted range (lower) | Interpreted range (upper) | Literature maximum |
|---|---|---|---|---|
| Surface disturbance | 3.2km (2mi) * | 5km (3.1mi) | 8km (5mi) | 20km (12.4mi) ◊ |
| Linear features | 400m (0.25mi) ‡ | 5km (3.1mi) | 8km (5mi) | 18km (11.2mi) ◊ |
| Energy development | 3.2km (2mi) ǂ | 5km (3.1mi) | 8km (5mi) | 20km (12.4mi) ◊ |
| Tall structures | 1km (0.6mi) ° | 3.3km (2mi) | 8km (5mi) | 18km (11.2mi) ◊ |
| Low structures | 200 m (0.12 mi) § | 2 km (1.2mi) | 5.1 km (3.2mi) | 5.1 km (3.2mi) « |
| Activities | 400 m (0.12 mi) ‡ | 400 m (0.12 mi) | 4.8 km (3mi) | 4.8 km (3mi) ψ |

# A Report on National Greater Sage-Grouse Conservation Measures

**Produced by:**

**Sage-grouse National Technical Team**

**December 21, 2011**

## Table of Contents


Introduction ..... 4

Goals and Objectives ..... 6

Conservation Measures ..... 11

Travel and Transportation ..... 11

Recreation ..... 12

Lands/Realty ..... 12

Range Management ..... 14

Wild Horse and Burro Management ..... 18

Minerals ..... 18

Fluid Minerals ..... 22

Solid Minerals ..... 24

Mineral Split Estate ..... 25

Wildfire Suppression, Fuels Management and Fire Rehabilitation ..... 25

Habitat Restoration ..... 27

Monitoring of Sage-grouse and Sagebrush Habitats ..... 28

Acronyms ..... 32

Glossary ..... 33

Literature Cited ..... 39

Appendices ..... 51

Appendix A. Life History Requirements of Greater Sage-grouse (excerpted from 75 FR 13910) ..... 51

Appendix B. Scientific Inference ..... 56

Appendix C. BMPs for how to make a pond that won't produce mosquitoes that transmit West Nile virus (from Doherty (2007)). ..... 61

Appendix D. Best Management Practices for Fluid Mineral Development.....63

Appendix E. Best Management Practices for Locatable Mineral Development .....68

Appendix F. Best Management Practices for Fire & Fuels (wo IM 2011-138) .....71

Appendix G. National Technical Team Members .....74

# Introduction

Sagebrush landscapes have changed dramatically over the last two centuries. The vast expanses of sagebrush crossed by early European settlers and used by sage-grouse have been lost, fragmented, or altered due to invasive plants, changes in fire regimes, and impact of land uses (Knick et al. 2003, Knick and Connelly 2011a). As a consequence, sage-grouse and many other wildlife species that depend on sagebrush have undergone long-term range-wide population declines. Sage-grouse populations now occupy approximately one-half of their pre-European settlement distribution (Schroeder et al. 2004). Anthropogenic habitat impacts and lack of regulatory mechanisms to protect against further losses provided the basis for warranting listing under the Endangered Species Act (ESA) in 2010 (75 FR 13910). The need to address higher priority species and limited funding precluded immediate listing action. However, a litigation settlement requires that a listing decision be made by the U.S. Fish and Wildlife Service (USFWS) by September, 2015.

The Bureau of Land Management (BLM) manages approximately 50% of the sagebrush habitats used by sage-grouse (Knick 2011). Therefore, management actions by BLM in concert with other state and federal agencies, and private land owners play a critical role in the future trends of sage-grouse populations. To ensure BLM management actions are effective and based on the best available science, the National Policy Team created a National Technical Team (NTT) in August of 2011. The BLM's objective for chartering this planning strategy effort was to develop new or revised regulatory mechanisms, through Resource Management Plans (RMPs), to conserve and restore the greater sage-grouse and its habitat on BLM-administered lands on a range-wide basis over the long term. The National Greater Sage-Grouse Planning Strategy Charter charged the NTT to serve as a scientific and technical forum to:

- Understand current scientific knowledge related to the greater sage-grouse.
- Provide specialized sources of expertise not otherwise available.
- Provide innovative scientific perspectives concerning management approaches for the greater sage-grouse.
- Provide assurance that relevant science is considered, reasonably interpreted, and accurately presented; and that uncertainties and risks are acknowledged and documented.
- Provide science and technical assistance to the Regional Management Team (RMT) and Regional Interdisciplinary Team (RIDT), on request.
- Articulate conservation objectives for the greater sage-grouse in measurable terms to guide overall planning.

- Identify science-based management considerations for the greater sage-grouse (e.g., conservation measures) that are necessary to promote sustainable sage-grouse populations, and which focus on the threats (75 FR 13910) in each of the management zones.[i]

The National Technical Team (NTT) met from August 28 through September 2, 2011, in Denver, Colorado, and a subset of the team met December 5-8 in Phoenix, Arizona, to further articulate the scientific basis for the conservation measures. Members of the team included resource specialists and scientists from the BLM, State Fish and Wildlife Agencies, USFWS, Natural Resources Conservation Service (NRCS) and U.S. Geological Survey (USGS).

This document provides the latest science and best biological judgment to assist in making management decisions. Fortunately, recent emphasis on sage-grouse conservation has resulted in a substantial number of publications dealing with a variety of aspects of sage-grouse ecology and management, summarized in the 2010 listing petition (75 FR 13910), as well as Knick and Connelly (2011b). Habitat requirements and other life history aspects of sage-grouse, excerpted from the USFWS listing decision (75 FR 13910), are summarized in Appendix A to provide context for the proposed conservation measures. We have attempted to describe the scientific basis for the conservation measures proposed within each program area. Perspectives on the nature and interpretation of the available science are in Appendix B.

The conservation measures described in this report are not an end point but, rather, a starting point to be used in the BLM's planning processes. Due to time constraints, they are focused primarily on priority sage-grouse habitat areas. General habitat conservation areas were not thoroughly discussed or vetted through the NTT, and the concept of connectivity between priority sage-grouse habitat areas will need more development through the BLM planning process.

[i] Identified in the Western Association of Fish and Wildlife Agencies (WAFWA) Conservation Strategy (Stiver et al. 2006).

# Goals and Objectives

The BLM, along with a host of other state and federal agencies who participated in development of the Greater Sage-grouse Comprehensive Conservation Strategy (Stiver et al. 2006), endorsed the goal of that document which was "to maintain and enhance populations and distribution of sage-grouse by protecting and improving sagebrush habitats and ecosystems that sustain these populations". Although it was understood that at least in the short term this goal of maintaining sage-grouse population size and distribution as based on trends from 1965 - 2003, or enhancing above these levels was aspirational, the NTT supports it as a guiding philosophy against which management actions and policies of BLM should be weighed. Therefore, the conservation measures and strategies that follow assume the goal and objectives below.

## Goal

**Maintain and/or increase sage-grouse abundance and distribution by conserving, enhancing or restoring the sagebrush ecosystem upon which populations depend in cooperation with other conservation partners.**

Until such time as more specific conservation objectives relative to sage-grouse distribution or abundance by sage-grouse management zone, state, or population are developed, BLM will strive to maintain or increase current distribution and abundance of sage-grouse on BLM administered lands in support of the range-wide goals. BLM will specifically address threats identified by the Fish and Wildlife Service in their 2010 listing decision (75 FR 13910).

Sage-grouse populations have the greatest chance of persisting when landscapes are dominated by sagebrush and natural or human disturbances are minimal (Aldridge et al. 2008, Knick and Hanser 2011, Wisdom et al. 2011). Within priority habitat, a minimum range of 50-70% of the acreage in sagebrush cover is required for long-term sage-grouse persistence (Aldridge et al. 2008, Doherty et al. 2010, Wisdom et al. 2011). Fire and invasion by exotic grasses are widespread causes for habitat loss, particularly in the western part of the sage-grouse range (Miller et al. 2011). Human land use, including tillage agriculture, historic grazing management, energy development, roads and power line infrastructure, and even recreation have contributed both individually and cumulatively to lower numbers of sage-grouse across the range (75 FR 13910, Knick et al. 2011).

### *New Paradigm*

Through the establishment of the National Sage-grouse Planning Strategy, the Bureau of Land Management has committed to a new paradigm in managing the sagebrush landscape. That new paradigm will require collaborative conservation efforts among private, state, tribal, and other federal partners to conserve sage-grouse. Land uses, habitat treatments, and anthropogenic disturbances will need to be managed below thresholds necessary to conserve not only local sage-grouse populations, but sagebrush communities and landscapes as well. Management priorities will need to be shifted and balanced to maximize benefits to

sage-grouse habitats and populations in priority habitats. Adequacy of management adjustments will be measured by science-based effectiveness monitoring of the biological response of sagebrush landscapes and sage-grouse populations. Ultimately, success will be measured by the maintenance and enhancement of sage-grouse populations well into the future.

***Objectives***

The overall objective is to protect priority sage-grouse habitats from anthropogenic disturbances that will reduce distribution or abundance of sage-grouse. Priority sage-grouse habitats are areas that have the highest conservation value to maintaining or increasing sage-grouse populations. These areas would include breeding, late brood-rearing, winter concentration areas, and where known, migration or connectivity corridors. These areas have been, or will be identified by state fish and wildlife agencies in coordination with respective BLM offices. Priority habitat designations must reflect the vision, goals and objectives of this overall plan if the conservation measures are to be effective. Additionally, there is an opportunity for synergy and collaboration with WAFWA in order to identify a consistent way to designate priority sage-grouse habitat areas and develop a range-wide priority habitat area map. This collaborative and overarching approach could help ensure activities immediately outside the priority areas do not impact priority habitat.

To reach this objective, it will be necessary to achieve the following sub-objectives for priority habitat:

- Designate priority sage-grouse habitats for each WAFWA management zone (Stiver et al. 2006) across the current geographic range of sage-grouse that are large enough to stabilize populations in the short term and enhance populations over the long term.
- To maintain or increase current populations, manage or restore priority areas so that at least 70% of the land cover provides adequate sagebrush habitat to meet sage-grouse needs.
- Develop quantifiable habitat and population objectives with WAFWA and other conservation partners at the management zone and/or other appropriate scales. Develop a monitoring and adaptive management strategy to track whether these objectives are being met, and allow for revisions to management approaches if they are not.[ii]
- Manage priority sage-grouse habitats so that discrete anthropogenic disturbances cover less than 3% of the total sage-grouse habitat regardless of ownership. Anthropogenic features include but are not limited to paved highways, graded gravel roads, transmission lines, substations, wind

[ii] As population trends within each Management Zone respond, long-term success can be judged based on comparisons with data from the 1965-2003 period for that specific Management Zone (Stiver et al., 2006).

[iii] Professional judgment as derived from Holloran 2005, Walker et al. 2007, Doherty et al. 2008, Doherty et al. 2011, Naugle et al. 2011a,b.

turbines, oil and gas wells, geothermal wells and associated facilities, pipelines, landfills, homes, and mines. [iii]

- In priority habitats where the 3% disturbance threshold is already exceeded from any source, no further anthropogenic disturbances will be permitted by BLM until enough habitat has been restored to maintain the area under this threshold (subject to valid existing rights).

- In this instance, an additional objective will be designated for the priority area to prioritize and reclaim/restore anthropogenic disturbances so that 3% or less of the total priority habitat area is disturbed within 10 years.

*Note to add context to above objective:* Disturbance can be described within categories as discrete (having a distinct measureable impact in space and time) or diffuse (pressure is exerted over broad spatial or temporal scales) (Turner and Gardner 1991). Most anthropogenic disturbance (roads, power lines, oil/gas wells, tall structures) are discrete disturbances. Livestock grazing is a diffuse disturbance. Fire can be either discrete or diffuse depending on its characteristics and the scales at which it is measured. Sage-grouse are extremely sensitive to discrete disturbance (Johnson et al. 2011, Naugle et al. 2011a,b) although diffuse disturbance over broad spatial and temporal scales can have similar, but less visible effects.

Spatial and temporal scales are important components in measuring and interpreting the effects of disturbance (Johnson and St-Laurent 2011). A discrete event might be significant to individuals or local communities but have little effect on the larger population or region (See Figure 2 in Appendix B). Therefore, defining the spatial extent (the region bounding the analysis), spatial and temporal scale (the dimension of the event), and the resolution (the precision of the measurement) are fundamental inputs into any assessment of disturbance (Wheatley and Johnson 2009).

Two spatial extents for measuring anthropogenic disturbance will be used: 1) the area contained within individual priority areas and 2) each one-mile section within the priority area. This hierarchical arrangement allows concentrated anthropogenic disturbance to exceed recommended thresholds within a smaller area, yet still maintain an overall level at the scale to which sage-grouse respond within priority areas.

(1) Large-scale disturbances that impact sage grouse distribution and abundance at any level will not be permitted within priority areas (subject to valid existing rights). Other, smaller scale proposed anthropogenic disturbances will not disturb more than a total of 3% of the acreage within each priority area.

[iii] Professional judgment as derived from Holloran 2005, Walker et al. 2007, Doherty et al. 2008, Doherty et al. 2011, Naugle et al. 2011a,b.

(2) Proposed anthropogenic surface disturbances within an individual priority area will be encouraged to occur in areas of existing development, or areas of non-suitable habitats. Suitable buffers, depending on the occurrence of adjacent seasonal habitats and local information (e.g. migratory vs. non-migratory populations; [Connelly et al. 2000]) may be applied in siting a proposed anthropogenic surface disturbance to protect surrounding suitable, undisturbed habitats.

(3) Concentrating or clustering disturbances locally while maintaining total disturbance below 3% at the priority habitat scale may cause some one-mile$^2$ analysis sections to exceed the 3% anthropogenic disturbance goal. For example, a sand and gravel mine can result in intensive development of 40 acres, effectively rendering that area unsuitable for sage-grouse. The actual 40-acre disturbance may not push total anthropogenic disturbance to more than 3% for the entire priority area, but obviously has a significant local impact. In these situations, 40 acres of off-site mitigation will be necessary to offset this loss of habitat. The priority is to implement off-site mitigation within the priority sage-grouse habitat, followed by general sage-grouse habitat.

If a project proponent agrees to site proposed anthropogenic surface disturbance within areas of existing development or areas of non-suitable habitat in a priority area, and the resulting localized total surface disturbance exceeds 3% (but the anthropogenic surface disturbance of the entire priority area does not exceed 3%), the need for off-site mitigation should be evaluated on a case-by-case basis.

Additionally, there are sub-objectives that must be met in general sage-grouse habitat. General sage-grouse habitat is occupied (seasonal or year-round) habitat outside of priority habitat. These areas have been, or will be identified by state fish and wildlife agencies in coordination with respective BLM offices.

It will be necessary to achieve the following sub-objectives for general habitat:

- Quantify and delineate general habitat for capability to provide connectivity among priority areas (Knick and Hanser 2011).
- Conserve, enhance or restore sage-grouse habitat and connectivity (Knick and Hanser 2011) to promote movement and genetic diversity, with emphasis on those habitats occupied by sage-grouse.
- Assess general sage-grouse habitats to determine potential to replace lost priority habitat caused by perturbations and/or disturbances and provide connectivity (Knick and Hanser 2011) between priority areas.
    - These habitats should be given some priority over other general sage-grouse habitats that provide marginal or substandard sage-grouse habitat.

- Restore historical habitat functionality to support sage-grouse populations guided by objectives to maintain or enhance connectivity. Total area and locations will be determined at the Land Use Plan level.
- Enhance general sage-grouse habitat such that population declines in one area are replaced elsewhere within the habitat.

# Conservation Measures

The following conservation measures are designed to achieve population and habitat objectives stated in this report. They are organized by resource programs.

## Travel and Transportation

The Travel and Transportation program is principally focused on road networks within the sage-grouse range. Roads can range from state or interstate highways to gravel and two-track roads. Within the sage-grouse range, 95% of the mapped sagebrush habitats are within 2.5 km (1.55 miles) of a mapped road; density of secondary roads exceeds 5 km/km$^2$ (3.1 miles/247 acres) in some regions (Knick et al. 2011).

Roads have multiple impacts on wildlife in terrestrial ecosystems, including:

1) Increased mortality from collision with vehicles;
2) Changes in behavior;
3) Loss, fragmentation, and alteration of habitat;
4) Spread of exotic species; and
5) Increased human access, resulting in facilitation of additional alteration and use of habitats by humans (Formann and Alexander 1998, Jackson 2000, Trombulak and Frissel 2000).

The effect of roads can be expressed directly through changes in habitat and sage-grouse populations and indirectly through avoidance behavior because of noise created by vehicle traffic (Lyon and Anderson 2003, 75 FR 13910).

<u>Priority sage-grouse habitat areas</u>

- Limit motorized travel to designated roads, primitive roads, and trails at a minimum.
- Travel management should evaluate the need for permanent or seasonal road or area closures.
- Complete activity level plans within five years of the record of decision. During activity level planning, where appropriate, designate routes with current administrative/agency purpose or need to administrative access only.
- Limit route construction to realignments of existing designated routes if that realignment has a minimal impact on sage-grouse habitat, eliminates the need to construct a new road, or is necessary for motorist safety
- Use existing roads, or realignments as described above to access valid existing rights that are not yet developed. If valid existing rights cannot be accessed via existing roads, then build any new road constructed to the absolute minimum standard necessary, and add the surface disturbance to the total disturbance in the priority area. If that disturbance exceeds 3 % for that area, then make additional, effective mitigation necessary to offset the resulting loss of sage-grouse habitat (see Objectives).

- Allow no upgrading of existing routes that would change route category (road, primitive road, or trail) or capacity unless the upgrading would have minimal impact on sage-grouse habitat, is necessary for motorist safety, or eliminates the need to construct a new road.
- Conduct restoration of roads, primitive roads and trails not designated in travel management plans. This also includes primitive route/roads that were not designated in Wilderness Study Areas and within lands with wilderness characteristics that have been selected for protection.
- When reseeding roads, primitive roads and trails, use appropriate seed mixes and consider the use of transplanted sagebrush.

## Recreation

Recreational activities in sagebrush habitats range from hiking, camping and hunting to lek viewing, and off-highway vehicle (OHV) use. Many of these activities are benign uses in sagebrush habitats. However, excessive use, such as repeated disturbance to leks for viewing that disrupts sage-grouse breeding activities, can have negative effects (75 FR 13910). Off-trail recreation by OHV users can fragment habitat and create corridors for spread of exotic plant species (Knick et al. 2011).

***Special Recreation Permits (SRP)***

- Only allow SRPs that have neutral or beneficial affects to priority habitat areas.

## Lands/Realty

The Lands and Realty program primarily influences rights-of-way (ROWs), land tenure adjustments, and proposed land withdrawals. Existing and proposed developments for ROWs (such as powerlines, pipelines, and renewable energy projects) and access to various mineral claims or energy development locations have the potential to cause habitat loss and fragmentation that decreases habitat and population connectivity. Roads also create corridors that facilitate spread of exotic plant species (Gelbard and Belnap 2003). In addition, roads and infrastructure networks can increase sage-grouse mortality from increased predation and collisions with vehicles. Sage-grouse may avoid areas because of noise from vehicle traffic (Lyon and Anderson 2003). Adjustments for land tenure and strategically-located land withdrawals can be used to increase connectivity within sage-grouse populations and sagebrush habitats (Knick and Hanser 2011). In addition, land acquisitions and withdrawals may be important conservation strategies because increased development on private lands, which is not subject to mitigation, will focus greater needs for conservation of sage-grouse and sagebrush on public lands (Knick et al. 2011).

***Rights of Way***

<u>Priority sage-grouse habitat areas</u>

- Make priority sage-grouse habitat areas exclusion areas for new ROWs permits. Consider the following exceptions:

- Within designated ROW corridors encumbered by existing ROW authorizations: new ROWs may be co-located only if the entire footprint of the proposed project (including construction and staging), can be completed within the existing disturbance associated with the authorized ROWs.
- Subject to valid, existing rights: where new ROWs associated with valid existing rights are required, co-locate new ROWs within existing ROWs or where it best minimizes sage-grouse impacts. Use existing roads, or realignments as described above, to access valid existing rights that are not yet developed. If valid existing rights cannot be accessed via existing roads, then build any new road constructed to the absolute minimum standard necessary, and add the surface disturbance to the total disturbance in the priority area. If that disturbance exceeds 3% for that area, then make additional effective mitigation necessary to offset the resulting loss of sage-grouse.

- Evaluate and take advantage of opportunities to remove, bury, or modify existing power lines within priority sage-grouse habitat areas. Sage-grouse may avoid powerlines because of increased predation risk (Steenhof et al. 1993, Lammers and Collopy 2007). Powerlines effectively influence (direct physical area plus estimated area of effect due to predator movements) at least 39% of the sage-grouse range (Knick et al. 2011). Deaths resulting from collisions with powerlines were an important source of mortality for sage-grouse in southeastern Idaho (Beck et al. 2006, 75 FR 13910)
- Where existing leases or ROWs have had some level of development (road, fence, well, etc.) and are no longer in use, reclaim the site by removing these features and restoring the habitat.

  *Planning Direction Note:* While engaged in this sage-grouse EIS planning process, relocate existing designated ROW corridors crossing priority sage-grouse habitat void of any authorized ROWs, outside of the priority habitat area. If relocation is not possible, undesignate that entire corridor during the planning process.

<u>General sage-grouse habitat areas</u>

- Make general sage-grouse habitat areas “avoidance areas” for new ROWs.
- Where new ROWs are necessary, co-locate new ROWs within existing ROWs where possible.

***Land Tenure Adjustment***

<u>Priority sage-grouse habitat areas</u>

- Retain public ownership of priority sage-grouse habitat. Consider exceptions where:
  - There is mixed ownership, and land exchanges would allow for additional or more contiguous federal ownership patterns within the priority sage-grouse habitat area.
  - Under priority sage-grouse habitat areas with minority federal ownership, include an additional, effective mitigation agreement for any disposal of federal land. As a final preservation measure consideration should be given to pursuing a permanent conservation easement.

- Where suitable conservation actions cannot be achieved, seek to acquire state and private lands with intact subsurface mineral estate by donation, purchase or exchange in order to best conserve, enhance or restore sage-grouse habitat.

***Proposed Land Withdrawals***

Priority sage-grouse habitat areas

- Propose lands within priority sage-grouse habitat areas for mineral withdrawal.
- Do not approve withdrawal proposals not associated with mineral activity unless the land management is consistent with sage-grouse conservation measures. (For example; in a proposed withdrawal for a military training range buffer area, manage the buffer area with sage-grouse conservation measures.)

## Range Management

Potential impacts of herbivory on sage-grouse and their habitat include:

1) Long-term effects of historic overgrazing on sagebrush habitat;

2) Sage-grouse habitat changes due to herbivory;

3) Direct effects of herbivores on sage-grouse, such as trampling of nests and eggs;

4) Altered sage-grouse behavior due to presence of herbivores; and

5) Impacts to sage-grouse and sage-grouse behavior from structures associated with grazing management (Beck and Mitchell 2000).

Managing livestock grazing to maintain residual cover of herbaceous vegetation so as to reduce predation during nesting may be the most beneficial for sage-grouse populations (Beck and Mitchell 2000, Aldridge and Brigham 2003). Other management objectives that control livestock movements and grazing intensities can be achieved broadly through rotational grazing patterns or locally through water and salt placements (Beck and Mitchell 2000). Treatments used to manipulate vegetation ultimately may have far greater effect on sage-grouse through long-term habitat changes rather than direct impacts of grazing itself (Freilich et al. 2003, Knick et al. 2011). An important objective in managing livestock grazing is to maintain residual cover of herbaceous vegetation to reduce predation during nesting (Beck and Mitchell 2000) and to maintain the integrity of riparian vegetation and other wetlands (Crawford et al. 2004). Proper livestock management (timing, location, and intensity) can assist in meeting sage-grouse habitat objectives and reduce fuels (Briske et al. 2011).

- Within priority sage-grouse habitat, incorporate sage-grouse habitat objectives and management considerations into all BLM grazing allotments through AMPs or permit renewals.

- Work cooperatively on integrated ranch planning within sage-grouse habitat so operations with deeded/BLM allotments can be planned as single units.
- Prioritize completion of land health assessments and processing grazing permits within priority sage-grouse habitat areas. Focus this process on allotments that have the best opportunities for conserving, enhancing or restoring habitat for sage-grouse. Utilize Ecological Site Descriptions (ESDs) to conduct land health assessments to determine if standards of range-land health are being met.
- Conduct land health assessments that include (at a minimum) indicators and measurements of structure/condition/composition of vegetation specific to achieving sage-grouse habitat objectives (Doherty et al. 2011). If local/state seasonal habitat objectives are not available, use sage-grouse habitat recommendations from Connelly et al. 2000b and Hagen et al. 2007.

***Implementing Management Actions after Land Health and Habitat Evaluations***

- Develop specific objectives to conserve, enhance or restore priority sage-grouse habitat based on ESDs and assessments (including within wetlands and riparian areas). If an effective grazing system that meets sage-grouse habitat requirements is not already in place, analyze at least one alternative that conserves, restores or enhances sage-grouse habitat in the NEPA document prepared for the permit renewal (Doherty et al. 2011b, Williams et al. 2011).
- Manage for vegetation composition and structure consistent with ecological site potential and within the reference state to achieve sage-grouse seasonal habitat objectives.
- Implement management actions (grazing decisions, AMP/Conservation Plan development, or other agreements) to modify grazing management to meet seasonal sage-grouse habitat requirements (Connelly et al. 2011c). Consider singly, or in combination, changes in:

    1) Season or timing of use;

    2) Numbers of livestock (includes temporary non-use or livestock removal);

    3) Distribution of livestock use;

    4) Intensity of use; and

    5) Type of livestock (e.g., cattle, sheep, horses, llamas, alpacas and goats) (Briske et al. 2011).
- During drought periods, prioritize evaluating effects of the drought in priority sage-grouse habitat areas relative to their needs for food and cover. Since there is a lag in vegetation recovery following drought (Thurow and Taylor 1999, Cagney et al. 2010), ensure that post-drought management allows for vegetation recovery that meets sage-grouse needs in priority sage-grouse habitat areas.

***Riparian Areas and Wet Meadows***

- Manage riparian areas and wet meadows for proper functioning condition within priority sage-grouse habitats.
    - Within priority and general sage-grouse habitats, manage wet meadows to maintain a component of perennial forbs with diverse species richness relative to site potential (e.g., reference state) to facilitate brood rearing. Also conserve or enhance these wet meadow complexes to maintain or increase amount of edge and cover within that edge to minimize elevated mortality during the late brood rearing period (Hagen et al. 2007, Kolada et al. 2009, Atamian et al. 2010).
- Where riparian areas and wet meadows meet proper functioning condition, strive to attain reference state vegetation relative to the ecological site description.
    - For example: Within priority sage-grouse habitat, reduce hot season grazing on riparian and meadow complexes to promote recovery or maintenance of appropriate vegetation and water quality. Utilize fencing/herding techniques or seasonal use or livestock distribution changes to reduce pressure on riparian or wet meadow vegetation used by sage-grouse in the hot season (summer) (Aldridge and Brigham 2002, Crawford et al. 2004, Hagen et al. 2007).
- Authorize new water development for diversion from spring or seep source only when priority sage-grouse habitat would benefit from the development. This includes developing new water sources for livestock as part of an AMP/conservation plan to improve sage-grouse habitat.
- Analyze springs, seeps and associated pipelines to determine if modifications are necessary to maintain the continuity of the predevelopment riparian area within priority sage-grouse habitats. Make modifications where necessary, considering impacts to other water uses when such considerations are neutral or beneficial to sage-grouse.

***Treatments to Increase Forage for Livestock/Wild Ungulates***

<u>Priority sage-grouse habitat areas</u>

- Only allow treatments that conserve, enhance or restore sage-grouse habitat (this includes treatments that benefit livestock as part of an AMP/Conservation Plan to improve sage-grouse habitat.[iv]
- Evaluate the role of existing seedings that are currently composed of primarily introduced perennial grasses in and adjacent to priority sage-grouse habitats to determine if they should be restored to sagebrush or habitat of higher quality for sage-grouse. If these seedings are part of an AMP/

[iv] Conserve or enhance means to allow no degradation and can mean that the improvement or livestock supplement is part of a grazing/AMP/Conservation Plan that facilitates meeting sage-grouse habitat objectives within a pasture or allotment.

Conservation Plan or if they provide value in conserving or enhancing the rest of the priority habitats, then no restoration would be necessary. Assess the compatibility of these seedings for sage-grouse habitat or as a component of a grazing system during the land health assessments (Davies et al. 2011).

- For example: Some introduced grass seedings are an integral part of a livestock management plan and reduce grazing pressure in important sagebrush habitats or serve as a strategic fuels management area.

***Structural Range Improvements and Livestock Management Tools***

Priority sage-grouse habitat areas

- Design any new structural range improvements and location of supplements (salt or protein blocks) to conserve, enhance, or restore sage-grouse habitat through an improved grazing management system relative to sage-grouse objectives. Structural range improvements, in this context, include but are not limited to: cattleguards, fences, exclosures, corrals or other livestock handling structures; pipelines, troughs, storage tanks (including moveable tanks used in livestock water hauling), windmills, ponds/reservoirs, solar panels and spring developments. Potential for invasive species establishment or increase following construction must be considered in the project planning process and monitored and treated post-construction.
- When developing or modifying water developments, use best management practices (BMPs, see Appendix C) to mitigate potential impacts from West Nile virus (Clark et al. 2006, Doherty 2007, Walker et al. 2007b, Walker and Naugle 2011).
- Evaluate existing structural range improvements and location of supplements (salt or protein blocks) to make sure they conserve, enhance or restore sage-grouse habitat.
    - To reduce outright sage-grouse strikes and mortality, remove, modify or mark fences in high risk areas within priority sage-grouse habitat based on proximity to lek, lek size, and topography (Christiansen 2009, Stevens 2011).
    - Monitor for, and treat invasive species associated with existing range improvements (Gelbard and Belnap 2003 and Bergquist et al. 2007).

***Retirement of Grazing Privileges***

- Maintain retirement of grazing privileges as an option in priority sage-grouse areas when base property is transferred or the current permittee is willing to retire grazing on all or part of an allotment. Analyze the adverse impacts of no livestock use on wildfire and invasive species threats (Crawford et al. 2004) in evaluating retirement proposals.

    *Planning direction Note:* Each planning effort will identify the specific allotment(s) where permanent retirement of grazing privileges is potentially beneficial.

## Wild Horse and Burro Management

Wild horses and burros have the potential to impact habitats used by sage-grouse by reducing grass, shrub, and forb cover and increasing unpalatable forbs and exotic plants including cheatgrass (Beever and Aldridge 2011). Effects of wild equids on habitats may be especially pronounced during periods of drought or vegetation stress. Wild equids have different grazing patterns than domestic livestock, thus increasing the magnitude of grazing across the entire landscape (Beever and Aldridge 2011).

***Ongoing Authorizations/Activities***

- Manage wild horse and burro population levels within established Appropriate Management Levels (AML).
- Prioritize gathers in priority sage-grouse habitat, unless removals are necessary in other areas to prevent catastrophic environmental issues, including herd health impacts.

***Proposed Authorization/Activities***

- Within priority sage-grouse habitat, develop or amend herd management area plans (HMAPs) to incorporate sage-grouse habitat objectives and management considerations for all BLM herd management areas (HMAs).
    - For all HMAs within priority sage-grouse habitat, prioritize the evaluation of all AMLs based on indicators that address structure/condition/composition of vegetation and measurements specific to achieving sage-grouse habitat objectives.
- Coordinate with other resources (Range, Wildlife, and Riparian) to conduct land health assessments to determine existing structure/condition/composition of vegetation within all BLM HMAs.
- When conducting NEPA analysis for wild horse and burro management activities, water developments or other rangeland improvements for wild horses in priority sage-grouse habitat, address the direct and indirect effects to sage-grouse populations and habitat. Implement any water developments or rangeland improvements using the criteria identified for domestic livestock identified above in priority habitats.

## Minerals

The primary potential risks to sage-grouse from energy and mineral development are:

1) Direct disturbance, displacement, or mortality of grouse;
2) Direct loss of habitat, or loss of effective habitat through fragmentation and reduced habitat patch size and quality; and
3) Cumulative landscape-level impacts (Bergquist et al. 2007, Walston et al. 2009, Naugle et al. 2011).

There is strong evidence from the literature to support that surface-disturbing energy or mineral development within priority sage-grouse habitats is not consistent with a goal to maintain or increase populations or distribution. None of the published science reports a positive influence of development on sage-grouse populations or habitats. Breeding populations are severely reduced at well pad densities commonly permitted (Holloran 2005, Walker et al. 2007a). Magnitude of losses varies from one field to another, but findings suggest that impacts are universally negative and typically severe.

Mechanisms that lead to avoidance and decreased fitness have not been empirically tested but rather suggested from multiple correlative and observational studies. For example, abandonment may increase if leks are repeatedly disturbed by raptors perching on power lines near leks (Ellis 1984), by vehicle traffic on nearby roads (Lyon and Anderson 2003), or by noise and human activity associated with energy development during the breeding season (Remington and Braun 1991, Holloran 2005, Kaiser 2006, Blickley and Patricelli *In review*). One recently completed research study in Wyoming (Blickley et al. *In press*), experimentally validates noise from natural gas drilling and roads resulted in a decline of 29% and 73% respectively in male peak attendance at leks relative to paired controls; declines were immediate and sustained throughout the experiment with low statistical support for a cumulative effect of noise over time. Collisions with nearby power lines and vehicles and increased predation by raptors may also increase mortality of birds at leks (Connelly et al. 2000). Alternatively, roads and power lines may indirectly affect lek persistence by altering productivity of local populations or survival at other times of the year. For example, sage-grouse mortality associated with power lines and roads occurs year-round (Beck et al. 2006, Aldridge and Boyce 2007), and ponds created by coal bed natural gas development may increase the risk of West Nile virus mortality in late summer (Walker et al. 2004, Zou et al. 2006, Walker et al. 2007b). Loss and degradation of sagebrush habitat can also reduce carrying capacity of local breeding populations (Swenson et al. 1987, Braun 1998, Connelly et al. 2000, 2000b, Crawford et al. 2004). Birds may avoid otherwise suitable habitat as the density of roads, power lines, or energy development increases (Lyon and Anderson 2003, Holloran 2005, Kaiser 2006, Doherty et al. 2008, Carpenter et al. 2010).

Negative responses of sage-grouse to energy development were consistent among studies regardless of whether they examined lek dynamics or demographic rates of specific cohorts within populations. Sage-grouse populations decline when birds avoid infrastructure in one or more seasons (Doherty et al. 2008, Carpenter et al. 2010) and when cumulative impacts of development negatively affect reproduction or survival (Aldridge and Boyce 2007), or both demographic rates (Lyon and Anderson 2003, Holloran 2005, Holloran et al. 2010). Avoidance of energy development at the scale of entire oil and gas fields should not be considered a simple shift in habitat use but rather a reduction in the distribution of sage-grouse (Walker et al. 2007). Avoidance is likely to result in true population declines if density dependence, competition, or displacement of birds into poorer-quality adjacent habitats lowers survival or reproduction (Holloran and Anderson 2005, Aldridge and Boyce 2007, Holloran et al. 2010). High site fidelity in sage-grouse also suggests that unfamiliarity with new habitats may also reduce survival, as in other grouse species (Yoder et al. 2004). Sage-grouse in the Powder River Basin were 1.3 times more likely to occupy winter habitats that had not been developed for energy (12 wells per 4 square kilometers or 12 wells per 1.5 square miles), and avoidance of developed areas was most pronounced when it occurred in high-quality winter habitat with abundant sagebrush (Doherty et al. 2008). In a similar study in Alberta, avoidance of otherwise suitable

wintering habitats within a 1.9-kilometer (1.2 mile) radius of energy development resulted in substantial loss of functional habitat surrounding wells (Carpenter et al. 2010).

Long-term studies in the Pinedale Anticline Project Area in southwest Wyoming present the most complete picture of cumulative impacts and provide a mechanistic explanation for declines in populations. Early in development, nest sites were farther from disturbed than undisturbed leks, the rate of nest initiation from disturbed leks was 24 percent lower than for birds breeding on undisturbed leks, and 26 percent fewer females from disturbed leks initiated nests in consecutive years (Lyon and Anderson 2003). As development progressed, adult females remained in traditional nesting areas regardless of increasing levels of development, but yearlings that had not yet imprinted on habitats inside the gas field avoided development by nesting farther from roads (Holloran 2005). The most recent study confirmed that yearling females avoided infrastructure when selecting nest sites, and yearling males avoided leks inside of development and were displaced to the periphery of the gas field (Holloran et al. 2010). Recruitment of males to leks also declined as distance within the external limit of development increased, indicating a high likelihood of lek loss near the center of developed oil and gas fields (Kaiser 2006). The most important finding from studies in Pinedale was that sage-grouse declines are explained in part by lower annual survival of female sage-grouse and that the impact on survival resulted in a population-level decline (Holloran 2005). High site fidelity but low survival of adult sage-grouse combined with lek avoidance by younger birds (Holloran et al. 2010) resulted in a time lag of 3–4 years between the onset of development activities and lek loss (Holloran 2005). The time lag observed by Holloran (2005) in the Anticline matched that for leks that became inactive 3–4 years after natural gas development in the Powder River Basin (Walker et al. 2007a). Analysis of seven oil and gas fields across Wyoming showed time lags of 2–10 years between activities associated with energy development and its measurable effects on sage-grouse populations (Harju et al. 2010).

Impacts as measured by the number of males attending leks are most severe near the lek, remain discernible out to >4 miles (Holloran 2005, Walker et al. 2007, Tack 2009, Johnson et al. 2011), and often result in lek extirpations (Holloran 2005, Walker et al. 2007). Negative effects of well surface occupancy were apparent out to 3.1 miles, the largest radius investigated, in 2 of 7 study areas in Wyoming (Harju et al. 2010). Curvilinear relationships show that lek counts decreased with distance to the nearest active drilling rig, producing well, or main haul road and that development within 3 to 4 miles of leks decrease counts of displaying males (Holloran 2005). All well-supported models in Walker et al. (2007) indicate a strong negative effect, estimated as proportion of development within either 0.5 miles or 2 miles, on lek persistence. A model with development at 4 miles had less support, but the regression coefficient indicated that negative impacts within 4 miles were still apparent. Two additional studies reported negative impacts apparent out to 8 miles on large lek occurrence (>25 males; Tack 2009) and out to 11.7 miles on lek trends (Johnson et al. 2011), the largest scales evaluated.

Past BLM conservation measures have focused on 0.25 mile No Surface Occupancy (NSO) buffers around leks, and timing stipulations applied to 0.6 mile buffers around leks to protect both breeding and nesting activities. Given impacts of large scale disturbances described above that occur across seasons and impact all demographic rates, applying NSO or other buffers around leks at any distance is unlikely to be effective. Even if this approach were to be continued, it should be noted that protecting even 75 to >80% of nesting

hens would require a 4-mile radius buffer (Table 1). Even a 4-mile NSO buffer would not be large enough to offset all the impacts reviewed above. A 4-mile NSO likely would not be practical given most leases are not large enough to accommodate a buffer of this size, and lek spacing within priority habitats is such that lek-based buffers may overlap and preclude all development.

We do not include timing restrictions on construction and drilling during the breeding season because they do not prevent impacts of infrastructure (e.g., avoidance, mortality) at other times of the year, during the production phase, or in other seasonal habitats that are crucial for population persistence (e.g., winter; Walker et al. 2007). Seasonal timing restrictions may be effective during the exploration phase. Instead, we recommend excluding mineral development and other large scale disturbances from priority habitats where possible, and where it is not limit disturbance as much as possible.

For these reasons, we believe the conservation strategy most likely to meet the objective of maintaining or increasing sage-grouse distribution and abundance is to exclude energy development and other large scale disturbances from priority habitats, and where valid existing rights exist, minimize those impacts by keeping disturbances to 1 per section with direct surface disturbance impacts held to 3% of the area or less.

**Table 1. Distance Of Greater Sage-Grouse Nests From Lek Of Capture[1]**

| % Nests within 2-mi. radius | % Nests Within 4-mi. radius | Location | Study |
|---|---|---|---|
| 46.4 (n = 13/28) | 85.7 (n = 24/28) | North Park, CO | Peterson (1980) |
| 59.5 (n = 182/306) | 85 (n = 260/306) | Idaho | Autenrieth (1981) |
| 71.8 (n = 51/71) | 90.1 (n = 64/71) | North Park, CO | Giesen (1995) |
| 49.5 (n = 192/388) | 77.1 (n = 299/388) | Moffat County, CO | Thompson et al. 2005, Thompson 2006 |
| 48.4 (n = 15/31) | 96.8 (n = 30/31) | Eagle and South Routt Counties, CO | Graham and McConnell 2004, Graham and Jones 2005 |
| 44.7 (n = 152/340) | 74.4 (n = 243/340) | Wyoming | Holloran and Anderson (2005) |
| 35.5 (n = 86/238) | 61 (n = 145/238) @ 3 miles (data unavailable at this time for 4 miles) | Montana | Moynahan and Lindberg (2006) |
| 35.5 (n = 27/76) | 76.3 (n = 58/76) | Montana | Tack (2009) |
| 50 (n = 495) | >80 (n = 495) | Oregon | Hagen (2011) |

[1]Data obtained from Colorado Greater Sage-grouse Conservation Plan and additional recent studies/plans.

## Fluid Minerals

### *Unleased Federal Fluid Mineral Estate*

*Alternative A*

- Close priority sage-grouse habitat areas to fluid mineral leasing. Upon expiration or termination of existing leases, do not accept nominations/expressions of interest for parcels within priority areas.
- Allow geophysical exploration within priority sage-grouse habitat areas to obtain exploratory information for areas outside of and adjacent to priority sage-grouse habitat areas. Allow geophysical operations only by helicopter-portable drilling methods and in accordance with seasonal timing restrictions and/or other restrictions that may apply.

*Alternative B*

- Close priority sage-grouse habitat areas to fluid mineral leasing. Consider an exception:
    - When there is an opportunity for the BLM to influence conservation measures where surface and/or mineral ownership is not entirely federally owned (i.e., checkerboard ownership). In this case, a plan amendment may be developed that opens the priority area for new leasing. The plan must demonstrate long-term population increases in the priority area through mitigation (prior to issuing the lease) including lease stipulations, off-site mitigation, etc., and avoid short-term losses that put the sage-grouse population at risk from stochastic events leading to extirpation.
- Allow geophysical exploration within priority sage-grouse habitat areas to obtain exploratory information for areas outside of and adjacent to priority sage-grouse habitat areas. Only allow geophysical operations by helicopter-portable drilling methods and in accordance with seasonal timing restrictions and/or other restrictions that may apply.

### *Leased Federal Fluid Mineral Estate*

Priority sage-grouse habitat areas (with varying levels of exploration & development)

Apply the following conservation measures through Resource Management Plan (RMP) implementation decisions (e.g., approval of an Application for Permit to Drill, Sundry Notice, etc.) and upon completion of the environmental record of review (43 CFR 3162.5), including appropriate documentation of compliance with NEPA. In this process evaluate, among other things:

1. Whether the conservation measure is "reasonable" (43 CFR 3101.1-2) with the valid existing rights; and
2. Whether the action is in conformance with the approved RMP.[v]

[v] Plan conformance means, "a resource management action shall be specifically provided for in the plan, or if not specifically mentioned, shall be clearly consistent with the terms, conditions, and decisions of the approved plan or amendment." 43 CFR 1601.0-5(b).

Provide the following conservation measures as terms and conditions of the approved RMP:

- Do not allow new surface occupancy on federal leases within priority habitats, this includes winter concentration areas (Doherty et al. 2008, Carpenter et al. 2010) during any time of the year. Consider an exception:
    - If the lease is entirely within priority habitats, apply a 4-mile NSO around the lek, and limit permitted disturbances to 1 per section with no more than 3% surface disturbance in that section.
    - If the entire lease is within the 4-mile lek perimeter, limit permitted disturbances to 1 per section with no more than 3% surface disturbance in that section. Require any development to be placed at the most distal part of the lease from the lek, or, depending on topography and other habitat aspects, in an area that is less demonstrably harmful to sage-grouse.
- Apply a seasonal restriction on exploratory drilling that prohibits surface-disturbing activities during the nesting and early brood-rearing season in all priority sage-grouse habitat during this period.
- Do not use Categorical Exclusions (CXs) including under the Energy Policy Act of 2005, Section 390 in priority sage-grouse habitats due to resource conflicts.
- Complete Master Development Plans in lieu of Application for Permit to Drill (APD)-by-APD processing for all but wildcat wells.
- When permitting APDs on existing leases that are not yet developed, the proposed surface disturbance cannot exceed 3% for that area. Consider an exception if:
    - Additional, effective mitigation is demonstrated to offset the resulting loss of sage-grouse (see Objectives).
        - When necessary, conduct additional, effective mitigation in 1) priority sage-grouse habitat areas or – less preferably – 2) general sage-grouse habitat (dependent upon the area-specific ability to increase sage-grouse populations).
        - Conduct additional, effective mitigation first within the same population area where the impact is realized, and if not possible then conduct mitigation within the same Management Zone as the impact, per 2006 WAFWA Strategy – pg 2-17.
- Require unitization when deemed necessary for proper development and operation of an area (with strong oversight and monitoring) to minimize adverse impacts to sage-grouse according to the Federal Lease Form, 3100-11, Sections 4 and 6.
- Identify areas where acquisitions (including subsurface mineral rights) or conservation easements, would benefit sage-grouse habitat.
- Require a full reclamation bond specific to the site. Insure bonds are sufficient for costs relative to reclamation (Connelly et al. 2000, Hagen et al. 2007) that would result in full restoration. Base the reclamation costs on the assumption that contractors for the BLM will perform the work.

- Make applicable Best Management Practices (BMPs, see Appendix D) mandatory as Conditions of Approval within priority sage-grouse habitat.

## Solid Minerals

### *Coal*

Priority sage-grouse habitat areas

- *Surface mines*: Find unsuitable all surface mining of coal under the criteria set forth in 43 CFR 3461.5.
- *Sub-surface mines:* Grant no new mining leases unless all surface disturbances (appurtenant facilities) are placed outside of the priority sage-grouse habitat area.
- For coal mining operations on existing leases:
    - *Sub-surface mining:* in priority sage-grouse habitat areas, place any new appurtenant facilities outside of priority areas. Where new appurtenant facilities associated with the existing lease cannot be located outside the priority sage-grouse habitat area, co-locate new facilities within existing disturbed areas. If this is not possible, then build any new appurtenant facilities to the absolute minimum standard necessary.

General sage-grouse habitat

- Apply minimization of surface-disturbing or disrupting activities (including operations and maintenance) where needed to reduce the impacts of human activities on important seasonal sage-grouse habitats. Apply these measures during activity level planning.
    - Use additional, effective mitigation to offset impacts as appropriate (determined by local options/needs).

### *Locatable Minerals*

Priority sage-grouse habitat areas

- Propose withdrawal from mineral entry based on risk to the sage-grouse and its habitat from conflicting locatable mineral potential and development.
    - Make any existing claims within the withdrawal area subject to validity patent exams or buy out. Include claims that have been subsequently determined to be null and void in the proposed withdrawal.
    - In plans of operations required prior to any proposed surface disturbing activities, include the following:
        - Additional, effective mitigation in perpetuity for conservation (In accordance with existing policy, WO IM 2008-204). Example: purchase private land and mineral rights or severed subsurface mineral rights within the priority area and deed to US Government).

        - Consider seasonal restrictions if deemed effective.
    - Make applicable Best Management Practices (see Appendix E) mandatory as Conditions of Approval within priority sage-grouse habitat.

***Non-energy Leasable Minerals (i.e. sodium, potash)***

Priority sage-grouse habitat areas

- Close priority habitat to non-energy leasable mineral leasing. This includes not permitting any new leases to expand an existing mine.
- For existing non-energy leasable mineral leases, in addition to the solid minerals BMPs (Appendix E), follow the same BMPs applied to Fluid Minerals (Appendix D), when wells are used for solution mining.

***Saleable Mineral Materials***

Priority sage-grouse habitat areas

- Close priority habitat to mineral material sales.
- Restore saleable mineral pits no longer in use to meet sage-grouse habitat conservation objectives.

**Mineral Split Estate**

Priority sage-grouse habitat areas

- Where the federal government owns the mineral estate, and the surface is in non-federal ownership, apply the conservation measures applied on public lands.
- Where the federal government owns the surface, and the mineral estate is in non-federal ownership, apply appropriate Fluid Mineral BMPs (see Appendix D) to surface development.

## Wildfire Suppression, Fuels Management and Fire Rehabilitation

These programs address the threats resulting from wildfires and post-wildfire effects along with a program (fuels management) designed to try to reduce these impacts. Together these programs provide a significant opportunity to influence sagebrush habitats that benefit sage-grouse. Wildfire, particularly in low elevation Wyoming big sagebrush systems, has resulted in significant habitat loss primarily because of subsequent invasion by cheatgrass and other exotic plant species (Miller et al. 2011). The number of fires and total acreage burned has increased throughout the sage-grouse range (Miller et al. 2011). Long-term monitoring following prescribed fire is important because treatments may not increase either yield or nutritional quality of forbs eaten by sage-grouse, and also may decrease abundance of insects that are important for growth of sage-grouse chicks (Beck et al. 2009, Rhodes et al. 2010). Therefore, it is critical

not only to conduct management actions that reduce the long-term loss of sagebrush but also to restore and recover burned areas to habitats that will be used by sage-grouse (Pyke 2011). Prescribed fire is a tool that can assist in the recovery of sagebrush habitat in some vegetation types (Davies et al. 2011).

**Fuels Management**

Priority sage-grouse habitat areas

- Design and implement fuels treatments with an emphasis on protecting existing sagebrush ecosystems.
    - Do not reduce sagebrush canopy cover to less than 15% (Connelly et al. 2000, Hagen et al. 2007) unless a fuels management objective requires additional reduction in sagebrush cover to meet strategic protection of priority sage-grouse habitat and conserve habitat quality for the species. Closely evaluate the benefits of the fuel break against the additional loss of sagebrush cover in the EA process.
    - Apply appropriate seasonal restrictions for implementing fuels management treatments according to the type of seasonal habitats present in a priority area.
    - Allow no treatments in known winter range unless the treatments are designed to strategically reduce wildfire risk around or in the winter range and will maintain winter range habitat quality.
    - Do not use fire to treat sagebrush in less than 12-inch precipitation zones (e.g., Wyoming big sagebrush or other xeric sagebrush species; Connelly et al. 2000, Hagen et al. 2007, Beck et al. 2009). However, if as a last resort and after all other treatment opportunities have been explored and site specific variables allow, the use of prescribed fire for fuel breaks that would disrupt the fuel continuity across the landscape could be considered, in stands where cheatgrass is a very minor component in the understory (Brown 1982).
    - Monitor and control invasive vegetation post-treatment.
    - Rest treated areas from grazing for two full growing seasons unless vegetation recovery dictates otherwise (WGFD 2011).
    - Require use of native seeds for fuels management treatment based on availability, adaptation (site potential), and probability of success (Richards et al. 1998). Where probability of success or native seed availability is low, non-native seeds may be used as long as they meet sage-grouse habitat objectives (Pyke 2011).
    - Design post fuels management projects to ensure long term persistence of seeded or pre-treatment native plants. This may require temporary or long-term changes in livestock grazing management, wild horse and burro management, travel management, or other activities to achieve and maintain the desired condition of the fuels management project (Eiswerth and Shonkwiler 2006).

- Design fuels management projects in priority sage-grouse habitat to strategically and effectively reduce wildfire threats in the greatest area. This may require fuels treatments implemented in a more linear versus block design (Launchbaugh et al. 2007).

During fuels management project design, consider the utility of using livestock to strategically reduce fine fuels (Diamond et al. 2009), and implement grazing management that will accomplish this objective Davies et al. 2011 and Launchbaugh et al. 2007). Consult with ecologists to minimize impacts to native perennial grasses.

**Fire operations**

- In priority sage-grouse habitat areas, prioritize suppression, immediately after life and property, to conserve the habitat.
- In general sage-grouse habitat, prioritize suppression where wildfires threaten priority sage-grouse habitat.
- Follow Best Management Practices (WO IM 2011-138, see appendix E.)

**Emergency Stabilization and Rehabilitation (ES&R)**

- Prioritize native seed allocation for use in sage-grouse habitat in years when preferred native seed is in short supply. This may require reallocation of native seed from ES&R projects outside of priority sage-grouse habitat to those inside it. Use of native plant seeds for ES&R seedings is required based on availability, adaptation (site potential), and probability of success Richards et al. 1998). Where probability of success or native seed availability is low, non-native seeds may be used as long as they meet sage-grouse habitat conservation objectives (Pyke 2011). Re-establishment of appropriate sagebrush species/subspecies and important understory plants, relative to site potential, shall be the highest priority for rehabilitation efforts.
- Design post ES&R management to ensure long term persistence of seeded or pre-burn native plants. This may require temporary or long-term changes in livestock grazing, wild horse and burro, and travel management, etc., to achieve and maintain the desired condition of ES&R projects to benefit sage-grouse (Eiswerth and Shonkwiler 2006).
- Consider potential changes in climate (Miller at al. 2011) when proposing post-fire seedings using native plants. Consider seed collections from the warmer component within a species' current range for selection of native seed. (Kramer and Havens 2009).

## Habitat Restoration

Habitat restoration cross-cuts all programs. It is an important tool to create and/or maintain a landscape that benefits sage-grouse.

- Prioritize implementation of restoration projects based on environmental variables that improve chances for project success in areas most likely to benefit sage-grouse (Meinke et al. 2009).
    - Prioritize restoration in seasonal habitats that are thought to be limiting sage-grouse distribution and/or abundance.
- Include sage-grouse habitat parameters as defined by Connelly et al. (2000), Hagen et al. (2007) or if available, State Sage-Grouse Conservation plans and appropriate local information in habitat restoration objectives. Make meeting these objectives within priority sage-grouse habitat areas the highest restoration priority.
- Require use of native seeds for restoration based on availability, adaptation (ecological site potential), and probability of success (Richards et al. 1998). Where probability of success or adapted seed availability is low, non-native seeds may be used as long as they support sage-grouse habitat objectives (Pyke 2011).
- Design post restoration management to ensure long term persistence. This could include changes in livestock grazing management, wild horse and burro management and travel management, etc., to achieve and maintain the desired condition of the restoration effort that benefits sage-grouse (Eiswerth and Shonkwiler 2006).
- Consider potential changes in climate (Miller et al. 2011) when proposing restoration seedings when using native plants. Consider collection from the warmer component of the species current range when selecting native species (Kramer and Havens 2009).
- Restore native (or desirable) plants and create landscape patterns which most benefit sage-grouse.
- Make re-establishment of sagebrush cover and desirable understory plants (relative to ecological site potential) the highest priority for restoration efforts.
- In fire prone areas where sagebrush seed is required for sage-grouse habitat restoration, consider establishing seed harvest areas that are managed for seed production (Armstrong 2007) and are a priority for protection from outside disturbances.

## Monitoring of Sage-grouse and Sagebrush Habitats

Given the degree of uncertainty associated with managing natural resources, adaptive management approaches that include rigorous monitoring protocols to support them are essential if conservation goals are to be realized (Walters 1986, Burgman et al. 2005, Stankey et al. 2005, Turner 2005, Lyons et al. 2008). Recent efforts to develop range-wide policy and conservation measures for sage-grouse have emphasized the importance of improving monitoring efforts on both sage-grouse distribution and population trends, and the habitat they depend on (Wambolt et al. 2002, Stiver et al. 2006, Reese and Boyer 2007, Connelly et al. 2011a).

Monitoring is necessary to provide an objective appraisal of the effects of potentially positive conservation actions, and to assess the relative negative effects of management actions to sage-grouse populations and their habitats. Adaptive management planning also reveals substantial gaps in knowledge about key processes and functional relationships (Walters 1987), and therefore helps to identify and prioritize research needs. Ideally, monitoring attributes of sage-grouse habitat and sage-grouse populations will allow linking real or potential habitat changes from natural events and management actions to vital rates of sage-grouse populations (Stiver et al. 2006, Naugle and Walker 2007). Population monitoring led by State wildlife agencies and consistent long-term habitat monitoring among all jurisdictions will enable managers to identify indicators associated with population change across large landscapes and to ameliorate negative effects with appropriate conservation actions (Burgman et al. 2005, Turner 2005).

Sage-grouse select habitats at multiple scales across large landscapes (Connelly et al. 2003, Stiver et al. 2006), which monitoring strategies for sage-grouse habitats must reflect. At landscape levels (RMP level), monitoring should track percent of sagebrush and cover and maturity of stands, preservation of key seasonal habitat components, and the degree of connectivity among populations, seasonal habitats and stands. At the project level, a truly effective monitoring strategy will include measures as to how plant communities respond, how that relates to structural and other sage-grouse habitat requirements, and how sage-grouse populations respond demographically. Quantitative data for habitat measurements should be collected that are sensitive to the land use change being proposed (Stiver et al 2006). Monitoring must occur over the proper time frames to evaluate temporal variation of important components of sage-grouse habitats (Stiver et al. 2006).

Recognizing the importance of monitoring both sage-grouse habitat and populations, BLM in November 2004, completed the National Sage-Grouse Habitat Conservation Strategy (USDI BLM 2004) to address conservation and management of sage-grouse. The overarching goal was to "provide a consistent and scientifically based approach for collection and use of monitoring data for sagebrush habitats, sage-grouse and other components of the sagebrush community." Four action items were identified to accomplish this goal: 1) Develop, cooperatively with our partners, appropriate monitoring strategies and protocols at the appropriate scale for sage-grouse habitat in conjunction with the development of the range-wide conservation action plan; 2) Develop, cooperatively with our partners, a sage-grouse habitat assessment methodology in conjunction with development of the range-wide conservation action plan; 3) Incorporate the sage-grouse habitat assessment framework into the land health assessment process for evaluating indicators of healthy rangelands; and 4) In conjunction with the development of the range-wide conservation action plan, issue guidance for collecting fine-scale monitoring and assessment information and incorporating requirements into implementation projects and plans.

To date, BLM has completed portions of the above action items. In August 2010, the Sage-Grouse Habitat Assessment Framework: Multi-scale Habitat Assessment Tool was completed (Stiver et al. 2010). The assessment framework provides policy makers, resource managers, and natural resource specialists a comprehensive framework for landscape conservation in sagebrush ecosystems with an emphasis on sage-grouse. Implementation policy directing consistent use of the assessment still needs to be completed by BLM in addition to other guidance identified in the strategy.

BLM has recently completed the agency's Assessment, Inventory, and Monitoring (AIM) Strategy (Toevs 2011). The AIM strategy identifies "core indicators" for reporting landscape level attributes. The AIM strategy has resulted in BLM adopting the Natural Resource Conservation Service's National Resource Inventory (NRI) methodology as part of BLM's Landscape Monitoring Project. The NRI protocols provide BLM a statistical framework for evaluating management actions, and programs and policies at a landscape or regional level. Initial NRI data collection occurred on all lands managed by BLM during the summer of 2011. During the summer of 2012 additional NRI monitoring sites are being incorporated to evaluate sagebrush habitats that contain approximately two-thirds of the sage-grouse populations west wide. At this time, the remaining sage-grouse populations have not been identified for long-term habitat monitoring due to funding short falls. In addition to prioritizing funding to fully achieve this objective, habitat monitoring protocols at a fine scale to evaluate impacts at a project level remain to be developed.

Estimates of sage-grouse population size are not available for any population, rather trends in population size are estimated through a lek count index. Exact estimates of sage grouse abundance, while desirable, are probably less important than trends and particularly how sage grouse respond to management actions.

Counts of males attending leks in the spring have been used by wildlife agencies as the primary index to population trends since Patterson suggested that this method might be useful in 1952 (Patterson 1952). Use of convenience sampling to monitor bird populations has been criticized (Ellingson and Lukacs 2003), and lek counts in particular have been challenged as inconsistently conducted, inherently biased and without any known relationship to population size (Beck and Braun 1980, Walsh et al. 2004, Sedinger 2007). Despite limitations of the method, lek counts remain the best available information on population trends over time, and pragmatic strategies to improve population estimation remain elusive (Reese and Bowyer 2007).

It is beyond the scope of this report to develop methodology to better estimate sage-grouse distribution and abundance, but rather to emphasize that WAFWA should convene a technical group for this purpose, and that this group should consider ways to:

1. Standardize, at least within management zones, lek count methodology.
2. Develop and implement methodology to estimate the number of leks in an unbiased manner (Walsh et al. 2004, Sedinger 2007), and determine the location of new or previously unknown leks (particularly important since priority habitat designations are based in large part on locations of leks).
3. Develop and implement methodology to estimate the proportion of males detected while attending leks, and explore degree and nature of variability.
4. Develop and explore methodology to estimate sex ratios within sage-grouse populations.
5. Use Geographic Information System (GIS) mapping technology and analytical tools to track changes in distribution over time, connectivity among populations and population segments, and explore spatially explicit models that link sage-grouse population performance with ecological indicators (Naugle and Walker 2007).

The standardization of monitoring methods and implementation of a defensible monitoring approach is vital if BLM and other conservation partners are to use the resulting information to guide implementation of conservation activities (Naugle and Walker 2007). Monitoring strategies for sage-grouse habitat and populations must be collaborative, as habitat occurs across varied land ownership (52% BLM, 8% USFS, 31% private 5% state, 4% BIA and other Federal; 75 FR 13910), and state fish and wildlife agencies have primary responsibility for population level management of wildlife, including monitoring.

# Acronyms

| | |
|---|---|
| AML | Appropriate Management Level |
| AMP | Allotment Management Plan |
| APD | Application of Permit to Drill |
| BLM | Bureau of Land Management |
| BMPs | Best Management Practices |
| CX | Categorical Exclusion |
| ERMA | Extensive Recreation Management Areas |
| ESA | Endangered Species Act |
| ESD | Ecological Site Description |
| ES&R | Emergency Stabilization and Rehabilitation |
| IM | Instruction Memorandum |
| MOU | Memorandum of Understanding |
| NEPA | National Environmental Policy Act |
| NGO | non-governmental organization |
| NMAC | National Multi-Agency Coordination Group |
| NRCS | Natural Resources Conservation Service |
| NPT | National Policy Team |
| NTT | National Technical Team |
| RIDT | Regional Interdisciplinary Team |
| RMP | Resource Management Plan |
| RMT | Regional Management Team |
| ROW | Right-of-Way |
| SRMA | Special Recreation Management Area |
| SRP | Special Recreation Permit |
| USFWS | U.S. Fish and Wildlife Service |
| USGS | U.S. Geological Survey |
| WAFWA | Western Association of Fish and Wildlife Agencies |

# Glossary

**2008 WAFWA Sage-grouse MOU:** A memorandum of understanding (MOU) among Western Association of Fish and Wildlife Agencies, U.S. Department of Agriculture, Forest Service, U.S. Department of the Interior, Bureau of Land Management, U.S. Department of the Interior, Fish and Wildlife Service, U.S. Department of the Interior, Geological Survey, U.S. Department of Agriculture, Natural Resources Conservation Service, and the U.S. Department of Agriculture, Farm Service Agency. The purpose of the MOU is to provide for cooperation among the participating state and federal land, wildlife management and science agencies in the conservation and management of sage-grouse (*Centrocercus urophasianus*) sagebrush (*Artemisia* spp.) habitats and other sagebrush-dependent wildlife throughout the western United States and Canada and a commitment of all agencies to implement the 2006 WAFWA Conservation Strategy.

**2011 Partnership MOU:** A partnership agreement among the United States Department of Agriculture Natural Resource Conservation Service, Forest Service, United State Department of the Interior, Bureau of Land Management, and Fish and Wildlife Service. 2011. This MOU is for range management – to implement NRCS practices on adjacent federal properties.

**Administrative Access:** A term used to describe access for resource management and administrative purposes such as fire suppression, cadastral surveys, permit compliance, law enforcement and military in the performance of their official duty, or other access needed to administer BLM-managed lands or uses.

**Avoidance Areas:** Areas to be avoided but that may be available for location of ROWs with special stipulations.

**Best Management Practices (BMPs):** A suite of techniques that guide or may be applied to management actions to aide in achieving desired outcomes. BMPs are often developed in conjunction with land use plans, but they are not considered a planning decision unless the plans specify that they are mandatory.

**Casual Use:** Casual use means activities ordinarily resulting in no or negligible disturbance of the public lands, resources, or improvements. For examples for rights of ways see 43 CFR 2801.5. For examples for locatable minerals see 43 CFR 3809.5.

**Conservation Plan:** The recorded decisions of a landowner or operator, cooperating with a conservation district, on how the landowner or operator plans, within practical limits, to use his/her land according to its capability and to treat it according to its needs for maintenance or improvement of the soil, water, animal, plant, and air resources.

**Conserve:** To cause no degradation or loss of sage-grouse habitat. Conserve can also refer to maintaining intact sagebrush steppe by fine tuning livestock use, watching for and treating new invasive species and maintaining existing range improvements that benefit sage-grouse etc.

**Ecological Site:** A distinctive kind of land with specific physical characteristics that differs from other kinds of land in its ability to produce a distinctive kind and amount of vegetation.

**Exploration:** Active drilling and geophysical operations to:

a. Determine the presence of the mineral resource; or
b. Determine the extent of the reservoir.

**Development:** Active drilling and production of wells

**Development Area:** Areas primarily leased with active drilling and wells capable of production in payable quantities.

**Enhance:** The improvement of habitat by increasing missing or modifying unsatisfactory components and/or attributes of the plant community to meet sage-grouse objectives. Examples include modifying livestock grazing systems to improve the quantity and vigor of desirable forbs, improving water flow in riparian areas by modifying existing spring developments to return more water to the riparian area below the development, or marking fences to minimize sage-grouse hits and mortality.

**General Sage-grouse Habitat:** Is occupied (seasonal or year-round) habitat outside of priority habitat. These areas have been identified by state fish and wildlife agencies in coordination with respective BLM offices.

**Integrated Ranch Planning:** A method for ranch planning that takes a holistic look at all elements of the ranching operations, including strategic and tactical planning, rather than approaching planning as several separate enterprises.

**Large Scale Anthropogenic Disturbances:** Features include but are not limited to paved highways, graded gravel roads, transmission lines, substations, wind turbines, oil and gas wells, geothermal wells and associated facilities, pipelines, landfills, agricultural conversion, homes, and mines.

**Late Brood Rearing Area:** Habitat includes mesic sagebrush and mixed shrub communities, wet meadows, and riparian habitats as well as some agricultural lands (e.g. alfalfa fields, etc).

**Lek:**[vi] A traditional courtship display area attended by male sage-grouse in or adjacent to sagebrush dominated habitat. A lek is designated based on observations of two or more male sage-grouse engaged in courtship displays. Sub-dominant males may display on itinerant strutting areas during population peaks. Such areas usually fail to become established leks. Therefore, a site where less than five males are observed strutting should be confirmed active for two years before meeting the definition of a lek (Connelly et al 2000, Connelly et al. 2003, 2004).

> **Lek Complex:** A lek or group of leks within 2.5 km (1.5 mi) of each other between which male sage-grouse may interchange from one day to the next. Fidelity to leks has been well documented.

[vi] Each State may have a slightly different definition of lek, active lek, inactive lek, occupied, and unoccupied leks. Regional planning will use the appropriate definition provided by the State of interest.

Visits to multiple leks are most common among yearlings and less frequent for adult males, suggesting an age-related period of establishment (Connelly et al. 2004).

**Active Lek:** Any lek that has been attended by male sage-grouse during the strutting season.

**Inactive Lek:** Any lek where sufficient data suggests that there was no strutting activity throughout a strutting season. Absence of strutting grouse during a single visit is insufficient documentation to establish that a lek is inactive. This designation requires documentation of either: 1) an absence of sage-grouses on the lek during at least 2 ground surveys separated by at least seven days. These surveys must be conducted under ideal conditions (April 1-May 7 (or other appropriate date based on local conditions), no precipitation, light or no wind, half-hour before sunrise to one hour after sunrise) or 2) a ground check of the exact known lek site late in the strutting season (after April 15) that fails to find any sign (tracks, droppings, feathers) of strutting activity. Data collected by aerial surveys should not be used to designate inactive status as the aerial survey may actually disrupt activities.

**Occupied Lek:** A lek that has been active during at least one strutting season within the prior 10 years.

**Unoccupied Lek:** A lek that has either been "destroyed" or "abandoned."

**Destroyed Lek:** A formerly active lek site and surrounding sagebrush habitat that has been destroyed and is no longer suitable for sage-grouse breeding.

**Abandoned Lek:** A lek in otherwise suitable habitat that has not been active during a period of 10 consecutive years. To be designated abandoned, a lek must be "inactive" (see above criteria) in at least four non-consecutive strutting seasons spanning the 10 years. The site of an "abandoned" lek should be surveyed at least once every 10 years to determine whether it has been re-occupied by sage-grouse.

**Master Development Plans:** A set of information common to multiple planned wells, including drilling plans, Surface Use Plans of Operations, and plans for future production.

**Mitigation:** Compensating for resource impacts by replacing or providing substitute resources or habitat.

**Notice-level Mining Activities:** To qualify for a Notice the mining activity must: 1) constitute exploration, 2) not involve bulk sampling of more than 1,000 tons of presumed ore, 3) must not exceed 5 acres of surface disturbance, and 4) must not occur in one of the special category lands listed in 43 CFR 3809.11(c). The Notice is to be filed in the BLM field office with jurisdiction over the land involved. The Notice does not need to be on a particular form but must contain the information required by 43 CFR 3809.301(b).

**Offsite Mitigation:** Compensating for resource impacts by replacing or providing substitute resources or habitat at a different location than the project area.

**Plan of Operations:** A Plan of Operations is required for all mining activity exploration greater than 5 acres or surface disturbance greater than casual use on certain special category lands. Special category lands are described under 43 CFR 3809.11(c) and include such lands as designated Areas of Critical Environmental Concern, lands within the National Wilderness Preservation System, and areas closed to off-road vehicles, among others. In addition, a plan of operations is required for activity greater than casual use on lands patented under the Stock Raising Homestead Act with Federal minerals where the operator does not have the written consent of the surface owner (43 CFR 3814). The Plan of operations needs to be filed in the BLM field office with jurisdiction over the land involved. The Plan of Operations does not need to be on a particular form but must address the information required by 43 CFR 3809.401(b).

**Priority Sage-grouse Habitat:** Areas that have been identified as having the highest conservation value to maintaining sustainable sage-grouse populations. These areas would include breeding, late brood-rearing, and winter concentration areas. These areas have been identified by state fish and wildlife agencies in coordination with respective BLM offices.

**Range Improvement:** The term range improvement means any activity, structure or program on or relating to rangelands which is designed to improve production of forage; change vegetative composition; control patterns of use; provide water; stabilize soil and water conditions; and provide habitat for livestock and wildlife. The term includes, but is not limited to, structures, treatment projects, and use of mechanical means to accomplish the desired results.

**Roads, Primitive Roads and Trails:** Roads, primitive roads or trails that have been specifically designated for motorized use through a public implementation-level National Environmental Policy Act process in accordance with 43 CFR, Part 8340.

**Reclamation:** Rehabilitation of a disturbed area to make it acceptable for designated uses. This normally involves re-contouring, replacement of topsoil, re-vegetation, and other work necessary to ensure eventual restoration of the site.

**Reference State:** The reference state is the state where the functional capacities represented by soil/site stability, hydrologic function, and biotic integrity are performing at an optimum level under the natural disturbance regime. This state usually includes, but is not limited to, what is often referred to as the potential natural plant community.

**Restoration:** Implementation of a set of actions that promotes plant community diversity and structure that allows plant communities to be more resilient to disturbance and invasive species over the long term. The long-term goal is to create functional, high quality habitat that is occupied by sage-grouse. Short-term goal may be to restore the landform, soils and hydrology and increase the percentage of preferred vegetation, seeding of desired species, or treatment of undesired species.

**State:** A state is comprised of an integrated soil and vegetation unit having one or more biological communities that occur on a particular ecological site and that are functionally similar with respect to the three attributes (soil/site stability, hydrologic function, and biotic integrity) under natural disturbance regimes.

**Stochastic:** Randomly determined event, chance event, a condition determined by predictable processes and a random element.

**Surface Disruption:** Resource uses and activities that are likely to alter the behavior of, displace, or cause stress to sage-grouse occurring at a specific location and/or time. Surface disruption includes those actions that alter behavior or cause the displacement of sage-grouse such that reproductive success is negatively affected, or the physiological ability to cope with environmental stress is compromised. Examples of disruptive activities may include noise, vehicle traffic, or other human presence regardless of the associated activity.

**Surface Disturbance:** Suitable habitat is considered disturbed when it is removed and unavailable for immediate sage-grouse use.

a. Long-term removal occurs when habitat is physically removed through activities that replace suitable habitat with long term occupancy of unsuitable habitat such as a road, powerline, well pad or active mine. Long-term removal may also result from any activities that cause soil mixing, soil removal, and exposure of the soil to erosive processes.

b. Short–term removal occurs when vegetation is removed in small areas, but restored to suitable habitat within a few years (< 5) of disturbance, such as a successfully reclaimed pipeline, or successfully reclaimed drill hole or pit.

c. Suitable habitat rendered unusable due to numerous anthropogenic disturbances

d. Anthropogenic surface disturbance are surface disturbances meeting the above definitions which result from human activities.

**Transition:** A shift between two states. Transitions are not reversible by simply altering the intensity or direction of factors that produced the change. Instead, they require new inputs such as revegetation or shrub removal. Practices, such as these, that accelerate succession are often expensive to apply.

**Unitization**: Operation of multiple leases as a single lease under a single operator

**Wildcat Well:** An exploratory oil well drilled in land not known to be an oil field.

**Wildland Fire:** Any non-structure fire that occurs in the vegetation and/or natural fuels. Includes both prescribed fire and wildfire (NWCG Memo #024-2010 April 30, 2010. www.nwcg.gov).

**Winter Concentration Areas:** Sage-grouse winter habitats which are occupied annually by sage-grouse and provide sufficient sagebrush cover and food to support birds throughout the entire winter (especially periods with above average snow cover). Many of these areas support several different breeding

populations of sage-grouse. Sage-grouse typically show high fidelity for these areas, and loss or fragmentation can result in significant population impacts.

# Literature Cited

75 FR 13910. 2010. Endangered and Threatened Wildlife and Plants: 12-month finding for petitions to list the greater sage-grouse as threatened or endangered.

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: Habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–26.

Aldridge, C. L., and R. M. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Canada. Journal of Wildlife Management 66:433-444.

Aldridge, C. L., and R. M. Brigham. 2003. Distribution, abundance, and status of the greater sage-grouse, *Centrocercus urophasianus*, in Canada. Canadian Field-Naturalist 117:25-34.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. Diversity and Distributions 17:983-994.

Armstrong, J. C. 2007. Improving sustainable seed yield in Wyoming big sagebrush. Provo, UT: Brigham Young University. 29 p. Thesis.

Atamian, M. T., M. S. Sedinger, J. S. Heaton, and E. J. Blomberg. 2010. Landscape-level assessment of brood rearing habitat for greater sage-grouse in Nevada. Journal of Wildlife Management -74:1533-1543.

Autenrieth, R. E. 1981. Sage grouse management in Idaho. Idaho Department of Fish and Game, Wildlife Bulletin 9, Boise, Idaho, USA.

Beck, J.L., and D. L. Mitchell. 2000. Influences of livestock grazing on sage-grouse habitat. Wildlife Society Bulletin 28:993-1002.

Beck, J.L. K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070-1078.

Beck, J.L., J.W. Connelly, and K.P. Reese. 2009. Recovery of greater sage-grouse habitat features in Wyoming big sagebrush following prescribed fire. Restoration Ecology 17:393-403.

Beck, T.D.I., and C.E. Braun. 1980. The strutting ground count: variation, traditionalism, management needs. Proceedings of the Western Association of Fish and Wildlife Agencies 60:558-566.

Beever, E.A., and C. L. Aldridge. 2011. Influences of free-roaming equids on sagebrush ecosystems, with a focus on greater sage-grouse. Pp. 273-290 in S. T. Knick and J. W. Connelly (editors). Greater sage-

grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press. Berkeley, CA.

Bergquist, E., P. Evangelista, T.J. Stohlgren, and N. Alley. 2007. Invasive species and coal bed methane development in the Powder River Basin, Wyoming. Environmental Monitoring and Assessment 128:381-394.

Blickely, J.L. and G.L. Patricelli. *In press*. Potential acoustical masking of greater sage-grouse display components by chronic industrial noise. Ornithological Monographs.

Blickley, J.L., D. Blackwood, and G.L. Patricelli. *In press.* Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. Conservation Biology.

Braun, C.E. 1998. Sage grouse declines in western North America: What are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139–56.Braun, C. E., T. Britt, and R. O. Wallestad. 1977. Guidelines for maintenance of sage grouse habitats. Wildlife Society Bulletin 5:99-106.

Braun, C.E., T. Britt, and R.O. Wallestad. 1977. Guidelines for maintenance of sage grouse habitats. Wildlife Society Bulletin 5:99-106.

Briske, D.D., J.D. Derner, D.G. Milchunas, and K.W. Tate. 2011. An evidence-based assessment of prescribed grazing practices. Pp. 23-74 in D.D. Briske. Conservation benefits of rangeland resources: assessment, recommendations, and knowledge gaps. USDA National Resources Conservation Service, Washington D.C.

Brown, J.K. 1982. Fuel and fire behavior prediction in big sagebrush. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. Research Paper INT-290. Ogden, UT.

Burgman, M.A., D.B. Lindenmayer, and J. Elith. 2005. Managing landscapes for conservation under uncertainty. Ecology 86:2007-2017.

Cagney, J., E. Bainter, B. Budd, T. Christiansen, V. Herren, M. Holloran, B. Rashford, M. Smith and J. Williams. 2010. Grazing Influence, Objective Development, and Management in Wyoming's Greater Sage-Grouse Habitat. Cooperative Extension Service Bulletin B-1203, University of Wyoming, Laramie, WY.

Carpenter, J., C. Aldridge, and M.S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management -74:1806-1814.

Christiansen, T. 2009. Fence marking to reduce greater sage-grouse collisions and mortality near Farson, Wyoming – summary of interim results. Wyoming Game and Fish Department unpublished interim report.

Clark, L., J. Hall, R. McLean, M. Dunbar, K. Klenk, R. Bowen, and C.A. Smeraski. 2006. Susceptibility of greater sage-grouse to experimental infection with West Nile virus. Journal of Wildlife Diseases 42:14-42.

Colorado Greater Sage-grouse Steering Committee. 2008. Colorado greater sage-grouse conservation plan. Colorado Division of Wildlife, Denver, Colorado, USA.

Connelly, J.W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000a. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. Wildlife Biology 6:227–32.

Connelly, J.W., C.A. Hagen, and M.A. Schroeder. 2011b. Characteristics and dynamics of greater sage-grouse populations. Pp. 53-67 in S.T. Knick and J.W. Connelly. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitat. Studies in Avian Biology 38. University of California Press, Berkeley, CA.

Connelly, J.W., S.T. Knick, C.E. Braun, W.L. Baker, E.A. Beever, T. Christiansen, K.E. Doherty, E.O. Garton, S.E. Hanser, D.H. Johnson, M. Leu, R.F. Miller, D.E. Naugle, S.J. Oyler-McCance, D.A. Pyke, K.P. Reese, M.A. Schroeder, S.J. Stiver, B.L. Walker, and M.J. Wisdom. 2011. Conservation of Greater Sage-Grouse: a synthesis of current trends and future management. Pp. 549–563 in S. T. Knick and J. W. Connelly (editors). Greater Sage-Grouse: ecology and conservation of a landscape species and habitats. Studies in Avian Biology (vol. 38), University of California Press, Berkeley, CA.

Connelly, J.W., E.T. Rinkes, and C.E. Braun. 2011. Characteristics of greater sage-grouse habitats: a landscape species at micro- and macroscales. Pp. 69-83 in S.T. Knick and J.W. Connelly. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitat. Studies in Avian Biology 38. University of California Press, Berkeley, CA.

Connelly, J.W., K.P. Reese, and M.A. Schroeder. 2003. Monitoring sage-grouse habitats and populations. University of Idaho, College of Natural Resources Experiment Station Bulletin 80 Moscow, Idaho, USA.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Connelly, J.W., S.T. Knick, M.A. Schroeder and S.J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming, USA. (available at http://sagemap.wr.usgs.gov)

Crawford, J.A., R.A. Olson, N.E. West, J.C. Mosley, M.A. Schroeder, T.D. Whitson, R.F. Miller, M.A. Gregg, and C.S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57: 2-19.

Davies, K.W., C.S. Boyde, J.L. Beck, J.D. Bates, T.J. Svejcar, and J.G. Gregg. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush. Biological Conservation 144:2573-2584.

Diamond, J.M., C.A. Call, and N. Devoe. 2009. Effects of targeted cattle grazing on fire behavior of cheatgrass-dominated rangeland in the northern Great Basin, USA. International Journal of Wildland Fire 18:944–950.

Doherty, M.K. 2007. Mosquito populations in the Powder River Basin, Wyoming: a comparison of natural, agricultural, and effluent coal-bed natural gas aquatic habitats. Thesis. Montana State University, Bozeman, Montanna, USA.

Doherty, K.E., D.E. Naugle, and B.L. Walker. 2010. Greater sage-grouse nesting habitat: The importance of managing at multiple scales. Journal of Wildlife Management 74:1544-1553.

Doherty, K.E., D.E. Naugle, B.L. Walker, and J.M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187-195.

Doherty, K.E., D.E. Naugle, H.E. Copeland, A. Pocewicz, and J.M. Kiesecker. 2011a. Energy development and conservation tradeoffs: systematic planning for greater sage-grouse in their eastern range. Pages 505-516 in S.T. Knick and J.W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, California, USA.

Doherty, K.E., D.E. Naugle, and J.S. Evans. 2010. A currency for offsetting energy development impacts: Horse-trading sage-grouse on the open market. PLoS One 5:e10339. Accessed 19 September 2011 http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone0010339

Doherty, K.E., J.L. Beck, and D.E. Naugle. 2011b. Comparing ecological site descriptions to habitat characteristics influencing greater sage-grouse nest site occurrence and success. Rangeland Ecology & Management 64: 344-351.

Eiswerth, M.E. and J.S.Shonkwiler. 2006. Examining post-wildfire reseeding on arid arid rangeland: a multivariate tobit modeling approach. Ecological Modeling 192:286-298.

Ellingson, A.R., and P.M. Lukacs. 2003. Improving methods for regional landbird monitoring: a reply to Hutto and Young. Wildlife Society Bulletin 31:896-902.

Ellis, K.L. 1984. Behavior of lekking sage grouse in response to a perched golden eagle. Western Birds 15:37 –8.

Formann, R T.T., and L.E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207-231.

Freilich, J.E., J.M. Emlen, J.J. Duda, D.C. Freeman, and P.J. Cafaro. 2003. Ecological effects of ranching: a six-point critique. BioScience 53:759-765.

Gelbard, J.L., and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology 17:420-432.

Giesen, K.M. 1995. Upland bird research: evaluation of livestock grazing and residual herbaceous cover on sage grouse nest success. Job final report, project number COW-167-R/Job 18/Wk.Pl. 3. Colorado Division of Wildlife, Colorado, USA.

Graham, L., and B. Jones. 2005. Northern Eagle/Southern Routt Greater Sage-Grouse Summary Report. Colorado Division of Wildlife, Steamboat Springs, Colorado, USA.

Graham, L., and C. McConnell. 2004. Radio-collared greater sage-grouse summary report: Southern Routt and Northern Eagle Counties, Colorado. Colorado Division of Wildlife, Steamboat Springs, Colorado, USA.

Hagen, C. 2011. Greater sage-grouse conservation assessment and strategy for Oregon: a plan to maintain and enhance populations and habitats. Oregon Department of Fish and Wildlife, Portland, Oregon, USA.

Hagen, C.A., J.W. Connelly, and M.A. Schroeder. 2007. A meta-analysis for greater sage-grouse nesting and brood rearing habitats. Wildlife Biology 13 (Supplement 1):42-50.

Harju, S.M., M.R. Dzialak, R.C. Taylor, L.D. Hayden-Wing, and J.B. Winstead. 2010. Thresholds and time lags in effects of energy development on greater sage-grouse populations. Journal of Wildlife Management 74:437–48.

Holloran, M.J. 2005. Greater sage-grouse (Centrocercus urophasianus) population response to natural gas field development in western Wyoming. Dissertation, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming.

Holloran, M.J., R.C. Kaiser, and W.A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Holloran, M.J. and S.H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742-752.

Jackson, S.D. 2000. Overview of Transportation Impacts on Wildlife Movement and Populations. Pp. 7-20 In Messmer, T.A. and B. West, (editors) Wildlife and Highways: Seeking Solutions to an Ecological and Socio-economic Dilemma. The Wildlife Society.

Johnson, C.J., and Martin-Hughes St-Laurent. 2011. Unifying framework for understanding impacts of human developments on wildlife. Pages 27-54 in D.E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

Johnson, D.H., M.J. Holloran, J.W. Connelly, S.E. Hanser, C.L. Amundson, and S.T. Knick. 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations. Pages 407-450 in S.T. Knick and J.W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, California, USA.

Kaiser, R.C. 2006. Recruitment by greater sage-grouse in association with natural gas development in western Wyoming. Thesis, University of Wyoming, Laramie.

Knick, S.T. 2011. Historical development, principal federal legislation, and current management of sagebrush habitats: implications for conservation. Pages 13-31 in S.T. Knick and J.W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, California, USA.

Knick, S.T., and J.W. Connelly. 2011a. Greater sage-grouse and sagebrush: an introduction to the landscape. Pp. 1-9 in S.T. Knick and J.W. Connelly. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitat. Studies in Avian Biology 38. University of California Press, Berkeley, CA.

Knick, S.T., and J.W. Connelly, editors. 2011b. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, CA.

Knick, S.T., D.S. Dobkin, J.T. Rotenberry, M.A. Schroeder, W.M. Vander Haegen, and C. van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634.

Knick, S.T. and S.E. Hanser. 2011. Connecting pattern and process in greater sage-grouse populations and sagebrush landscapes. Pages 383-405 in S.T. Knick and J.W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, California, USA.

Knick S.T., S.E. Hanser, R.F. Miller, D.A. Pyke, M.J. Wisdom, S.P. Finn, E.T. Rinkes and C.J. Henny. 2011. Ecological Influence and Pathways of Land Use in Sagebrush. Pp. 203-251 in S.T. Knick and J.C. Connelly (editors), Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology (vol. 38), University of California Press, Berkley, CA.

Kolada, E.J., M.L. Casazza, and J.S. Sedinger. 2009. Ecological factors influencing nest survival of greater sage-grouse in Mono County, California. Journal of Wildlife Management 73:1341-1347.

Kramer, A.T. and K. Havens. 2009. Plant conservation genetics in a changing world. Trends in Plant Science 14:599-607.

Lammers, W.M., and M.W. Collopy. 2007. Effectiveness of avian predator perch deterrents on electric transmission lines. Journal of Wildlife Management 71:2752-2758.

Launchbaugh, K., B. Brammer, M.L. Brooks, S. Bunting, P. Clark, J. Davison, M. Fleming, R. Kay, M. Pellant, D. A. Pyke, and B. Wylie. 2007. Interactions among livestock grazing, vegetation type, and fire behavior in the Murphy Wildland Fire Complex in Idaho and Nevada, July 2007. U.S. Geological Survey Open-File Report 2008–1214. (http://pubs.usgs.gov/ofr/2008/1214).

Lyon, A.G. and S.H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31: 486-491.

Lyons, J.E., M.C. Runge, H.P. Laskowski, and W.L. Kendall. 2008. Monitoring in the context of structured decision-making and adaptive management.

Meinke, C.W., S.T. Knick, and D.A. Pyke. 2009. A spatial model to prioritize sagebrush landscapes in the intermountain west (U.S.A.) for restoration. Restoration Ecology 17:652-659.

Miller, R.F., S.T. Knick, D.A. Pyke, C.W. Meinke, S.E. Hanser, M.J. Wisdom, and A.L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pp. 145-184 in S.T. Knick and J.W. Connelly (editors). Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, CA.

Moynahan, B.J. and M.S. Lindberg. 2006. Nest locations of greater sage-grouse in relationship to leks in north-central Montana. Unpublished report.

Naugle, D.E. and B.L. Walker. 2007. A collaborative vision for integrated monitoring of greater sage-grouse populations. Pp. 57-62 in K.P. Reese and R.T. Bowyer (editors). Monitoring populations of sage-grouse: proceedings of a symposium at Idaho State University. University of Idaho College of Natural Resources Station Bulletin 88. University of Idaho, Moscow, ID.

Naugle, D.E., K.E. Doherty, B.L. Walker, H.E. Copeland, M.J. Holloran, and J.D. Tack. 2011a. Sage-grouse and cumulative impacts of energy development. Pages 55-70 in D.E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

Naugle, D.E., K.E. Doherty, B.L. Walker, M.J. Holloran, and H.E. Copeland. 2011b. Energy development and greater sage-grouse. Pages. 489-503 in S.T. Knick and J.W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, California, USA.

NWCG Memo #024-2010 April 30, 2010. www.nwcg.gov

Patterson, R.L. 1952. The sage grouse in Wyoming. Sage Books, Denver, Colorado. USA.

Petersen, B.E. 1980. Breeding and nesting ecology of female sage grouse in North Park, Colorado. Thesis. Colorado State University, Fort Collins, USA.

Pyke, D.A. 2011. Restoring and rehabilitating sagebrush habitats. Pp. 531-548 in S. T. Knick and J. W. Connelly (editors). Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press. Berkeley, CA.

Reese, K.P., and R.T. Bowyer (editors). 2007. Monitoring populations of sage-grouse. College of Natural Resources Experiment Station Bulletin 88. University of Idaho, Moscow, ID.

Remington, T.E., and C.E. Braun. 1991. How surface coal mining affects sage grouse, North Park, Colorado. Proceedings, Issues and Technology in the Management of Impacted Western Wildlife. Thorne Ecological Institute 5:128-132.

Rhodes, E.C., J.D. Bates, R.N. Sharp, and K.W. Davies. 2010. Fire effects on cover and dietary resources of sage-grouse habitat. Journal of Wildlife Management 74:755-764.

Richards, R.T., J.C. Chambers, and C. Ross. 1998. Use of native plants on federal lands: policy and practice. Journal of Range Management 51:625-632.

Schroeder, M.A., C.L. Aldridge, A.D. Apa, J.R. Bohne, C.E. Braun, S.D. Bunnell, J.W. Connelly, P.A. Deibert, S.C. Gardner, M.A. Hilliard, G.D. Kobriger, S.M. McAdam, C.W. McCarthy, J.J. McCarthy, D.L. Mitchell, E.V. Rickerson, and S.J. Stiver. 2004. Distribution of sage grouse in North America. Condor 106:363–76.

Sedinger, J.S. 2007. Improving understanding and assessment of greater sage-grouse populations. Pp. 43-56 in K.P. Reese and R.T. Bowyer (editors). Monitoring populations of sage-grouse: proceedings of a

symposium at Idaho State University. University of Idaho College of Natural Resources Station Bulletin 88. University of Idaho, Moscow, ID.

Steenhof, K., M.N. Kochert, and J.A. Roppe. 1993. Nesting by raptors and common ravens on electrical transmission line towers. Journal of Wildlife Management 57:271-281.

Stankey, G.H., R.N. Clark, and B.T. Bormann. 2005. Adaptive management of natural resources: theory, concepts, and management institutions. Gen. Tech. Rep. PNW-GTR-654. Portland, OR: U.S. Department of Agriculture, Forest Service, Northwest Research Station.

Stevens, B.S. 2011. Impacts of fences on greater sage-grouse in Idaho: Collision, mitigation, and spatial ecology. Thesis, University of Idaho, Moscow, Idaho, USA.

Stiver, S.J., A.D. Apa, J.R. Bohne, S.D. Bunnell, P.A. Deibert, S.C. Gardner, M.A. Hilliard, C.W. McCarthy, and M.A. Schroeder. 2006. Greater sage-grouse comprehensive strategy. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming, USA.

Stiver, S.J., E.T. Rinkes, and D.E. Naugle. 2010. Sage-Grouse Habitat Assessment Framework. , Bureau of Land Management Unpublished Report. U.S. Department of Interior, Bureau of Land Management, Idaho State Office, Boise, ID.

Swenson, J.E., C.A. Simmons, and C.D. Eustace. 1987. Decrease of sage grouse *Centrocercus urophasianus* after ploughing of sagebrush steppe. Biological Conservation 41:125–32.

Tack, J.D. 2009. Sage-grouse and the human footprint: implications for conservation of small and declining populations. Thesis. University of Montana, Missoula, Montana, USA.

Thompson, T.R. 2006. Dispersal ecology of greater sage-grouse in northwestern Colorado: evidence from genetic and demographic data: 2006 Annual Progress Report. Colorado Division of Wildlife, Grand Junction, Colorado, USA.

Thompson, T.R., K.P. Reese, and A.D. Apa. 2005. Dispersal ecology of greater sage-grouse in northwestern Colorado: Annual Report 2005. Colorado Division of Wildlife, Grand Junction, Colorado, USA.

Thurow, T.L., and C.A. Taylor, Jr. 1999. Viewpoint: the role of drought in range management. Journal of Range Management 52:413-419.

Toevs, G.R., J.J. Taylor, C.S. Spurrier, W.C. MacKinnon, and M.R. Bobo. 2011. Assessment, Inventory, and Monitoring Strategy: For integrated renewable resource management. U.S. Department of Interior, Bureau of Land Management, National Operations Center, Denver, CO.

Trombulak, S.C., and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18-30.

Turner, M.G. 2005. Landscape ecology in North America: Past, present, and future. Ecology 86:1967-1974.

Turner, M.G., and R.H. Gardner (editors). 1991. Quantitative methods in landscape ecology. Springer-Verlag, New York, NY.

U.S. Department of Interior, Bureau of Land Management. 2004. National Sage-Grouse Habitat Conservation Strategy. WO IM2005-024. Washington D.C. Online:

Walker, B.L., and D.E. Naugle. 2011. West Nile virus ecology in sagebrush habitat and impacts on greater sage-grouse populations. Pages 127-144 in S.T. Knick and J.W. Connelly (editors). Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, California, USA.

Walker, B.L., D.E. Naugle, and K.E. Doherty. 2007a. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644-2654.

Walker, B.L., D.E. Naugle, K.E. Doherty, and T.E. Cornish. 2004. Outbreak of West Nile virus in greater sage-grouse and guidelines for monitoring, handling, and submitting dead birds. Wildlife Society Bulletin 32:1000–6.

Walker, B.L. D.E. Naugle, K.E. Doherty, and T.E. Cornish. 2007b. West Nile Virus and greater sage-grouse: estimating infection rate in a wild bird population. Avian Diseases 51:691-696.

Wambolt, C.L., A.J. Harp, B.L. Welch, N. Shaw, J.W. Connelly, K.P. Reese, C.E. Braun, D.A. Klebenow, E.D.McArthur, J.G. Thompson, L.A.Torell, and J.A. Tanaka. 2002. Conservation of Greater Sage-Grouse on Public Lands in the Western U.S.: Implications of Recovery and Management Policies. PACWPL Policy Paper SG-02-02, Caldwell, ID: Policy Analysis Center for Western Public Lands. 41p.

Walsh, D.P., G.C. White, T.E. Remington, and D.C. Bowden. 2004. Evaluation of the lek count index for greater sage-grouse. Wildlife Society Bulletin 32:56-68.

Walston, L.J., B.L. Cantwell, and J.R. Krummel. 2009. Quantifying spatiotemporal changes in a sagebrush ecosystem in relation to energy development. Ecography 32:943-952.

Walters, C.J. 1986. Adaptive Management of Renewable Resources. MacMillan, New York, New York. 374pp.

Walters, C.J. 1987. Challenges in adaptive management of riparian and coastal ecosystems. Conservation Ecology 1(2):1 [online] http://www.ecologyandsociety.org/vol1/iss2/art1/

Wheatley, M., and C. Johnson. 2009. Factors limiting our understanding of ecological scale. Ecological Complexity 6:150-159.

Williams, M.I., G.B. Paige, T.L. Thurow, A.L. Hild, and K.G. Gerow. 2011. Songbird relationships to shrub-steppe ecological site characteristics. Rangeland Ecology & Management 64:109-118.

Wisdom, M.J., C.W. Meinke, S.T. Knick, and M.A Schroeder. 2011. Factors associated with extirpation of sage-grouse. Page 451-472 in S.T. Knick and J.W. Connelly (editors). Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California press, Berkeley, California, USA.

Wyoming Game and Fish Department. 2011. Wyoming Game and Fish Department Protocols for Treating Sagebrush to Benefit Sage-Grouse. Unpublished report. 5 pp.

Yoder J.M., D.A. Swanson, and E.A. Marschall. 2004. The cost of dispersal: Predation as a function of movement in ruffed grouse. Behavioral Ecology 15:469–76.

Zou, L., S.N. Miller, and E.T. Schmidtmann. 2006. Mosquito larval habitat mapping using remote sensing and GIS: Implications of coalbed methane development and West Nile virus. Journal of Medical Entomology 43:1034–41.

*Code of Federal Regulations Cited*

43 CFR 8340

43 CFR 3809.5

43 CFR 2801.5

43 CFR 3461.5

43 CFR 3101.1-2

43 CFR 3162.5

43 CFR 1601.0-5(b)

*BLM Washington Office Instruction Memorandums*

WO IM 2011–138, Sage-grouse Conservation Related to Wildland Fire and Fuels Management

WO IM 2008-204, Offsite Mitigation
*Other Federal, State and Interagency Memorandums/Reports*

WAFWA Sage-grouse Strategy MOU, 2008

# Appendices

## Appendix A. Life History Requirements of Greater Sage-grouse (excerpted from 75 FR 13910)

Greater sage-grouse depend on a variety of shrub-steppe habitats throughout their life cycle, and are considered obligate users of several species of sagebrush (e.g., *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush), *A. t.* ssp. *vaseyana* (mountain big sagebrush), and *A. t. tridentata* (basin big sagebrush)) (Patterson 1952, Braun et al. 1976, Connelly et al. 2000a, Connelly et al. 2004, Miller et al. 2011). Greater sage-grouse also use other sagebrush species such as *A. arbuscula* (low sagebrush), *A. nova* (black sagebrush), *A. frigida* (fringed sagebrush), and *A. cana* silver sagebrush (Schroeder et al. 1999, Connelly et al. 2004,). Thus, sage-grouse distribution is strongly correlated with the distribution of sagebrush habitats (Schroeder et al. 2004). Sage-grouse exhibit strong site fidelity (loyalty to a particular area even when the area is no longer of value) to seasonal habitats, which includes breeding, nesting, brood rearing, and wintering areas (Connelly et al. 2004, Connelly et al. 2011b). Adult sage-grouse rarely switch between these habitats once they have been selected, limiting their adaptability to changes.

During the spring breeding season, male sage-grouse gather together to perform courtship displays on areas called leks. The proximity, configuration, and abundance of nesting habitat are key factors influencing lek location (Connelly et al., 1981, and Connelly et al., 2000b, cited in Connelly et al., 2011). Leks can be formed opportunistically at any appropriate site within or adjacent to nesting habitat (Connelly et al. 2000a) and, therefore, lek habitat availability is not considered to be a limiting factor for sage-grouse (Schroeder et al. 1999). Nest sites are selected independent of lek locations, but the reverse is not true (Bradbury et al. 1989,Wakkinen et al. 1992). Thus, leks are indicative of nesting habitat.

Females have been documented to travel more than 20 km (12.5 mi) to their nest site after mating (Connelly et al. 2000a), but distances between a nest site and the lek on which breeding occurred is variable (Connelly et al. 2004, Connelly et al. 2011b). Average distance between a female's nest and the lek on which she was first observed ranged from 3.4 km (2.1 mi) to 7.8 km (4.8 mi) in five studies examining 301 nest locations (Schroeder et al. 1999).

Productive nesting areas are typically characterized by sagebrush with an understory of native grasses and forbs, with horizontal and vertical structural diversity that provides an insect prey base, herbaceous forage for pre-laying and nesting hens, and cover for the hen while she is incubating (Gregg 1991Schroeder et al. 1999, Connelly et al. 2000a, Connelly et al. 2004, Connelly et al. 2011b). Sage-grouse also may use other shrub or bunchgrass species for nest sites (Klebenow 1969, Connelly et al. 2000a, Connelly et al. 2004). Shrub canopy and grass cover provide concealment for sage-grouse nests and young, and are critical for reproductive success (Barnett and Crawford 1994, Gregg et al. 1994, DeLong et al.1995, Connelly et al. 2004).

Hens rear their broods in the vicinity of the nest site for the first 2-3 weeks following hatching (within 0.2-5 km (0.1-3.1 mi)), based on two studies in Wyoming (Connelly et al. 2004). Forbs and insects are essential nutritional components for chicks (Klebenow and Gray 1968, Johnson and Boyce 1991, Connelly et al. 2004). Therefore, early brood-rearing habitat must provide adequate cover (sagebrush canopy cover of 10 to 25 percent; Connelly et al. 2000a) adjacent to areas rich in forbs and insects to ensure chick survival during this period (Connelly et al. 2004, Hagen et al. 2007).

All sage-grouse gradually move from sagebrush uplands to more mesic areas (moist areas such as streambeds or wet meadows) during the late brood-rearing period (3 weeks post-hatch) in response to summer desiccation of herbaceous vegetation (Connelly et al. 2000a). Summer use areas can include sagebrush habitats as well as riparian areas, wet meadows and alfalfa fields (Schroeder et al. 1999). These areas provide an abundance of forbs and insects for both hens and chicks (Schroeder et al. 1999, Connelly et al. 2000a).

As vegetation continues to desiccate through the late summer and fall, sage-grouse shift their diet entirely to sagebrush (Schroeder et al. 1999). Sage-grouse depend entirely on sagebrush throughout the winter for both food and cover (Connelly et al. 2011a). Sagebrush stand selection is influenced by snow depth (Patterson 1952, Hupp and Braun 1989), availability of sagebrush above the snow to provide cover (Connelly et al. 2004, and references therein) and, in some areas, topography (e.g., elevation, slope and aspect, Beck 1977, Crawford et al. 2004).

Many populations of sage-grouse migrate between seasonal ranges in response to habitat distribution (Connelly et al. 2004). Migration can occur between winter and breeding and summer areas, between breeding, summer and winter areas, or not at all. Migration distances of up to 161 km (100 mi) have been recorded (Patterson 1952), however, distances vary depending on the locations of seasonal habitats (Schroeder et al. 1999). Migration distances for female sage-grouse generally are less than for males (Connelly et al. 2004), but in one study in Colorado, females travelled further than males (Beck 1977). Almost no information is available regarding the distribution and characteristics of migration corridors for sage-grouse (Connelly et al. 2004). Sage-grouse dispersal (permanent moves to other areas) is poorly understood (Connelly et al. 2004, Knick and Hanser 2011) and appears to be sporadic (Dunn and Braun 1986). Estimating an "average" home range for sage-grouse is difficult due to the large variation in sage-grouse movements both within and among populations. This variation is related to the spatial availability of habitats required for seasonal use and annual recorded home ranges have varied from 4 to 615 square kilometers ($km^2$) (1.5 to 237.5 square miles ($mi^2$)), Connelly et al. *2011b*).

## Literature Cited:

Barnett, J.K., and J. A. Crawford. 1994. Pre-laying nutrition of sage grouse hens in Oregon. Journal of Range Management, 47:114-118.

Beck, T.D.I. 1977. Sage grouse flock characteristics and habitat selection in winter. Journal of Wildlife Management 41:18-26.

Bradbury, J.W., R.M. Gibson, C.E. McCarthy, and S.L. Vehrencamp. 1989. Dispersion of displaying male sage grouse. II. The role of female dispersion. Behavioral Ecology and Sociobiology 24:15-24.

Braun, C.E., M.F. Baker, R.L. Eng, J.W. Gashwiler, and M.H. Schroeder. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin 88:165-171.

Connelly, J.W., W.J. Arthur, and O.D. Markham. 1981. Sage grouse leks on recently disturbed sites. Journal of Range Management 52:153-154.

Connelly, J.W., C.A. Hagen, and M.A. Schroeder. 2011a. Characteristics and dynamics of greater sage-grouse populations. Pp. 53-67 in S.T. Knick and J.W. Connelly. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitat. Studies in Avian Biology 38. University of California Press, Berkeley, CA.

Connelly, J.W., E.T. Rinkes, and C.E. Braun. 2011b. Characteristics of greater sage-grouse habitats: a landscape species at micro and macro scales. Pp. 69-83 in S.T. Knick and J.W. Connelly, editors. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitat. Studies in Avian Biology 38. University of California Press, Berkeley, CA.

Connelly, J.W., S.T. Knick, C.E. Braun, W.L. Baker, E.A. Beever, T. Christiansen, K.E. Doherty, E.O. Garton, C.A. Hagen, S.E. Hanser, D.H. Johnson, M. Leu, R.F. Miller, D.E. Naugle, S.J. Oyler-McCance, D.A. Pyke, K.P. Reese, M.A. Schroeder, S.J. Stiver, B.L. Walker, and M.J. Wisdom. 2011. Conservation of greater sage-grouse: a synthesis of current trends and future management. Studies in Avian Biology. 46 pp.

Connelly, J.W., M.A. Schroeder, A.R. Sands and C.E. Braun. 2000a. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Connelly, J.W., A.D. Apa, R.B. Smith, and K.P. Reese. 2000b. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. Wildlife Biology 6:227-232.

Connelly, J. W., S. T. Knick, M. A. Schroeder and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming, USA.

Crawford, J.A., R.A. Olson, N.E. West, J.C. Mosley, M.A. Schroeder, T.D. Whitson, R.F. Miller, M.A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Rangeland Ecology & Management 57:2-19.

DeLong, A.K., J.A. Crawford and D. C. DeLong, Jr. 1995. Relationships between vegetational structure and predation of artificial sage grouse nests. Journal of Wildlife Management 59:88-92.

Dunn, P.O., and C.E. Braun. 1986. Late summer-spring movements of juvenile sage grouse. Wilson Bulletin 98:83-92.

Gregg, M.A. 1991. Use and selection of nesting habitat by sage grouse in Oregon. M.S. Thesis, Oregon State University, Corvallis, Oregon, USA. 46pp.

Gregg, M.A., J.A. Crawford, M.S. Drut and A.K. DeLong. 1994. Vegetational cover and predation of sage grouse nests in Oregon. Journal of Wildlife Management 58:162-166.

Hagen, C.A., J.W. Connelly, and M.A. Schroeder. 2007. A meta-analysis for greater sage-grouse nesting and brood rearing habitats. Wildlife Biology 13 (Supplement 1):42-50.

Hupp, J.W. and C.E. Braun. 1989. Topographic distribution of sage grouse foraging in winter. Journal of Wildlife Management 53:823-829.

Johnson, G.D. and M.S. Boyce. 1991. Survival, growth, and reproduction of captive-reared sage grouse. Wildlife Society Bulletin 19: 88-93.

Klebenow, D.A. 1969. Sage grouse nesting and brood habitat in Idaho. Journal of Wildlife Management 33:649-661.

Klebenow, D.A. and G.M. Gray. 1968. Food habits of juvenile sage grouse. Journal of Range Management 21:80-83.

Knick, S.T. and S.E. Hanser. 2011. Connecting pattern and process in greater sage-grouse populations and sagebrush landscapes. Pages 383-405 *in* S.T. Knick and J.W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, California, USA.

Miller, R.F., S.T. Knick, D.A. Pyke, C.W. Meinke, S.E. Hanser, M.J. Wisdom, and A.L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. S. T. Knick and J. W. Connelly (editors). Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, CA.

Patterson, R.L. 1952. The sage grouse in Wyoming. Sage Books, Denver, Colorado. USA.

Schroeder, M.A., J.R. Young, and C.E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Pages 1-28 *in* A. Poole and F. Gill, editors. The birds of North America, No 425. The Birds of North America, Philadelphia, Pennsylvania, USA.

Schroeder, M.A., C.L. Aldridge, A.D. Apa, J.R. Bohne, C.E. Braun, S. D. Bunnell, J.W. Connelly, P.A. Deibert, S.C. Gardner, M.A. Hilliard, G.D. Kobriger, S.M. McAdam, C.W. McCarthy, J.J. McCarthy, D.L. Mitchell, E.V. Rickerson, and S.J. Stiver. 2004. Distribution of sage grouse in North America. Condor 106:363-376.

Wakkinen, W.L., K.P. Reese, and J.W. Connelly. 1992. Sage grouse nest locations in relation to leks. Journal of Wildlife Management 56:381-383.

## Appendix B. Scientific Inference

When making natural resource management decisions, managers desire a high level of certainty that their management actions will have the anticipated outcome (Ratti and Garton 1994, Garton et al. 2005). Unfortunately, natural systems have inherent complexity and stochasticity that make certainty in wildlife management decisions challenging (Williams et al. 2002). In an effort to ameliorate some of this uncertainty, managers use quality, published scientific investigations which are reliant upon thoughtful research design (Ratti and Garton 1994, Garton et al. 2005) to guide population and habitat management decisions. When relevant peer reviewed literature does not exist, managers have to resort to best professional judgment and/or unpublished studies. In addition, when using published and unpublished literature, managers must also be cognizant of the research findings for certainty of the conclusions, the scientific method, and if the findings can be applied from the data and results (Murphy and Noon 1991).

Most wildlife research is located along a continuum of field studies (Ratti and Garton 1994, Garton et al. 2005; Fig. 1) and provides varying degrees of reliable knowledge (Romesburg 1981, Hurlbert, 1984, Eberhardt and Thomas 1991). The more rigorous the research design, results, and conclusions, the more confident managers can be in the anticipated outcome (Ratti and Garton 1994, Garton et al. 2005). Research that bases its results and interpretation on an integrated research process includes field level experiments, field study, and modeling (Fig. 1). If designed appropriately, these research efforts can provide for a more broad-based application of research results as opposed to descriptive natural history studies (Ratti and Garton 1994, Garton et al. 2005) (Fig. 1).

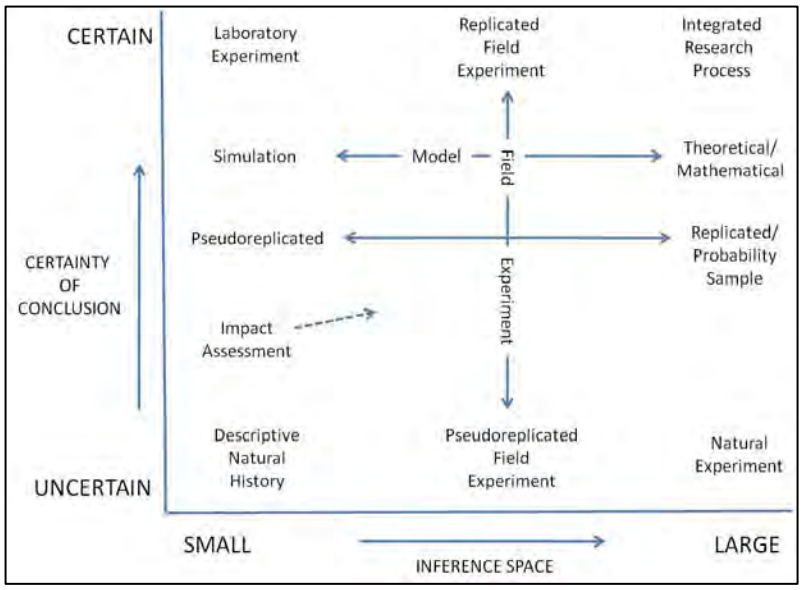



Figure 1. The spectrum of types of wildlife studies that can produce results and conclusions with a large amount of certainty over a very large area of applicability (adapted from Ratti and Garton 1994 and Garton et al. 2005).

Because sage-grouse research has been on-going for over 60 years, managers have access to published literature from several studies (metareplication (Johnson 2002)) that includes different years, study areas, methods, and investigators (Johnson 2002) which leads to more certainty in conclusions (for example see Hagen et al. 2007). In contrast, for some management actions, access to published and unpublished literature may be limited to a single descriptive study. A single descriptive study and/or professional judgment has the lowest level of certainty and lowest inference space. Unfortunately, it may be the only information available on the subject. Ultimately, the result is succinctly summarized by Anderson et al. (2001:312) who stated, "In the long run, science is safeguarded by repeated studies to ascertain what is real and what is merely a spurious result from a single study."

Management in sagebrush ecosystems is further complicated by new forms of development or the unprecedented pace at which traditional uses are increasing. Wind and other renewable energy sources are being proposed and developed in areas that previously had undergone little development. The applicability of results from previous research in other regions on oil and gas development to these new forms of land use is unknown, but is the best information currently available. We also do not know how sagebrush and sage-grouse respond to the increasing intensity of all uses ranging from traditional commodity development to nonconsumptive activities, such as recreation and OHV travel that is occurring across their range. Although previous research can guide management decisions, the changes due to the cumulative effect of this new level of increased development may take years to be fully expressed in habitat and population response.

No single research study, or even a series of studies, regardless of design, and/or inference extent can provide complete certainty in their conclusion(s). As a result, managers must be vigilant in their judgment of research study design, its inference space, and applicability to their management issue when making management decisions. This report cites a large number of published and unpublished studies that can be placed along the continuum of certainty of conclusion and inference space (Fig. 1). Many of the studies cited are from different researchers, study sites, methodologies, and/or years which assists and improves the certainty of the conclusion and inference space (Fig. 1), but ultimately, it is incumbent upon managers to assess their level of risk (consequences of being wrong) with management decisions based upon the cited findings.

The large spatial scales occupied by sage-grouse seasonally (as much as 1,700 mi $^2$; Leonard et al. 2000) have made research on how they respond to habitat perturbations difficult to conduct. Although strength of inference is strongest for replicated experiments, studies of this nature have not been conducted on large scale perturbations such as oil and gas developments, wind farms, coal mines, powerlines, etc. We therefore relied on retrospective and correlational studies that looked at changes in sage-grouse distribution, abundance or demographic rates over time following these developments. We gave greater credence to conclusions obtained from multiple studies conducted at different locations at different times that showed similar results.

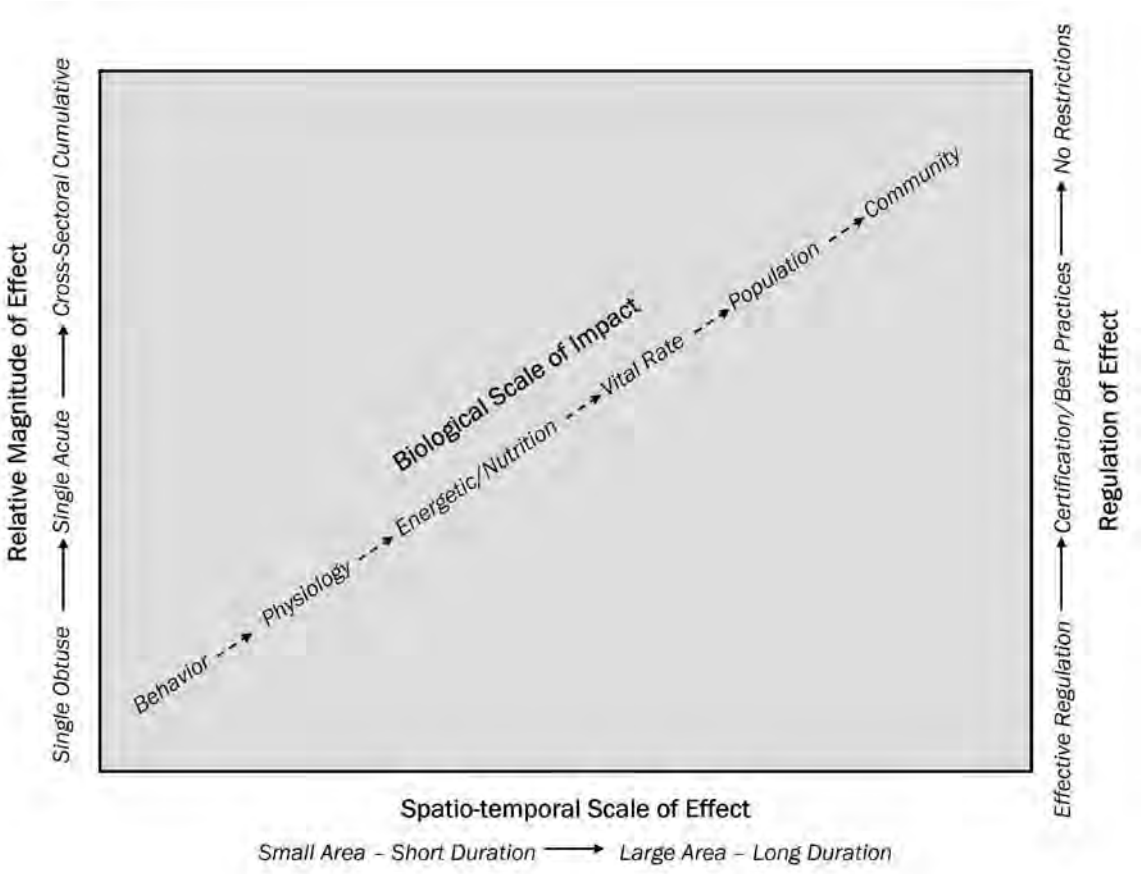



Figure 2. Schematic representation of a typology for classifying and predicting the impacts of human-wildlife interactions (as modified from Johnson and St-Laurent 2011).

Conservation measures described in this report are derived from interpretation of the best available scientific studies using our best professional judgment. Because there is a degree of uncertainty about the

effectiveness of these conservation measures, we recommend a rigorous adaptive management process be employed, with population and habitat monitoring as well as feedback loops so that conservation measures or policies that are ineffective can be changed (Lyons et al. 2008).

## Literature Cited:

75 FR 13910. 2010. Endangered and Threatened Wildlife and Plants: 12-month finding for petitions to list the greater sage-grouse as threatened or endangered.

Anderson, D.R., K.P. Burnham, W.R. Gould, and S. Cherry. 2001. Concerns about finding effects that are actually spurious. Wildlife Society Bulletin 29:311-316.

Eberhardt, L.L., and J.M. Thomas. 1991. Designing environmental field studies. Ecological Monographs 61:53-73.

Garton, E.O., J.T. Ratti, and J.H. Giudice. 2005. Research and Experimentation Design. Pages 43 – 71 in C. E. Braun, editor. Techniques for wildlife investigations and management. Sixth edition. The Wildlife Society, Bethesda, Maryland, USA.

Hagen, C.A., J.W. Connelly, and M.A. Schroeder. 2007. A meta-analysis for greater sage-grouse nesting and brood rearing habitats. Wildlife Biology 13 (Supplement 1):42-50.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Johnson, D.H. 2002. The importance of replication in wildlife research. Journal of Wildlife Management 66:919-932.

Knick, S.T., and J.W. Connelly (editors). 2011. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, CA.

Leonard, KM., K.P. Reese, and J.W. Connelly2000. Distribution, movements and habitats of sage grouse *Centrocercus urophasianus* on the Upper Snake River Plain of Idaho: changes from the 1950s to the 1990s. Wildl. Biol. 6:265-270.

Lyons, J.E., M.C. Runge, H.P. Laskowski, and W.L. Kendall. 2008. Monitoring in the context of structured decision-making and adaptive management.

Murphy, D.D. and B.D. Noon. 1991. Coping with uncertainty in wildlife biology. Journal of Wildlife Management 55:773-782.

Patterson, R.L. 1952. The sage grouse in Wyoming. Sage Books, Denver, Colorado. USA.

Ratti, J.T. and E.O. Garton. 1994. Research and Experimental Design. Page 1-23 in T.A. Bockhout (editor). Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.

Romesburg, H.C. 1981. Wildlife science: gaining reliable knowledge. Journal of Wildlife Management 45:293-313.

Schroeder, M.A., J.R. Young, and C.E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Pages 1-28 *in* A. Poole and F. Gill, editors. The birds of North America, No 425. The Birds of North America, Philadelphia, Pennsylvania, USA.

Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press, New York, New York, USA.

## Appendix C. BMPs for how to make a pond that won't produce mosquitoes that transmit West Nile virus (from Doherty (2007)).

The following are seven distinct site modifications that if adhered to, would minimize exploitation of CBNG ponds by *Culex tarsalis*:

1. Increase the size of ponds to accommodate a greater volume of water than is discharged. This will result in un-vegetated and muddy shorelines that breeding *Cx. tarsalis* avoid (De Szalay and Resh 2000). This modification may reduce *Cx. tarsalis* habitat but could create larval habitat for *Culicoides sonorensis*, a vector of blue tongue disease, and should be used sparingly (Schmidtmann et al. 2000). Steep shorelines should be used in combination with this technique whenever possible (Knight et al. 2003).

2. Build steep shorelines to reduce shallow water (>60 cm) and aquatic vegetation around the perimeter of impoundments (Knight et al. 2003). Construction of steep shorelines also will create more permanent ponds that are a deterrent to colonizing mosquito species like *Cx. tarsalis* which prefer newly flooded sites with high primary productivity (Knight et al. 2003).

3. Maintain the water level below that of rooted vegetation for a muddy shoreline that is unfavorable habitat for mosquito larvae. Rooted vegetation includes both aquatic and upland vegetative types. Avoid flooding terrestrial vegetation in flat terrain or low lying areas. Aquatic habitats with a vegetated inflow and outflow separated by open water produce 5-10 fold fewer Culex mosquitoes than completely vegetated wetlands (Walton and Workman 1998). Wetlands with open water also had significantly fewer stage III and IV instars which may be attributed to increased predator abundances in open water habitats (Walton and Workman 1998).

4. Construct dams or impoundments that restrict down slope seepage or overflow by digging ponds in flat areas rather than damming natural draws for effluent water storage, or lining constructed ponds in areas where seepage is anticipated (Knight et al. 2003).

5. Line the channel where discharge water flows into the pond with crushed rock, or use a horizontal pipe to discharge inflow directly into existing open water, thus precluding shallow surface inflow and accumulation of sediment that promotes aquatic vegetation.

6. Line the overflow spillway with crushed rock, and construct the spillway with steep sides to preclude the accumulation of shallow water and vegetation.

7. Fence pond site to restrict access by livestock and other wild ungulates that trample and disturb shorelines, enrich sediments with manure and create hoof print pockets of water that are attractive to breeding mosquitoes.

## Literature Cited:

De Szalay, F.A. and V.H. Resh. 2000. Factors influencing macroinvertebrate colonization of seasonal wetlands: responses to emergent plant cover. Freshwater Biology. 45: 295-308.

Doherty, M.K. 2007. Mosquito populations in the Powder River Basin, Wyoming: a comparison of natural, agricultural and effluent coal bed natural gas aquatic habitats. M.S. Thesis. Montana State University, Bozeman, U.S.A.

Knight, R.L., W.E. Walton, G.F. Meara, W.K. Riesen and R. Wass. 2003. Strategies for effective mosquito control in constructed treatment wetlands. Ecological Engineering. 21: 211-232.

Schmidtmann, E.T., R.J. Bobian, R.P. Beldin. 2000. Soil chemistries define aquatic habitats with immature populations of the *Culicoides variipennis* complex (Diptera: *Ceratopogonidae*). Journal of Medical Entomology. 37: 38-64.

Walton, W.E., and P.D. Workman. 1998. Effect of marsh design on the abundance of mosquitoes in experimental constructed wetlands in Southern California. Journal of the American mosquito control Association 14:95-107.

# Appendix D. Best Management Practices for Fluid Mineral Development

Priority Habitats - BMPs are continuously improving as new science and technology become available and therefore are subject to change. Include from the following BMPs those that are appropriate to mitigate effects from the approved action.

**Roads**

- Design roads to an appropriate standard no higher than necessary to accommodate their intended purpose.
- Locate roads to avoid important areas and habitats.
- Coordinate road construction and use among ROW holders.
- Construct road crossing at right angles to ephemeral drainages and stream crossings.
- Establish speed limits on BLM system roads to reduce vehicle/wildlife collisions or design roads to be driven at slower speeds.
- Establish trip restrictions (Lyon and Anderson 2003) or minimization through use of telemetry and remote well control (e.g., Supervisory Control and Data Acquisition).
- Do not issue ROWs to counties on newly constructed energy development roads, unless for a temporary use consistent with all other terms and conditions included in this document.
- Restrict vehicle traffic to only authorized users on newly constructed routes (use signing, gates, etc.)
- Use dust abatement practices on roads and pads.
- Close and rehabilitate duplicate roads.

**Operations**

- Cluster disturbances, operations (fracture stimulation, liquids gathering, etc.), and facilities.
- Use directional and horizontal drilling to reduce surface disturbance.
- Place infrastructure in already disturbed locations where the habitat has not been restored.
- Consider using oak (or other material) mats for drilling activities to reduce vegetation disturbance and for roads between closely spaced wells to reduce soil compaction and maintain soil structure to increase likelihood of vegetation reestablishment following drilling.
- Apply a phased development approach with concurrent reclamation.
- Place liquid gathering facilities outside of priority areas. Have no tanks at well locations within priority areas (minimizes perching and nesting opportunities for ravens and raptors and truck traffic). Pipelines must be under or immediately adjacent to the road (Bui et al. 2010).

- Restrict the construction of tall facilities and fences to the minimum number and amount needed.
- Site and/or minimize linear ROWs to reduce disturbance to sagebrush habitats.
- Place new utility developments (power lines, pipelines, etc.) and transportation routes in existing utility or transportation corridors.
- Bury distribution power lines.
- Corridor power, flow, and small pipelines under or immediately adjacent to roads.
- Design or site permanent structures which create movement (e.g. a pump jack) to minimize impacts to sage-grouse.
- Cover (e.g., fine mesh netting or use other effective techniques) all drilling and production pits and tanks regardless of size to reduce sage-grouse mortality.
- Equip tanks and other above ground facilities with structures or devices that discourage nesting of raptors and corvids.
- Control the spread and effects of non-native plant species (Evangelista et al. 2011). (E.g. by washing vehicles and equipment.)
- Use only closed-loop systems for drilling operations and no reserve pits.
- Restrict pit and impoundment construction to reduce or eliminate threats from West Nile virus (Doherty 2007).
- Remove or re-inject produced water to reduce habitat for mosquitoes that vector West Nile virus. If surface disposal of produced water continues, use the following steps for reservoir design to limit favorable mosquito habitat:
    - Overbuild size of ponds for muddy and non-vegetated shorelines.
    - Build steep shorelines to decrease vegetation and increase wave actions.
    - Avoid flooding terrestrial vegetation in flat terrain or low lying areas.
    - Construct dams or impoundments that restrict down slope seepage or overflow.
    - Line the channel where discharge water flows into the pond with crushed rock.
    - Construct spillway with steep sides and line it with crushed rock.
    - Treat waters with larvicides to reduce mosquito production where water occurs on the surface.
- Limit noise to less than 10 decibels above ambient measures (20-24 dBA) at sunrise at the perimeter of a lek during active lek season (Patricelli et al. 2010, Blickley et al. *In preparation*).
- Require noise shields when drilling during the lek, nesting, broodrearing, or wintering season.
- Fit transmission towers with anti-perch devices (Lammers and Collopy 2007).

- Require sage-grouse-safe fences.
- Locate new compressor stations outside priority habitats and design them to reduce noise that may be directed towards priority habitat.
- Clean up refuse (Bui et al. 2011).
- Locate man camps outside of priority habitats.

**Reclamation**

- Include objectives for ensuring habitat restoration to meet sage-grouse habitat needs in reclamation practices/sites (Pyke 2011). . Address post reclamation management in reclamation plan such that goals and objectives are to protect and improve sage-grouse habitat needs.
- Maximize the area of interim reclamation on long-term access roads and well pads including reshaping, topsoiling and revegetating cut and fill slopes.
- Restore disturbed areas at final reclamation to the pre-disturbance landforms and desired plant community.
- Irrigate interim reclamation if necessary for establishing seedlings more quickly.
- Utilize mulching techniques to expedite reclamation and to protect soils.

General sage-grouse habitat

*Best Management Practices*

Make applicable BMPs mandatory as Conditions of Approval within general sage-grouse habitat. BMPs are continuously improving as new science and technology become available and therefore are subject to change. At a minimum include the following BMPs:

**Roads**

- Design roads to an appropriate standard no higher than necessary to accommodate their intended purpose.
- Do not issue ROWs to counties on energy development roads, unless for a temporary use consistent with all other terms and conditions included in this document.
- Establish speed limits to reduce vehicle/wildlife collisions or design roads to be driven at slower speeds.
- Coordinate road construction and use among ROW holders.
- Construct road crossing at right angles to ephemeral drainages and stream crossings.
- Use dust abatement practices on roads and pads.

- Close and reclaim duplicate roads, by restoring original landform and establishing desired vegetation.

**Operations**

- Cluster disturbances, operations (fracture stimulation, liquids gathering, etc.), and facilities.
- Use directional and horizontal drilling to reduce surface disturbance.
- Clean up refuse (Bui et al. 2010).
- Restrict the construction of tall facilities and fences to the minimum number and amount needed.
- Cover (e.g., fine mesh netting or use other effective techniques) all drilling and production pits and tanks regardless of size to reduce sage-grouse mortality.
- Equip tanks and other above ground facilities with structures or devices that discourage nesting of raptors and corvids.
- Use remote monitoring techniques for production facilities and develop a plan to reduce the frequency of vehicle use.
- Control the spread and effects from non-native plant species. (e.g. by washing vehicles and equipment.)
- Restrict pit and impoundment construction to reduce or eliminate augmenting threats from West Nile virus (Dougherty 2007).

**Reclamation**

- Include restoration objectives to meet sage-grouse habitat needs in reclamation practices/sites (Pyke 2011). Address post reclamation management in reclamation plan such that goals and objectives are to enhance or restore sage-grouse habitat.

**Literature Cited:**

Blickley, J.L., D. Blackwood, and G.L. Patricelli. In preparation. Experimental evidence for avoidance of chronic anthropogenic noise by greater sage-grouse. University of California-Davis, California, USA.

Bui, T.D., J.M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. Condor 112:65-78.

Doherty, M.K. 2007. Mosquito populations in the Powder River Basin, Wyoming: a comparison of natural, agricultural and effluent coal-bed natural gas aquatic habitats. M.S. thesis, Montana State University, Bozeman, Montana, USA.

Evangelista, P.H., A.W. Crall, and E. Bergquist. 2011. Invasive plants and their response to energy development. Pages 115-129 in D.E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

Lammers, W.M., and M.W. Collopy. 2007. Effectiveness of avian predator perch deterrents on electric transmission lines. Journal of Wildlife Management 71:2752-2758.

Lyon, A.G. and S.H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31: 486-491.

Patricelli, G.L., J.L. Blickley, and S. Hooper. 2010. Incorporating the impacts of noise pollution into greater sage-grouse conservation planning. 27th Meeting of the Western Agencies Sage and Columbian Sharp-tailed Grouse Technical Committee Workshop. Twin Falls, Idaho, USA.

Pyke, D.A. 2011. Restoring and rehabilitating sagebrush habitats. Pp. 531-548 in S.T. Knick and J.W. Connelly (editors). Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press. Berkeley, CA.

# Appendix E. Best Management Practices for Locatable Mineral Development

BMPs are continuously improving as new science and technology become available and therefore are subject to change. Include from the following BMPs those that are appropriate to mitigate effects from the approved action.

**Roads**

- Design roads to an appropriate standard no higher than necessary to accommodate their intended purpose.
- Locate roads to avoid important areas and habitats.
- Coordinate road construction and use among ROW holders.
- Construct road crossing at right angles to ephemeral drainages and stream crossings.
- Establish speed limits on BLM system roads to reduce vehicle/wildlife collisions or design roads to be driven at slower speeds.
- Do not issue ROWs to counties on mining development roads, unless for a temporary use consistent with all other terms and conditions included in this document.
- Restrict vehicle traffic to only authorized users on newly constructed routes (e. g., use signing, gates, etc.)
- Use dust abatement practices on roads and pads.
- Close and reclaim duplicate roads, by restoring original landform and establishing desired vegetation.

**Operations**

- Cluster disturbances associated with operations and facilities as close as possible.
- Place infrastructure in already disturbed locations where the habitat has not been restored.
- Restrict the construction of tall facilities and fences to the minimum number and amount needed.
- Site and/or minimize linear ROWs to reduce disturbance to sagebrush habitats.
- Place new utility developments (power lines, pipelines, etc.) and transportation routes in existing utility or transportation corridors.
- Bury power lines.
- Cover (e.g., fine mesh netting or use other effective techniques) all pits and tanks regardless of size to reduce sage-grouse mortality.
- Equip tanks and other above ground facilities with structures or devices that discourage nesting of raptors and corvids.

- Control the spread and effects of non-native plant species (Gelbard and Belnap 2003, Bergquist et al. 2007).
- Restrict pit and impoundment construction to reduce or eliminate threats from West Nile virus (Doherty 2007).
- Remove or re-inject produced water to reduce habitat for mosquitoes that vector West Nile virus. If surface disposal of produced water continues, use the following steps for reservoir design to limit favorable mosquito habitat:
    - Overbuild size of ponds for muddy and non-vegetated shorelines.
    - Build steep shorelines to decrease vegetation and increase wave actions.
    - Avoid flooding terrestrial vegetation in flat terrain or low lying areas.
    - Construct dams or impoundments that restrict down slope seepage or overflow.
    - Line the channel where discharge water flows into the pond with crushed rock.
    - Construct spillway with steep sides and line it with crushed rock.
    - Treat waters with larvicides to reduce mosquito production where water occurs on the surface.
- Require sage-grouse-safe fences around sumps.
- Clean up refuse (Bui et al. 2010).
- Locate man camps outside of priority sage-grouse habitats.

**Reclamation**

- Include restoration objectives to meet sage-grouse habitat needs in reclamation practices/sites. Address post reclamation management in reclamation plan such that goals and objectives are to protect and improve sage-grouse habitat needs.
- Maximize the area of interim reclamation on long-term access roads and well pads including reshaping, topsoiling and revegetating cut and fill slopes.
- Restore disturbed areas at final reclamation to pre-disturbance landform and desired plant community.
- Irrigate interim reclamation as necessary during dry periods.

Utilize mulching techniques to expedite reclamation.

**Literature Cited:**

Bergquist, E., P. Evangelista, T. J. Stohlgren, and N. Alley. 2007. Invasive species and coal bed methane development in the Powder River Basin, Wyoming. Environmental Monitoring and Assessment 128:381-394.

Bui, T.D., J.M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. Condor 112:65-78.

Doherty, M.K. 2007. Mosquito populations in the Powder River Basin, Wyoming: a comparison of natural, agricultural and effluent coal bed natural gas aquatic habitats. Thesis. Montana State University, Bozeman, U.S.A.

Gelbard, J.L., and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology 17:420-432.

# Appendix F. Best Management Practices for Fire & Fuels (wo IM 2011-138)

*Fuels Management BMPs:*

1. Where applicable, design fuels treatment objective to protect existing sagebrush ecosystems, modify fire behavior, restore native plants, and create landscape patters which most benefit sage-grouse habitat.

2. Provide training to fuels treatment personnel on sage-grouse biology, habitat requirements, and identification of areas utilized locally.

3. Use fire prescriptions that minimize undesirable effects on vegetation or soils (e.g., minimize mortality of desirable perennial plant species and reduce risk of hydrophobicity).

4. Ensure proposed sagebrush treatments are planned with interdisciplinary input from BLM and /or state wildlife agency biologist and that treatment acreage is conservative in the context of surrounding sage-grouse seasonal habitats and landscape.

5. Where appropriate, ensure that treatments are configured in a manner (e.g., strips) that promotes use by sage-grouse (See Connelly et al., 2000*)

6. Where applicable, incorporate roads and natural fuel breaks into fuel break design.

7. Power-wash all vehicles and equipment involved in fuels management activities prior to entering the area to minimize the introduction of undesirable and/or invasive plant species.

8. Design vegetation treatment in areas of high frequency to facilitate firefighting safety, reduce the risk of extreme fire behavior; and to reduce the risk and rate of fire spread to key and restoration habitats.

9. Give priority for implementing specific sage-grouse habitat restoration projects in annual grasslands first to sites which are adjacent to or surrounded by sage-grouse key habitats. Annual grasslands are second priority for restoration when the sites not adjacent to key habitat, but within 2 miles of key habitat. The third priority for annual grasslands habitat restoration projects are sites beyond 2 miles of key habitat. The intent is to focus restoration outward from existing, intact habitat.

10. As funding and logistics permit, restore annual grasslands to a species composition characterized by perennial grasses, forbs, and shrubs.

11. Emphasize the use of native plant species, recognizing that non-native species may be necessary depending on the availability of native seed and prevailing site conditions.

12. Remove standing and encroaching trees within at least 100 meters of occupied sage-grouse leks and other habitats (e.g., nesting, wintering, and brood rearing) to reduce the availability of perch sites for avian predators, as appropriate, and resources permit.

13. Protect wildland areas from wildfire originating on private lands, infrastructure corridors, and recreational areas.

14. Reduce the risk of vehicle or human-caused wildfires and the spread of invasive species by planting perennial vegetation (e.g., green-strips) paralleling road rights-of-way.

15. Strategically place and maintain pre-treated strips/areas (e.g., mowing, herbicide application, and strictly managed grazed strips) to ail in controlling wildfire should wildfire occur near key habitats or important restoration areas (such as where investments in restoration have already been made).

*Fire Management BMPs:*

1. Develop state-specific sage-grouse toolboxes containing maps, a list of resource advisors, contact information, local guidance, and other relevant information.

2. Provide localized maps to dispatch offices and extended attack incident commanders for use in prioritizing wildfire suppression resources and designing suppression tactics.

3. Assign a sage-grouse resource advisor to all extended attack fires in or near key sage-grouse habitat areas. Prior to the fire season, provide training to sage-grouse resource advisors on wildfire suppression organization, objectives, tactics, and procedures to develop a cadre of qualified individuals.

4. On critical fire weather days, pre-position additional fire suppression resources to optimize a quick and efficient response in sage-grouse habitat areas.

5. During periods of multiple fires, ensure line officers are involved in setting priorities.

6. To the extent possible, locate wildfire suppression facilities (i.e., base camps, spike camps, drop points, staging areas, heli-bases) in areas where physical disturbance to sage-grouse habitat can be minimized. These include disturbed areas, grasslands, near roads/trails or in other areas where there is existing disturbance or minimal sagebrush cover.

7. Power-wash all firefighting vehicles, to the extent possible, including engines, water tenders, personnel vehicles, and ATVs prior to deploying in or near sage-grouse habitat areas to minimize noxious weed spread.

8. Minimize unnecessary cross-country vehicle travel during fire operations in sage-grouse habitat.

9. Minimize burnout operations in key sage-grouse habitat areas by constructing direct fireline whenever safe and practical to do so.

10. Utilize retardant and mechanized equipment to minimize burned acreage during initial attack.

11. As safety allows, conduct mop-up where the black adjoins unburned islands, dog legs, or other habitat features to minimize sagebrush loss.

## Literature Cited:

Connelly, J.W., M.A Schroeder, A.R. Sands, and C.E. Braun 2000. Guidelines to Manage Sage-grouse Populations and Their Habitats. Wildlife Society Bulletin 28:967-985.

## Appendix G. National Technical Team Members

| | |
|---|---|
| Raul Morales | *BLM, Nevada* (Team Lead) |
| Tony Apa | *Colorado Fish, Wildlife and Parks* |
| Charlie Beecham | *BLM, Colorado* |
| Travis Bargsten | *BLM, Wyoming* |
| Pat Deibert | *U.S. Fish and Wildlife* |
| Shawn Espinosa | *Nevada Department of Wildlife* |
| Mary Fiagerlle | *BLM, Nevada* |
| Tim Griffiths | *Natural Resources Conservation Service* |
| Christian Hagan | *Oregon Dept. of Fish and Wildlife* |
| Doug Havlina | *BLM, National Interagency Fire Center* |
| Don Kemner | *Idaho Fish and Game* |
| Steve Knick | *U.S. Geological Survey* |
| Ben Kniola | *BLM, Washington Office-310* |
| Lauren Mermejo | *BLM, Utah* |
| Dave Naugle | *Natural Resources Conservation Service* |
| Mike Pellant | *BLM, Nevada* |
| Rob Perrin | *BLM, Washington Office-250* |
| Frank Quamen | *BLM, National Operations Center* |
| Tom Rinkes | *BLM, Idaho* |
| Jason Robinson | *Utah Department of Wildlife Resources* |
| Jeff Rose | *BLM, Oregon* |
| Robin Sell | *BLM, Colorado* |
| David Wood | *BLM, Montana* |

# Dynamics of Greater Sage-grouse (*Centrocercus urophasianus*) Populations in Response to Transmission Lines in Central Nevada

Progress Report: Year 9

December 2011

Dan Nonne, Erik Blomberg, James Sedinger

Department of Natural Resources and Environmental Sciences

University of Nevada – Reno

1664 N. Virginia St. MS 146

Reno, NV 89512

**ABSTRACT** We monitored greater sage-grouse (*Centrocercus urophasianus*) associated with13 breeding leks to characterize demographic processes in a ~6500 $km^2$ area in Eureka County, Nevada. The long-term goal of this ten-year study is to assess the impact of NV Energy's Falcon-Gondor transmission line on sage grouse population dynamics. We used mark-recapture, lek observations, nest & brood monitoring, vegetation sampling, and radio telemetry to estimate key demographic parameters. We have banded a total of 1287 unique sage grouse during the nine years of the study. Additionally, we have radio-collared 199 female and 61 male sage-grouse during this time. We have also monitored 373 nests, of which 119 were successful. From 2009-2011, we captured and marked 352 chicks at hatch and recaptured 67 of the marked chicks at approximately one month of age. From 2003-2007, counts of common ravens along the transmission line corridor and raven-associated disturbances at leks increased dramatically, however, in 2008 raven counts declined to levels observed immediately following line construction. Raven counts have since rebounded and in 2011 counts approached 2007 levels.

We used our male banding data to evaluate the relative importance of annual variation in resource availability, as indexed by normalized difference vegetation indices (NDVI), to sage-grouse population dynamics. Annual variation in NDVI had a strong positive influence on per-capita recruitment ($\beta = 0.78$; 95% CI = 0.37 to 1.19), and recruitment was over 9-times greater following the year of highest NDVI ($f = 0.77 \pm 0.18$ SE) compared to the year of lowest NDVI ($f = 0.08 \pm 0.03$ SE). We found a similar positive influence on male survival, but the effect was not as strong ($\beta = 0.28$; 95% CI = -0.07 to 0.62) as for recruitment. Using this analysis we also demonstrated negative effects of exotic grassland footprint on lek-level recruitment ($\beta = -0.62$; 95% CI = -0.82 to -0.41) and annual survival ($\beta = -0.29$; 95% CI = -0.55 to -0.03).

We also used our male banding data to estimate differences in lek attendance and survival between males with radio-collars and banded-only males. Model average results indicate radio-collared male sage-grouse were less likely to attend a lek in a given year ($\gamma$=0.702 ± 0.201 SE) or less likely to be detected on a lek (P*= 0.332 ± 0.153 SE) if present than banded-only males ($\gamma$=0.275 ± 0.219 SE; P*= 0.615 ± 0.155 SE). Although results suggested a significant impact of radio-collars on male breeding behavior, no substantial support for an influence of radio-collars on male survival was found.

We evaluated the utility of lek counts for estimating annual and long term population trends, using our male banding data to generate independent estimates of population growth ($\lambda$) and male breeding propensity. A linear regression comparing annual lek count trends to realized $\lambda$, annual variation in breeding propensity, and unexplained error, showed that lek counts produced a good fit to realized $\lambda$ ($R^2$ = 0.760). However, the remaining error was sufficient to cause discrepancies between lek counts and realized $\lambda$ in 4 of 7 intervals. For this reason, we caution use of lek counts for making inferences regarding short-term changes in sage-grouse populations.

Female survival showed strong seasonal variation, with the lowest monthly survival occurring during the spring breeding season (March-May; $\Phi_B$ = 0.947 ± 0.007) and during the fall (August-October; $\Phi_F$ = 0.922 ± 0.009). We detected a substantial cost of reproduction on survival, where females that successfully raised ≥ 1 chick to 45 days of age had lower annual survival ($\Phi_A$ = 0.498 ± 0.057) than unsuccessful females ($\Phi_A$ = 0.610 ± 0.026). NDVI had an overall positive association with female survival; survival during the spring breeding season increased in years with higher plant production ($\beta$ = 0.513; 95% CI = 0.096 to 0.930).

We evaluated factors influencing female reproductive success using a multi-state model, where female success was modeled as a function of previous year's reproductive state and

NDVI. Females who were previously successful had a higher overall probability of success ($\Psi_S$ = 0.277 ± 0.089) compared to previously unsuccessful hens ($\Psi_U$ = 0.094 ± 0.025). NDVI had a strong positive influence on female success ($\beta$ = 1.336; 95% CI = 0.142 to 2.529), and we detected a more than 4-fold increase in success between the years of highest and lowest NDVI.

Estimated nest survival has remained relatively constant over the course of this study. Using data from 2005-2011, model averaged daily nest survival was 0.950 (± 0.009 SE) resulting in an overall probability of nest survival for a 37-day nest period of 0.149 (± 0.007 SE). Model results suggested a lower daily survival rate for the day following flushing a hen from a nest (0.908 ± 0.029 SE) compared to the day a hen was not flushed (0.950 ± 0.009 SE). However, there was not a substantial difference between overall nest survival probabilities from a nest that was flushed once (0.152 ±0.007 SE) compared with a nest that was not flushed (0.160 ±0.006 SE). We continue to find no convincing support for a meaningful impact of the Falcon-Gondor line on nest survival.

Overall we have demonstrated an important association between annual plant production (indexed by NDVI) and sage-grouse survival (males and females), reproductive success (females), recruitment (males), and population growth (males). These results highlight the important association between sage-grouse populations and climatic processes in our arid study system. We were also able to identify and quantify potential sources of bias associated with monitoring sage-grouse by modeling observer impacts on nest survival, impacts of radio-collar transmitters on male survival and behavior, and error associated with count-based indices.

## INTRODUCTION

Sage-grouse populations have declined range-wide since the mid 1960's, with some states showing stabilizing trends in the past two decades (Connelly et al. 2004). Sage-grouse are an obligate of sagebrush with both adults and young using this vegetation for food and shelter throughout the year and subsisting solely on it during the winter months (Beck 1977, Dalke et al. 1963, Wallestad et al. 1975). Human disruption of the sagebrush biome has contributed to approximately 530,000 square kilometers of sagebrush steppe habitat loss (Crawford et al. 2004, Connelly et al. 2004, Dalke et al. 1963). Given the amount of sagebrush steppe lost and sage-grouse dependency on sagebrush, it is believed that the loss and degradation of habitat is an important cause of population decline (Connelly et al. 2000).

Elevated structures, such as utility lines can provide perches for avian predators that are higher than those supplied by local vegetation and topography (Ellis 1984, Braun 1998). The only post-hoc study of the impact of utility lines on sage-grouse suggested general lower lek attendance at leks closer to utility lines, but was unable to account for confounding factors that may have influenced both utility line placement and sage-grouse populations (Hall and Haney 1997). It is hypothesized that avian predators of sage grouse adults (raptors) and nests (corvids) may use utility poles and towers to increase their hunting efficiency, in turn reducing adult survival or nest success and triggering population declines in nearby leks (Hall and Haney 1997, Alstatt 1995). Alternatively, the perceived threat of predation associated with utility lines may cause sage-grouse to avoid utility lines, leading to sage-grouse abandonment leks, nest sites, and brood rearing areas near utility lines (Hall and Haney 1997, Braun 1998).

Recent indirect evidence supports an avoidance hypothesis, in that lek locations have been found to have the least long range visibility in combination with greatest short range visibility

that local topography will allow (Aspbury et al. 2004). In short, male sage-grouse may be choosing lek locations that maximize their visibility to female grouse near a lek, while reducing long range visibility to predators (Aspbury et al. 2004).

In fall 2003 Sierra Pacific Power Company (now NV Energy) began construction of a 345 kilovolt transmission line between Falcon and Gondor, Nevada (FG line). Construction of the FG line was completed in the spring of 2004 and was energized in May of that year. The FG line is approximately 290 km long and has 735 towers that vary in height from 23 to 40 m, depending on topography. The FG line runs through the middle Eureka County's prime sage grouse habitat (M. Podborny, NDOW, personal communication).

**OBJECTIVES**

The goal of this study is to assess impacts of the FG line on population dynamics of greater sage-grouse in the region. The basic study design calls for estimation of key demographic parameters (male lek attendance over time, movement between leks, adult survival rates, nest success, brood survival, recruitment, and population size) as a function of distance from the line. Under the hypothesis that the line negatively affects local sage-grouse, we expect demographic responses to the line to be greatest for leks and/or individuals nearest the line. Distance from line will be directly incorporated into models of demographic parameters to assess this hypothesis. For parameters in which we hypothesize a time delayed response (e.g., adult survival following an increase in raptors) the appropriate analysis includes a time by distance interaction. Thus, though it may not be immediate, we expect (under the hypothesis of an impact of line) a greater decline in adult survival for leks near the line than for leks distant from the line.

To this end, several leks at varying distances from the FG line were chosen to be monitored for ten years. At each of these leks a regime of capture-mark-recapture and observations

throughout the strutting season was initiated. We also radio tagged a sample of hens captured each year and followed these hens throughout the breeding, nesting, and brood-rearing seasons. From 2005-2011, we used a combination of Passive Integrated Transponder (PIT) tags and patagial tags to permanently mark sage grouse chicks. Also in 2005, we began what has become an annual fall trap with Nevada Department of Wildlife (NDOW) to increase number of radio-tagged individuals in the population, hunter band returns and number of radio tagged young.

**STUDY AREA**

The study site is located in east central Nevada within Eureka County (Fig. 1). It is bounded by the Cortez and Simpson Park Mountains to the west and the Diamond and Sulphur Spring Mountains to the East. This area includes Denay, Pine, Kobeh, Diamond, Horse Creek, Grass, and Garden valleys. The study area encompasses approximately 6500 $km^2$ of sagebrush steppe and pinyon-juniper mountain ranges with many ephemeral streams. Sage-grouse utilize two main sagebrush communities in the study area. At low elevations (< ~7000 ft), a Wyoming big sagebrush (*A. tridentata wyomingensis*) community is dominant, with pockets of black sagebeush (*A. nova*) and basin big sagebrush (*A. tridentata tridentata*), as well as rubber rabbitbrush (*Chrysothamnus nauseosus*), greasewood (*Sarcobatus vermiculatus*), and some scattered Utah juniper (*Juniperus osteosperma*). At higher elevations (> ~7000 ft), a mixed mountain big sagebrush (*A. tridentata vaseyana*)/low sagebrush (*Artemisia arbuscula*) community is most prevalent, with some intermixed common snowberry (*Symphoricarpos albus*), western serviceberry (*Amelanchier alnifolia*), and bitterbrush (*Purshia tridentata*). Large expanses of singleleaf pinyon (*Pinus monophylla*)/Utah Juniper forest are also common in the study area and in many cases are found mid-elevation between the two sagebrush communities. Common annual and perennial forbs include phlox (*Phlox* spp.), cateyes (*Cryptantha* spp.), tansy

mustard (*Descurainia pinnata*), bur buttercup (*Ceratocephala testiculata*), woolystar (*Eriastrum* spp.), lupine (*Lupinus* spp.), desert parsley (*Lomatium* spp.), and desert buckwheat (*Eriogonum* spp.). Grasses consist of blue grass (*Poa* spp.), cheatgrass (*Bromus tectorum*), crested wheat (*Agropyron cristatum*), indian rice grass (*Achnatherum hymenoides*), and squirrel tail (*Elymus elymoides*). Sage-grouse were generally associated with 2 distinct populations centered on Roberts Creek Mountain and the Cortez Mountain Range. Movements of sage-grouse between these two populations appear to be relatively infrequent.

The study area includes 120 km of the FG line and focuses on thirteen active leks at various distances from the FG line (Fig. 1). Five of these leks have been monitored by NDOW and Bureau of Land Management (BLM) for the past thirty years. Long term data show male lek attendance at these leks has been declining since the early ‘70s with some signs of stabilization in the late ‘90s (Fig. 2).

## METHODS

### Field Methods

***Mark Recapture*** - The predominant trapping method used to capture adult sage grouse was night spotlighting (Giesen et al. 1982). We used a high candlepower spotlight to disorient birds while a dip net was placed over them, with white noise generated throughout to mask researcher movement. Binoculars and eyeshine were used to increase the distance at which birds are detected (Wakkinen et al. 1992). To supply power for the spotlight and white noise we used either an ATV or a portable generator strapped to a backpack frame. Small diameter mesh (Giesen et al. 1982) or rubber netting was used to decrease damage to plumage. Other methods were tried such as ground mounted rocket nets (Giesen et al. 1982) and walk-in traps (Schroeder et al. 1991), but were not as successful.

During the breeding season, we captured individuals on each study lek and surrounding area approximately once a week. During the late summer/early fall trap, known brood rearing areas and ridges were scouted one week before the trap, and then intensively trapped for three nights during the new moon in August or September. Upon capture, birds were aged, sexed, weighed, and a series of morphological measurements were taken (length of 1st primary, 5th primary, wing chord, tarsus, foot, and number of tail feathers). Each bird was banded with a National Band and Tag metal band, size 16 for males and 14 for females (Walsh 2002), and all adults and those young that were large enough were banded with a colored plastic band engraved with three character alpha-numeric code for re-sighting during lek observations. All hens captured during the lekking season and a subset of hens captured during the fall trap were fitted with a radio collar. A subset of males were radio tagged in both spring and fall. We used radios from Advanced Telemetry Systems, model number A4060. Each radio weighed approximately 22 g, had a battery life of 383-766 days, and a range of 1-5 miles depending on terrain.

***Lek Observations*** - We monitored ten viable leks in 2003, eleven leks in 2004 & 2005 twelve leks in 2006 & 2007, and 13 leks in 2008-2010, within 20 km of the transmission line. Six leks were within 5 km of the FG line and seven leks were greater than 5 km away. Leks were selected by evaluating previously collected data from BLM and the NDOW. Precise locations of monitored study leks are shown in Figure 1.

Each study lek was observed approximately once a week throughout the breeding season, March through May. Observers arrived on the leks 1/2 hour before first light, and remained until strutting activity ceased or birds disbursed (Walsh 2002). During these periods, researchers monitored leks from mobile blinds with high-powered (15x60) spotting scopes and binoculars. We occasionally included a mobile observation tower to facilitate band reading where terrain

permitted and vegetation characteristics required it. In 2011, we placed trail cameras on leks to generate additional band reads. We counted the number of males and females, marked and unmarked, on leks every 30 minutes during each observation period. We also recorded individual band codes (resights) and behavioral interactions with potential predators. For lek disturbances, bird behavior, time, number of birds affected, and type of predator/disturbance were recorded.

***Radio Telemetry -*** During the nesting season (late March to mid June) each hen was located at least once weekly either visually or by triangulation. Nesting hens were monitored twice weekly, and hens with broods were monitored once a week until 45 days post hatch (Schroeder 1997). Following nest failure hens were returned to the breeding season regime above. If a nest failed after strutting ceased the hen was monitored for survival approximately once a week. After all radio-collared hens had fledged their young or failed, they were monitored approximately once a month using fixed-wing aircraft until the next breeding season. In 2008, 2009, and 2010, all birds were monitored more intensively from August – October to document patterns in fall mortality (further description and results in Blomberg et al. 2010).

***Nest Monitoring & Vegetation Sampling -*** Upon locating a nesting hen, a visual check point at least twenty meters away was marked with a cairn of rocks or local debris and a GPS point recorded. If environmental conditions were favorable (no storm on the horizon and no predators seen nearby) the hen was approached and flushed from the nest. Size of clutch was recorded, eggs were floated to determine stage of incubation, and each egg's length & width was measured. Age of each nest was estimated using egg float data, assuming incubation began with laying of the last egg and one egg was laid every 1.3 days (average laying time per egg [Dalke et al. 1963]). Within 24 hours the nest was checked again from a distance to confirm the hen's

return. Nest monitoring followed a twice weekly regime until hatch or failure. A nest was determined successful/hatched if the hen was located nearby with chicks or if at least one egg was present with crown removed and/or the shell membrane was present and detached.

Vegetation was measured at each nest site within 3 days of hatch, or on the predicted hatch date for failed nests. We placed two perpendicular 10 m transects centered at the nest and recorded the percent shrub cover for each meter along the transect (Gregg 1994). In addition, five 20 X 50 cm Daubenmire plots were placed along each transect, where percent cover of grass and forbs was estimated and all plants were measured and identified to species. The same data collected for the Daubenmire plots were also collected for the $m^2$ area around the nest bowl (Sveum 1998). These same vegetation measurements are also made at 24 random points, located throughout the study area each year.

***Brood Trapping, Monitoring, & Vegetation*** - Within three days of hatch broods were trapped and processed (Gregg 2001). Like Gregg (2001) we found hens to still be brooding their young during the hours before dawn within 2 to 3 days after hatch. Hens were flushed and the young were gathered by hand and placed in a cloth sack, which was then placed inside a researcher's jacket to maintain chick body temperature. Processing involved weighing the individual chicks, measuring their tarsus, foot, and length of bill to back of the head, as well as uniquely marking each individual (Carver et al. 1999, Becker et al. 1997). In 2005 and 2006 we used passive integrated transponder (PIT) tags. In 2007 we included patagial wing tags (#1 fish fingerling tags), and double marked all chicks with one PIT and one wing tag. In 2008 we completely shifted to using only patagial wing tags in both wings, and continued this practice through 2011. After processing, chicks were placed in another cloth sack which was also placed inside a researcher's jacket and checked periodically to determine condition. Once processing was

completed, the entire brood was released together and researchers moved away from the brood in the direction opposite where the hen was last heard or seen. Throughout processing the brood the hen's position was periodically determined via radio or visual check, and we remained in the area long enough to confirm reassociation of the hen and chicks.

After capture, broods were checked once a week, hens were flushed and chicks counted to determine fledging and survival rates. In 2008, we modified brood check procedures to increase the precision of our brood count estimates. From initial capture to ~ 30 days of age, each brood was flushed weekly during the early morning while the chicks were still congregated near the hen. Following 30 days, chicks were counted while roosting at night using a spotlight and binoculars/spotting scope. We continued to collect a daytime location once a week for vegetation monitoring, however lower importance was placed on obtaining a mid-day flush count. Each daytime location was recorded using a GPS and we returned in 3-6 days to measure vegetation. Vegetation measurements were the same as those for 10 m nest transects. In addition to the vegetation measurements, we placed 5 pit traps filled with nontoxic glycerin glycol along one of the transect lines to assess arthropod densities (Gregg 2001).

In 2009 we began recapturing chicks at ~ 28 days of age to measure growth rates and collect feather samples for stable isotope analysis, and in 2011 we began additional recaptures of chicks at ~ 45 days and ~80 days of age to calculate more precise estimates of chick survival.
. We located broods at night using the hen's radio signal, and attempted to capture as many chicks from the brood as possible using our normal spotlighting techniques as described above. Captured chicks were identified by their patagial tags, weighed, and measures of head, foot, tarsus, and wing chord were taken. On the 28 day recapture occasion, we collected feathers from the secondary, lower, mid and upper covert, scapular, and back feather tracts for stable isotope

analysis. On the 80 day recapture occasion, female chicks that were large enough were equipped with an 11-gram radio-transmitter.

***Raptor/Corvid Surveys*** - Three transects were located along the FG line in the north, central, and southern portions of the study area. The northern transect had 9 points, the central had 9 points, and the southern had 5 points. We attempted to survey each transect once every 10 days. Starting times (1 hr after sunrise or at 13:00 hrs) and starting direction (north or south) were alternated. Surveys were not conducted if there was precipitation, fog, or if wind speeds exceeded 19 km/hr. Observers spent 10 minutes at each point, identified all raptor and corvid species, number of individuals, activity (perched or flying), location if perched (power line, deterrent, fence, etc), and whether it was within ¼ mile of the line or beyond.

***Predator Indices*** - In 2011, we instituted the use of trail cameras to develop indices of nest predator abundance and evaluate correlations between predator abundance and road densities. We created two sets of random camera locations per survey area located < 30m and >50m from a road. Cameras were placed within 4 survey areas to include low elevation habitat (Kobeh and Pine valleys) and high elevation habitat (Roberts Creek Mountain and the Potato Patch/Cottonwood Canyon area) associated with the Roberts Creek and Cortez populations of sage-grouse. Camera locations were randomly generated using ArcGIS and cameras were deployed from 3-5 days at each location. Cameras were baited with a scent-bait comprised of a mixture of rotting chicken, tuna, and various commercially available coyote lures. Cameras were oriented north or south to minimize random pictures caused by movement of the sun, were set at low sensitivity, and to take a burst of three pictures with a five-minute cool down between bursts.

**Quantitative Analyses**

For 2011 we've conducted demographic analyses in Program MARK (White and Burnham 1999) using data from our marked individuals to answer specific research questions regarding various sage-grouse life history stages. We will discuss the specific MARK models briefly, and then focus on each individual life stage analysis.

***Male analyses*** – Using our male banding data, we have conducted a Pradel model analysis to estimate population growth and recruitment of males, and a robust design analysis to estimate rates of annual lek attendance and annual survival. Pradel models allow for direct estimation of population growth rate ($\lambda$) and recruitment ($f$) from capture recapture data using a reverse-time sampling approach (Pradel 1996). Robust design models estimate rates of temporary emigration by dividing encounters of marked individuals into primary (e.g., a calendar year) and secondary (e.g., months within the year) occasions, where the population in considered open between primary occasions, but assumed to be closed among secondary occasions within each primary occasion. This allows for estimation of temporary emigration ($\gamma$) based on differences in detection probabilities between primary and secondary occasions, as well as estimation of apparent survival rates that are robust to error associated with temporary emigration (Kendal and Nichols 1995, Kendal et al. 1997). We have used these two analyses to support 3 independent studies that focus on: (1) the influence of climatic processes and habitat disturbance on sage-grouse population dynamics; (2) the influence of male breeding propensity on trends derived from lek counts; and (3) the effect of radio-collars on male survival and behavior.

***General modeling approach –*** All demographic analyses were conducted in a general linear modeling framework, and we used an information theoretic approach to model selection (Burnham and Anderson 2002). We evaluated support for explanatory covariates based on their

inclusion in competitive models ($\Delta$AIC <3.0), and their $\beta$ coefficients and associated estimates of variance. All covariates were z-standardized (mean = 0.0, standard deviation = 1.0).

***Female analyses*** - From our female radio-telemetry data, we conducted a known-fate survival analysis to estimate monthly and annual survival of radio collared hens. A known fate analysis estimates period survival from animals whose fates are known for each sampling interval (as opposed to band recoveries where status is not known unless the animal is recovered during an interval). In addition to the known fate analysis, we used our female telemetry data to conduct a multistate analysis, which estimates the probability of transitioning to a defined state based on previous status and explanatory covariates. We used the multistate approach to evaluate determinants of female breeding success and assess heterogeneity in individual quality. We used our nest monitoring data to estimate daily nest survival probabilities and evaluate the influence of ecological covariates on nest success. Using weekly counts of chicks associated with our radio-collared hens, we conducted a Lukac's young survival model to quantify survival rates of chicks from hatch to 45 days. The Lukac's models estimate period survival rates based on repeated counts of young present with marked adults, where detection probability is explicitly incorporated using variation in counts through time.

***Climate and disturbance influence on sage-grouse population dynamics*** - Sage-grouse are adapted to persist in arid environments despite dynamic climatic processes (e.g., drought) that lead to large annual variation in resource availability. We were interested in understanding how sage-grouse vital rates respond to stochastic variation in resources, what the net effect on population growth was, and how habitat disturbance at the landscape scale altered the relationship between resource availability and population processes. To characterize annual variation in resource availability, we estimated annual normalized difference vegetation indices

(NDVI) for our study area using Landsat 4-5 satellite imagery obtained from the Unites States Geological Survey Earth Explorer data viewer (http://edcsns17.cr.usgs.gov/NewEarthExplorer). NDVI provides an index to landscape greenness that is highly correlated with green-leaf area and is commonly used as a surrogate estimate of net primary productivity (Box et al. 1989, Paruelo and Lauenroth 1995). We applied annual NDVI values as group covariates in MARK analyses of male *f* (Pradel Models) and Φ (Robust Design), and tested for the overall effect of resource availability to population growth using a regression where annual λ (Pradel Models) was modeled as a function of NDVI. To evaluate how habitat loss might alter the relationship between resource availability and population dynamics, we also tested for an effect of wildfire and conversion to exotic grassland on Φ and *f*. Here, we quantified the cumulative footprint of wildfires within 5 km of each lek, and applied this value as a lek-level group covariate (Fig 3). We modeled exotic grassland impacts as an additive effect, as well as an interactive effect with NDVI. The later structure allowed us to assess whether the males breeding at leks impacted by fire experienced different population dynamics in response to variable resources compared to males the breed at non-impacted leks. A manuscript describing this analysis is currently in review at the journal Ecosphere.

***Impacts of radio-collars on males*** **-** During our normal spring trapping activities, we marked a subset of male sage-grouse with 22 gram radio-collars in addition to the unique metal and plastic tarsal bands. We used our spring male capture, recapture, and resight data in a robust design framework to estimate differences in detection probability, lek attendance, or survival between males with and without radio-collars. Temporal variation in model structure was similar to previous robust design analyses, and we modeled annual survival ($\Phi$) as a function of NDVI, temporary emigration ($\gamma$) as a function of male density, and allowed full time variation in

encounter and recapture probabilities. Each of the 9 primary occasions (year) was broken up into 3 secondary occasions (3-4 week intervals) which were selected to split the amount physical resights and recaptures relatively evenly amongst the secondary occasions across all years. True detection probability (P*) was calculated annually from the apparent detection probability estimates ($P_1$-$P_3$) for each of the secondary occasions for the corresponding year. The radio covariate was modeled as a time-varying covariate, which allowed new and previously marked individuals to enter the radio-collar cohort upon capture if equipped with a radio-collar. We applied the radio covariate to various combinations of the survival, immigration, detection, and recapture parameters to evaluate any potential relationships between individual parameters and wearing a radio-collar.

***The influence of breeding propensity on lek count trend estimate –*** Lek counts are used universally to track changing abundance of sage-grouse populations, and in some cases are used to infer changes in male abundance from one year to the next (annual population growth). One previously untested assumption is whether variation in male breeding propensity (the proportion of males that attempt to breed in a given year) may introduce sampling error into lek count trends. For each year of the study we estimated annual rates of male breeding propensity (1-$\gamma$) using robust design models, apparent annual population growth using our lek counts ($\lambda_A$), and realized $\lambda$ ($\lambda_R$) using Pradel models. We then used a linear regression to partition the variance in $\lambda_A$ that was associated with realized rate of growth ($\lambda_R$), breeding propensity, and unexplained error. Additionally, we assessed sources of variation in breeding propensity (Age, average male body condition, male density, NDVI, and exotic grassland impacts) to determine if we could identify any general explanations for temporal variation in breeding propensity. Finally, we compared long-term estimates of population growth from lek counts and Pradel models to

evaluate the utility of lek counts for quantifying long-term population trends. A manuscript describing this analysis in greater detail is currently in review at the journal Ecological Applications.

***Female survival and costs of reproduction –*** We conducted a know-fate survival analysis to evaluate temporal variation in female monthly survival rates, to evaluate reproductive costs to survival, and to test for other ecological effects which may influence temporal variation or reproductive costs. We summarized telemetry data into monthly (i.e., the calendar month) encounter histories for each individual. Because monthly telemetry records were incomplete during the winter for some study years, we aggregated November through February telemetry records into a single 4-month interval, and estimated monthly survival during this period as $\Phi_W^{1/4}$. We used individual and group covariate effects to test hypotheses regarding the cost of reproductive activities on subsequent survival, while controlling for potential confounding factors associated with individual age and environmental conditions. We began by evaluating temporal variation in survival by modeling the effects of year, month, and season (where monthly survivals were aggregated based on biologically meaningful time intervals; Breeding = March-May, Summer = June-July; Fall = August – October; Winter = November-February). Using the best supported temporal structure, we then considered the influence of reproductive success as direct effects (effect is applied to the time period immediately following nesting or brooding) and carry-over effects (effect is applied to a later time period). We tested for 2 general forms of reproductive costs; costs associated with successfully hatching a nest, and cost associated with successfully raising a brood. Finally, we considered additional effects of hen age and annual variation in resource variability (indexed by NDVI). We assigned hens a minimum age based on their known age at capture (Chick = 0; subadult = 1; adult = 2), which increased by

one for each year they remained part of the study and incorporated as a time-varying covariate into the analysis. NDVI was applied as a group covariate, and we tested for different seasonal effects of resource availability using models where NDVI effects were applied to specific combinations of seasonal intervals (e.g., the effect of NDVI was different for breeding vs. summer intervals). Where appropriate, we considered interactive effects between covariates (e.g., an interaction between female success and age). We constructed this analysis using telemetry data from March 2003 through February 2011, so as to include 8 complete study years.

***Female breeding success and reproductive heterogeneity –*** Understanding heterogeneity among individuals has recently become a prominent topic in animal ecology. In the case of sage-grouse, reproductive heterogeneity may be an especially important topic, because if there is substantial heterogeneity recruitment (and as a consequence population growth) may be driven by a small subset of high-quality females. We conducted a multi-state analysis where we assigned individuals into successful or unsuccessful breeding states for each year of the study, and estimated the probability of hen success in a given year as a function of previous reproductive status, and other ecological covariates. Hens were considered successful if they hatched a nest and raised $\geq 1$ chick to 45 days of age, and were considered unsuccessful if they either 1) were not found on a nest; 2) failed all nesting attempts; or 3) nested successfully but lost their entire brood prior to 45 days. We modeled the annual probability of transition to the successful state ($\Psi$; analogous to annual probability of success) as a function of previous reproductive state, minimum hen age, and NDVI. For the NDVI covariate, we considered direct (effect of $NDVI_t$ on $\Psi_t$) and carryover (effect of $NDVI_{t-1}$ on $\Psi_t$) effects. Because we did not begin monitoring broods until 2005, this analysis is restricted to females monitored from 2005-2010.

***Nest survival -*** For 2011, we developed a revised nest survival analysis to document potential observer effects on nest survival. Because the data necessary to model observer effects were not collected in 2003-2004, we omitted nests from those years for this analysis. This analysis includes 343 nests initiated from 2005-2011, of which 107 were successful. We modeled daily nest survival rate as a function of different combinations of disturbance, vegetation, spatial, temporal and demographic covariates. Temporal covariates included year and day, an index of annual raven abundance, population, season trapped, and Julian date of nest initiation. Demographic covariates included hen age, nest attempt, and clutch size, respectively. Nest vegetation covariates included percent cover within nest meter$^2$, average forb height within nest meter$^2$, average grass height within nest meter$^2$, average forb height within Daubenmire plots, average grass height within Daubenmire plots, percent shrub cover on the 10m transects, percent sagebrush cover on the 10m transects, and percent non sagebrush shrub cover along 10m transects. Spatial covariates, measured as total area (ha) within 1km of the nest, included wildfire, pinyon-juniper forest, all sagebrush habitat, Wyoming sagebrush habitat, and mountain sagebrush habitat. We also included nest site elevation, distance of nest from the nearest road, and distance of nest from the Falcon-Gondor power line as spatial covariates. Finally, we modeled both a nest visitation and nest flushing time-varying covariate to estimate visitor impacts on nest survival. Vegetative spatial covariates were generated from the Southwest Regional GAP database, The NDOW wildfire data layer, a roads data layer, and a data layer that delineated Falcon-Gondor. Covariates new to this year's analysis included the index of raven densities, and whether a nest was visited or flushed on a given day.

We used a systematic procedure for building competing models of daily nest survival across covariate types and spatial scales. First, we ran a series of basic models that only considered

variation in time structure, and the most competitive of these models was used as the basis for subsequent models. Single covariates were then added to the best time model, and variables with meaningful betas were retained and further combined into more complex models. Interactions between individual covariates were then included and retained if model fitness was improved. After all other model structures were considered, we included visitation and flushed from nest covariates to evaluate the potential impact of observers on nest survival.

***Chick survival to 45 days -*** Lukacs young survival models expand on the standard Cormack-Jolly Seber (CJS) approach by allowing the inclusion of a family size parameter in addition to detection probability and apparent survival parameters. This model design allows us to estimate chick survival using brood count data instead of physical recaptures of marked individuals which is required in normal CJS analyses. We used flush count data collected from 2005-2011 to estimate chick survival from hatch until approximately 45 days. We allowed annual time variation in model selection with constraints on weekly survival. Due to data limitations, the survival parameters for the first 2 weeks and last 4 weeks were constrained together. We modeled full weekly time variation in the detection probabilities with a year constraint grouping 2005-2008 and years 2009-2011 together. This constraint was modeled due a priori knowledge of a change in brood monitoring protocol instituted in 2008 that increased chick detection.

## RESULTS

### Field Results

***Banding -*** During spring trapping we have banded a total of 1023 sage grouse (824 males and 199 females) over nine years of the project (Table 1). During fall trapping, we have banded 264 sage-grouse (155 females, 96 males, and 13 unknown gender chicks) over 7 years. We banded 16 sage-grouse during the 2011 fall trap (12 females and 4 males). With multiple captures of

the same individual within the same year included, we have captured a total of 1674 sage grouse over 9 years of this study.

***Lek Observations*** **-** We conducted 108 total lek observations during the 2011 breeding season. The total number of males observed across all leks continued to show signs of stabilization (Table 2). We observed increased male attendance on 6 leks (Modarelli, Lone Mountain, Kobeh, Gable Canyon), 1 lek no change (Horse Creek) and decreased male attendance on 4 leks (Dome House, Big Pole, Buckhorn, Quartz Road). We discovered either a new lek or movement of the Pony Express lek this year which had a high count of 11 males. We observed no males strutting on Camp lek for the second straight year. The maximum number of females observed attending leks increased substantially between 2010 and 2011 due to one morning's observation of 18 females on Quartz Road lek in 2011 (Table 2). In 2011, we generated 107 total resights of 42 unique individuals, 3 of which were from trail cameras places on leks. Total resights of color-banded individuals by year are summarized in Table 1.

***Raptor Surveys*** **-** In the first 9 years of the study we conducted 199 raptor surveys for a total of 1529 points. The average number per point for each of the most common raptor species has remained relatively stable over the past nine years, however the average number per point Red-tailed hawks (*Buteo jamaicensis),* the most abundant raptor seen, increased threefold between 2010-2011 (Table 3). The average numbers of common ravens seen per point increased dramatically between 2003 and 2007, declined drastically during 2008 to the second lowest level since the project was initiated, and have again increased over the past 3 years to near 2007 levels (Fig 4). A similar, but less pronounced, pattern in common ravens sightings at sage grouse leks has been observed (Fig. 5). Additionally, sage-grouse reactions to raven presence were less apparent in 2011 than in previous years.

***Brood/Chick Monitoring -*** We captured and marked 120, 122, and 110 unique individual chicks from 2009-2011, respectively, and recaptured 14, 26, and 27 of them at approximately 28 days of age. Additionally, we recaptured 19 at approximately 45 days and 7 at approximately 80 days in 2011. Over the past 4 seasons, we have had some success capturing and radio-collaring chicks during the late summer that were marked as day-olds (2008 = 3; 2009 = 2; 2010 = 2; 2011=8). Of these, 4 died between fall and the following spring. One female chick hatched near the Buckhorn Mine in 2009 was monitored through the nesting season in 2010, and unsuccessfully nested in Horse Creek Valley ~ 7.4 km SE of her natal nest. A male chick hatched in the Buckhorn Mine area in 2009 survived through fall 2010, and remained in the Buckhorn Mine area when his signal was last heard. One female chick hatched in 2010 at the north end of the Simpson Park Mountains currently has an active radio and unsuccessfully nested within 1 km of her natal site in 2011. A male marked as a day-old chick in the Buckhorn Mine area was shot and recovered by a hunter in the fall of 2010 in the Cortez Mountains above the Buckhorn Mine. A male marked as a day-old chick in 2009 in the Cortez Mountains west of Cottonwood Canyon was recaptured and radio-collared as an adult in the spring of 2011 and died in late fall of 2011. A female marked as a day-old chick in the summer of 2010 in the Roberts was recaptured with her mother during the late summer of 2011 while associated mother's current brood. In the summer of 2011, 6 female chicks from radio-marked hens were captured and equipped with radio-collars and as of December 2011, 5 are still alive. The female chick that died was originally captured near the nest, captured again 80 days later ~13km from her nest site, and then moved back towards her natal area where her collar was recovered ~4 months later within 1km from her nest site.

***Radio Telemetry & Known Fate -*** A total of 199 females and 61 males have been radio collared during spring in the 9 years of the study. During the fall (in collaboration with NDOW) we have radio collared 140 females of which 83 have been adult birds (>1 year old) and 76 have been young of the year (YOY) hens. We have also radioed 16 YOY males during the fall. The number of females monitored per year and breeding rates are summarized in Table 4.

**Quantitative Analyses**

***Climate and disturbance influence on sage-grouse population dynamics -*** The greatest cumulative support was for models of survival and recruitment that included additive effects of NDVI and exotic grassland, as well as an interaction between the two variables (Table 5). The only recruitment model receiving support showed annual variation in NDVI corresponded closely with temporal variation in recruitment (Fig 6). NDVI covariate values had a strong positive effect on recruitment ($\beta = 0.78$; 95% CI = 0.37 to 1.19), and we observed over a 9-fold increase in per-capita recruitment (defined as recruits in year *t* per returning individual that was present in year *t-1*) following the year of highest NDVI ($f = 0.77 \pm 0.18$ SE) compared to the year of lowest NDVI ($f = 0.08 \pm 0.03$ SE). Lek-level recruitment was negatively correlated with the extent of exotic grassland surrounding the lek, and the interaction between exotic grassland and NDVI received stronger support ($\beta = -0.62$; 95% CI = -0.82 to -0.41) than an additive effect of exotic grassland alone ($\beta = -0.02$; 95% CI = -0.19 to 0.16). The interaction effect showed that leks impacted by exotic grasslands did not experience high rates of recruitment, even during years of high resource availability, but instead had low and stable recruitment of males throughout the study (Fig 7). In contrast, in the year of highest NDVI, leks that were not impacted by exotic grasslands experienced levels of recruitment nearly 70% greater than the population average ($f = 1.30 \pm 0.26$ SE).

Robust design survival models also indicated a positive influence of NDVI on survival (Fig. 6), however, 95% confidence intervals of parameter coefficients overlapped 0.0 (β = 0.28; 95% CI = -0.07 to 0.62), and the effect did not produce a comparable level of annual variation in Φ as for *f* (Table 6). We found a general negative impact of exotic grasslands on lek-level survival (β = - 0.29; 95% CI = -0.55 to -0.03) that again interacted with NDVI. The interaction effect did not, however, differ significantly from 0.0 (β = 0.21; 95% CI = -0.50 to 0.08). We thus observed strong support for an interaction effect between NDVI and exotic grassland in recruitment models, whereas support for an interaction effect between NDVI and exotic grasslands was weaker in survival models. Conversion of sagebrush to exotic grassland therefore appeared to disrupt the relationship between resource availability and recruitment, while lowering adult survival was not as directly associated with available resources (Fig 7).

A substantial amount of the overall variation in population growth was explained by annual variation in NDVI (Fig 8); the general linear model relating $\lambda_t$ to $NDVI_t$ explained approximately 95 % of the variance in population growth during the course of our study ($R^2 = 0.95$, $F_6 = 88.69$, $P < 0.001$). Male abundance fluctuated widely during our study, from a high of 612 males in 2005 to a low of 172 males in 2010 (Table 7).

These results demonstrate the important relationship between climate-driven variation in food resources and sage-grouse population dynamics. To better understand how climatic processes influence annual variation in NDVI, we ran a regression comparing NDVI to annual variation in precipitation and evaporation (derived from nearby National Climatic Data Center weather stations). This regression demonstrated a strong association between NDVI and these two climate variables ($R^2 = 0.71$, $F_7 = 6.09$, $P = 0.046$), where NDVI was higher (and consequently the sage-grouse experienced greater fitness) following years of high levels of precipitation and

cool springs with low rates of evaporation. This analysis also further clarifies the negative influence of exotic grassland conversion on sage-grouse vital rates, and shows these negative impacts occur primarily through a reduction in high rates of recruitment during favorable conditions. Consequently habitat restoration following wildfire should concentrate on mitigating fire effects on native plant communities known to be important to reproductive components (e.g., chick survival).

***Impacts of radio-collars on males –*** Top models suggested a significant negative effect of having a radio-collar on both the encounter and recapture probabilities (**β** = -0.262 95% CI = -0.441 to -0.083) and a significant positive effect on **γ** (**β** = 0.542 CI = 0.061 to 1.024), however inclusion of an effect of radio-collar on survival did not improve model fitness and confidence intervals on radio-collar beta on survival overlapped zero (**β** = -0.101 95% CI:-0.456 – 0.254) (Table 8). Model average results indicate radio-collared male sage-grouse were less likely to attend a lek in a given year (mean $\gamma$ = 0.702 ± 0.201 SE) or less likely to be detected on a lek (mean P* = 0.332 ± 0.153 SE) if present than banded-only males (mean $\gamma$ = 0.275 ± 0.219 SE; mean P* = 0.615 ± 0.155 SE)(Fig. 9), however no support for an effect of radio-collars on male survival was found. This preliminary analysis supports that equipping males with radio-collars may substantially alter their breeding behavior by lowering either the overall probability of breeding or rates of lek attendance for males that do attempt to breed. We suggest that researchers who making inferences about male sage-grouse behavior or demographic rates that are generated from radio-collared males should viewed cautiously.

***The influence of breeding propensity on lek count trend estimates -*** Effects of male density, exotic grasslands, male age, and male condition were all included in one or more competitive Robust design model of $\gamma$. Of these, there was relatively little support for meaningful effects of

male condition and age. A lag effect of male density, and landscape conversion to exotic grassland received greater support. Inclusion of exotic grassland impacts substantially improved model fit, and all competitive models contained this effect (Table 9). Parameter coefficients show a negative relationship between exotic grassland impact at leks and rates of temporary absence ($\beta$ = -2.15, 95% CI = -4.18 to 0.18), suggesting breeding propensity was higher at leks impacted by wildfire. However, the large range of variance and confidence intervals that slightly overlapped 0.0 indicates uncertainty about this effect. Male density, indexed by autoregressed counts of males attending leks, was positively related to temporary emigration (and hence negatively related to breeding propensity). Inclusion of density as a linear or quadratic effect improved overall model fit (Table 9), and parameter coefficients indicated stronger support for the linear effect ($\beta$ = 0.70, 95% CI = 0.19 to 1.21) compared to the quadratic effect ($\beta$ = 0.39, 95% CI = -0.13 to 0.92). Model-averaged estimates of $\gamma$ indicate a general decline in breeding propensity following years of high density (Fig 10).

The most competitive Pradel $\lambda$ model indicated a positive relationship between NDVI and $\lambda_R$ ($\beta$ = 0.37, 95% CI = 0.21 to 0.54)(Table 10). Estimates of general population trajectory (i.e., increase or decline) were similar between $\lambda_A$ and $\lambda_R$, however, annual estimates of $\lambda_A$ only fell within 95% confidence intervals of model-averaged $\lambda_R$ in 3 of 7 intervals (Fig. 11). Nevertheless, variance partitioning indicated a strong relationship between $\lambda_A$ and $\lambda_R$, where 76% of the variance in lek counts reflected variation in realized population growth (semipartial $R^2$ = 0.76). Variation in breeding propensity explained approximately 18% of the variance in $\lambda_A$ (semipartial $R^2$ = 0.18), indicating that 75% of the total error in lek count estimates of population growth was attributed to annual variation in male breeding propensity (based on the ratio of variance associated with breeding to total variance not associated with $\lambda_R$). Approximately 94%

of the overall variation in lek counts could be attributed to realized growth and breeding propensity ($R^2$ = 0.94, $F_7$=37.81, $P$ =0.001). The remaining 25% of total error (6 % of the total variance in lek counts) was attributed to other sources of unidentified error. Long-term estimates of $\lambda_A$ ($\lambda_A$ = 0.896 ± 0.047) and $\lambda_R$ ($\lambda_R$ = 0.912 ± 0.051) showed substantially greater agreement than annual estimates. Confidence intervals from the two estimates widely overlapped, indicating the two long-term estimates were not significantly different from each other.

This analysis demonstrates that annual variation in lek counts should not be used to infer rate of population change from one year to the next, because in the absence of marked individuals it is impossible to disentangle true population decline from temporary absence due to low breeding propensity. For this reason, inferences from lek counts should be restricted to detecting general patterns and quantifying long-term trends. A secondary result of this analysis is that male breeding propensity was highest at leks impacted by exotic grasslands. At this point the biological mechanisms for this phenomenon are unclear, however this result has important implications for monitoring populations following disturbance, because high rates of breeding propensity among remaining individuals may partially obscure the true population-level impact of disturbance, relative to control leks.

***Female survival and costs of reproduction –*** The best modeled structure of monthly female survival (Table 11) included an effect of season (Spring, Summer, Fall, Winter), effects of successfully hatching a nest on summer survival and successfully raising a brood on fall survival, an effect of hen age, and independent effects of NDVI on spring survival, and on summer/fall survival. The model also contained an interaction between the effect of successfully raising a brood on fall survival, and age. Monthly survival was highest during the winter (November-February; $\Phi_W$ = 0.983 ± 0.003), followed by summer (June-July; $\Phi_S$ = 0.980 ± 0.006), breeding

(March-May; $\Phi_B = 0.947 \pm 0.007$), and fall (August-October; $\Phi_F = 0.922 \pm 0.009$)(Fig 12). There was a negative effect of nesting successfully on summer survival ($\beta = -0.401$; 95% CI = -0.842 to 0.041), and also a negative effect of successfully raising a brood on fall survival ($\beta = -0.176$; 95% CI = -0.400 to 0.048). The net negative effect of successfully reproducing resulted in annual survival rates for successful hens of $0.498 \pm 0.057$, compared to annual survival of $0.610 \pm 0.026$ for unsuccessful hens (Fig 12). Survival generally decreased with hen age ($\beta = -0.090$; 95% CI = -0.258 to 0.078), but this effect interacted with successfully raising a brood ($\beta = -0.221$; 95% CI = -0.452 to 0.010), such that survival decreased with age primarily for successful females (Fig 13). Finally, we found independent and opposing effects of NDVI on seasonal survival. During the spring, survival increased in years with higher NDVI ($\beta = 0.513$; 95% CI = 0.096 to 0.930). In contrast, summer and fall survival was lower in years with higher NDVI ($\beta = -0.162$; 95% CI = -0.380 to 0.057). The net effect, however, was a general positive association between NDVI and annual survival (Fig 14).

Evaluating reproductive costs is a cornerstone of the study of life history evolution, and our research represents the first such assessment for sage-grouse. We continue to show the spring breeding season and fall period contain the highest mortality rates for female sage-grouse, and this analysis confirms previous analyses showing much of the increased mortality during the fall can be attributed to costs associated with successfully raising a brood. Additionally, the overall positive association between annual female survival (Fig 14) and NDVI shows the same climatic processes that influence male survival also act on the female segment of the population. This analysis allows us to better understand the underlying mechanisms for this positive association, because we have demonstrated the positive effect of NDVI is primarily related to increased survival during the spring breeding season. One biologic explanation for this result may be that

increased availability of high-quality food resources in “good” years (e.g., years with earlier or more rapid green-up) reduces the time females must devote to foraging, allowing them to increase the number of resources they devote to predator avoidance.

***Female breeding success and reproductive heterogeneity -*** The best-performing multistate model (Table 12) allowed the probability of female success to vary according to previous reproductive state, and included a direct effect of NDVI on the current year’s reproductive success. Females who successfully raised a brood in year *t-1* were more than twice as likely to raise a brood again in the year *t* ($\Psi_S = 0.277 \pm 0.089$) compared to females who were unsuccessful in year *t-1* ($\Psi_U = 0.094 \pm 0.025$). There was a direct positive effect of NDVI on female breeding success ($\beta = 1.336$; 95% CI = 0.142 to 2.529); years with high resource availability produced higher rates of female success for both reproductive states (Fig 15). For previously successful hens, annual probability of success ranged from $0.438 \pm 0.134$ in 2006, to a low of $0.141 \pm 0.075$ in 2008. For previously unsuccessful hens, annual probability of success ranged from $0.191 \pm 0.067$ in 2006, to a low of $0.047 \pm 0.022$ in 2008 (Fig 15). The overall probability of female success, averaged across all individuals from 2006-2010, was $0.123 \pm 0.026$.

The implications of this analysis are three-fold. First, the probability of reproductive success is generally very low. Second, in spite of this low overall success rate, there appears to be substantial reproductive heterogeneity within this population. Although overall success is low, females who are successful once are far more likely to be successful again than females who repeatedly fail. Because of this effect, the loss of one high-quality hen will have a substantially greater influence at the population level than the loss of one low-quality hen. Finally, the positive influence of NDVI on reproductive success reinforces the importance of environmental

conditions and resource availability to sage-grouse population dynamics, and provides one potential mechanism for the positive association we have found between annual recruitment rates and NDVI in other analyses.

***Nest Success -*** Overall model-averaged daily nest survival for the study area was 0.951 (± 0.009 SE) with an overall probability of nest success based on a 37-day nesting period of 0.152 (± 0.007 SE). The best model contained additive, positive effects of clutch size (β = 0.327, 95% CI = 0.180 to 0.474), distance from nearest road (β = 0.116, 95% CI = -0.032 to 0.264), grass height within 100 $m^2$ of the nest (β = 0.175, 95% CI = 0.003 to 0.323), coverage of non-sagebrush shrubs within 100 $m^2$ of the nest (β = 0.171, 95% CI = 0.008 to 0.334), distance from Falcon-Gondor (β = 0.157, 95% CI = -0.008 to 0.321), and nest site elevation (β = 0.116, 95% CI = -0.040 to 0.273) (Table 13)(Fig 16). In addition, we found negative effects of the season the hen was trapped (β = -0.230, 95% CI= -0.371 to -0.088), total hectares of wildfire-impacted area within a 1 km radius of the nest (β = -0.142, 95% CI = -0.302 to 0.017), and flushing a hen from a nest (β = -0.112, 95% CI = -0.230 to 0.006) (Fig 16). Finally, there were negative interactions between distance from road and wildfire (β = -0.181, 95% CI = -0.401 – 0.039) as well as road distance and distance from Falcon-Gondor (β = -0.112, 95% CI = -0.250 – 0.025)(Fig. 17).

The interaction between wildfire and road distance continued to perform well in model selection (Table 13). This interaction suggests that benefit of being further away from roads on nest survival is effectively removed in the presence of wildfire scarring, which supports our continued documentation of negative impacts of invasive grasses on sage-grouse vital rates (Fig 17). The interaction between distance from Falcon-Gondor and distance from roads on nest survival is not as intuitively clear (Fig 17). Although, one possible explanation is that the probability of nest survival increases as a nests distance from both Falcon-Gondor and roads

increases, however we feel that this interaction is an artifact of various spatial factors that are confounded with distance from the Falcon-Gondor line, such as elevation and overall habitat quality.

The visitation covariate was used to detect a difference between the daily nest survival rate on days a nest was visited and on days a nest was not visited, however models considering this covariate did not perform well in model selection (Table 13), and suggested no substantial negative impact of visiting a nest and nest survival ($\beta = 0.066$, 95% CI = -0.148 – 0.279). Model results suggested a lower daily survival rate for the day following flushing a hen from a nest (0.908 ± 0.029 SE) compared to the day a hen was not flushed (0.950 ± 0.009 SE). However, there was not a substantial difference between overall nest survival probabilities from a nest that was flushed (0.152 ±0.007 SE) compared with a nest that was not flushed (0.160 ±0.006 SE) (Fig 18). Given the results from this analysis, we feel that the data gained from a more active nest monitoring protocol, i.e. better estimates of clutch size, initiation date, cause of nest failures, higher probability of chick captures, are worth the slight decrease in daily nest survival rates.

***Chick Survival –*** Model-averaged results supported a large amount of annual variation in chick survival, with noticeable boom and bust periods (Fig 19). Additionally, top models supported a population-level interaction during the first 2 weeks survival post-hatch (Table 14). Here, chicks associated with Robert Creek Mountain had significantly lower survival (0.354 ±0.057 SE) during the first 2 weeks than chicks associated with the Cortez Mountains (0.533 ±0.056 SE) (Fig 20), which we hypothesize is related to differences in the average distance a brood must move to reach high quality brood habitat from their natal habitat between the Roberts and Cortez range. A quadratic relationship between hatch date and survival was also supported, suggesting chicks from early or late nests had a higher probability of surviving until 6 weeks than chicks

hatched around the mean hatching date (Fig 21). The quadratic interaction with hatch date could potentially be explained by a density-dependent predator response. Chicks hatched from early nests may have an advantage because predators have not adjusted their foraging behavior to look for chicks. As more chicks hatch, predators start to key in on the abundant food source, lowering chick survival. However, as the season progresses, the weaker chicks have already been removed from the landscape, and overall chick survival increases again. A similar hypothesis could be made in a density-dependant resource acquisitioning framework, in which intraspecific competition for resources drives the quadratic trend.

Overall chick survival to 45 days ranged from a high of 0.485 (±0.040 SE) in 2005 to a low of 0.053 (±0.015 SE) in 2007 (Fig 19). Our best models support that chick survival has steadily increased after the period of extremely low survival in 2007. In 2011, chick survival was estimated to be 0.409 (±0.028 SE). Chick survival estimates in all years other than 2007 were comparable to other studies of chick survival (Walker 2008, Dahlgren 2009). The fluctuations in chick survival illustrate one of the challenges with monitoring sage-grouse demographic rates across short time scales. The boom-bust nature of chick survival is most likely tied to plant productivity and precipitation events during key periods of the year. Studies that are monitoring sage-grouse during a short period that consist of all wet or all dry years potentially could misinterpret their results, leading to biased estimates of chick survival. Lastly, studies that attempt to artificially inflate nest survival through predator or raven control have to consider the interactions between environmental conditions and chick survival. Inflating the probability of nest survival may have no effect on sage-grouse recruitment if the experimental phase occurs during period of low chick survival.

## CONCLUSIONS

We've continued to document demographic differences between the Roberts Creek and Cortez populations; however the unexplained proportion of this effect has declined as we have continued to integrate more mechanistic components to our analyses. In particular, we have shown wildfire impacts to be important determinants of male survival and nest success, and the overall high impact of fire in the Cortez range likely contributes to lower demographic rates there. However, we have preliminary results that support the costs of reproduction on female survival are less severe in the Cortez population than in the Roberts Creek population, which also coincides with higher chick survival estimates in the Cortez range. A potential hypothesis for the discrepancies in brood rearing/survival demographic rates between the 2 populations is that the average distance a brood must move from nesting habitat to high quality brood rearing habitat is much shorter in the Cortez range than in the Roberts Creek range. The increased distance that the average Roberts Creek brood flock has to move may not only be lowering chick survival, but decreasing the fitness of a successful female, lowering the probability of her survival.

The sage-grouse population in our study area continued to appear to have stabilized based on patterns in lek attendance and male capture-recapture estimates. Increased captures of new males on our study leks in 2011 suggested that recruitment was higher into this spring than the 2 years prior. The fall trap with NDOW was moderately successful in 2011, we continued to have great success in the Cortez range but substantially fewer grouse were seen in the Roberts Creek range. Despite the lack of chicks seen in the fall trap in the Roberts, estimates of chick survival were significantly higher in 2011 than the 2 years prior. We are predicting that recruitment of this year's chick cohort will be apparent in next year's capture-recapture data.

Our male capture/recapture analysis has allowed us to quantify male demographics and better evaluate the efficacy of male-based population monitoring. Our results have major implications for the application of lek counts. We suggest that interpretation of short-term fluctuations in lek counts be discouraged, as these changes may be subject to sampling error associated with variation in male breeding propensity. Lek count use and interpretation should therefore be limited to quantifying long-term trends. Additionally, the preliminary results from our male radio-collar capture/recapture data suggest additional errors with lek counts that involve radio-collared male individuals.

Modeling observer effect on nest survival is not a novel concept (Sedinger 1990, Rotella et al. 2000, Jehle et al. 2004, Bentzen et al. 2008), however research on observer effects in nest survival of sage-grouse has not been conducted previously. Despite the lack of rigorous evidence for visitation effects, previous authors have repeatedly suggested that sage-grouse nest abandonment due to observer disturbance are substantial (Fischer *et al*. 1993, Sveum *et al*. 1998, Wik 2002, Chi 2004, Holloran *et al*. 2005, Kaiser 2006, Baxter *et al*. 2008). Critics have suggested that the lower nest survival estimates maximum likelihood approaches normally produce, compared to apparent nest survival estimates, are a result of increased abandonment due to the more aggressive monitoring methodology (Connelly *et al.* 2011). However, minimizing the observer impact during nest such as by radio triangulation, longer intervals between nest checks, or delaying when observers start looking for nests, increases the probability of missing nests completely and further inflates apparent nest survival estimates. Our results support that our current monitoring protocols, including the abandonments associated with flushing, are not significantly lowering overall nest success rates, or overly biasing our nest survival estimates.

Our new chick survival analysis framework will allow us to develop more precise estimates of chick survival using less invasive and time intensive measures. We plan to add more covariates to the analysis over the next year that will allow us to gauge the relative importance of food availability, movement rates, and various environmental factors on overall chick survival. Additionally, we will continue to collect novel descriptive data on the behavior of sage-grouse with known mothers. Our capture of a juvenile female with her mother's current brood, in the summer of 2011, was the first record of fledged offspring being associated with her mother's brood. Also, our records of juvenile females returning to be within a kilometer of their natal sites offer insights to sage-grouse dispersal.

One of the more interesting results of our demographic analyses has been evidence for heterogeneity in survival of females related to their reproductive status. The positive effect of hatching a nest on monthly and annual survival, and the positive effect of clutch size on nest success, suggests that high-quality females are substantially more successful than their low-quality counterparts. However, this year we have identified decreased fall survival for females that successfully raise broods, and the effect may be more pronounced for the Roberts Creek population. Thus, there may be a trade-off between individual quality and costs of reproduction, and factors that influence survival of high-quality brood hens in the fall may be of particular management concern.

We've documented a positive association between NDVI and multiple sage-grouse vital rates, including male annual survival, female monthly survival during the breeding season, per-capita recruitment of males, and female breeding success. For female sage-grouse, breeding season survival was 8% greater, and breeding success was over 400% greater, in the year of highest compared to lowest NDVI. For male sage-grouse, annual survival was 37% greater, and per-

capita recruitment was more than 900% greater, in the year of highest compared to lowest NDVI. The consequences of low plant production to sage-grouse populations therefore appear to be slight reductions in adult survival and major reductions in reproductive output. The net effect of these demographic fluctuations was a strong positive relationship between NDVI and sage-grouse population growth. In our study system patterns in NDVI were driven by annual variation in precipitation and evaporation ($R^2 = 0.71$, $F_7 = 6.09$, $P = 0.046$). These results emphasize the importance of climatic processes for driving temporal dynamics of sage-grouse populations, and have provided us with new insights into how sage-grouse respond to environmental variation in the arid Great Basin.

**Literature Cited**

Alstatt. A.L. 1995. The potential impact of raven predation on sage-grouse production in Nevada. MS Thesis. University of Nevada, Reno.

Anderson, D.R., K.P. Burnham, and W.L. Thompson. 2000. Null hypothesis testing: problems prevalence and an alternative. Journal of Wildlife Management 64:912-923.

Aspbury, A.S., and R.M. Gibson. 2004. Long-range visibility of greater sage grouse leks: a GIS-based analysis. Animal Behavior. 67:1127-1132.

Baxter, R. J., J. T. Flinders, and D. L. Mitchel. 2008. Survival, movements, and reproduction of translocated greater sage-grouse in Strawberry Valley, Utah. Journal of Wildlife Management 72: 179-186.

Beck, J.L., and D.L. Mitchell. 2000. Influences of livestock grazing on sage grouse habitat. Wildlife Society Bulletin 28:993-1002.

Beck, T.D.I. 1977. Sage grouse flock characteristics and habitat selection during winter. Journal of Wildlife Management. 41:18-26.

Becker, P.H., and W. Wendeln. 1997. A new application for transponders in population ecology of the Common Tern. Condor 99:534-538.

Bentzen, R. L., A. N. Powell, and R. S. Suydam. 2008. Factors influencing nesting success of King Eiders on northern Alaska's coastal plain. Journal of Wildlife Management 72: 1781-1789.

Blomberg, E. J., D. V. Nonne, and J. S. Sedinger. 2010. Dynamics of Greater Sage-grouse (*Centrocercus urophasianus*) Populations in Response to Transmission Lines in Central Nevada: Year 8 Progress Report. Unpublished report, University of Nevada, Reno.

Box, E. O., B. N. Holben, and V. Kalb. 1989. Accuracy of the AVHRR vegetation index as a predictor of biomass, primary productivity and net co2 flux. Vegetatio 80:71-89.

Boyko, A.R., R.M. Gibson, and J.R. Lucas. 2004. How predation risk affects temporal dynamics of avian leks: Greater Sage Grouse versus Golden Eagles. American Naturalist 163:154-165.

Braun, C.E. 1998. Sage-grouse declines in western North America: what are the problems? Proceeding of the Western Association of State Fish and Wildlife Agencies 78:139-156.

Bureau of Land Management. 2001. Falcon to Gondor 345kv Transmission Project: Environmental impact statement and resource management plan amendments. Bureau of Land Management. Battle Mountain, Nevada USA.

Carver, A.V., L.W. Burger, and L.A. Brennan. 1999. Passive integrated transponders and patagial tag markers for Northern Bobwhite chicks. Journal of Wildlife Management 63:162-166.

Connelly, J.W., A.D. Apa, R.B. Smith and K.P. Reese. 2000. Effects of predation and hunting on adult sage-grouse (*Centrocercus urophasianus*) in Idaho. Wildlife Biology 6:227-232.

Connelly, J.W., S.T. Knick, M.A. Schroeder, and S.J. Stiver. 2004. Conservation Assessment of Greater Sage-Grouse and Sagebrush Habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming.

Connelly, J.W., M.A. Schroeder, A.R. Sands, and C.E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin. 28:967-985.

Connelly, J.W., W.L. Wakkinen, A.D. Apa, and K.P. Reese. 1991. Sage grouse use of nest sites in Southeastern Idaho. Journal of Wildlife Management 55:521-524.

Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and Dynamics of greater sage-grouse populations. Studies in Avian Biology 38: 53-68.

Crawford, J.A., and M.A. Gregg. 2001. Survival of sage grouse chicks in the Northern Great Basin. 2000 Annual Report. Unpublished.

Crawford, J.A., R.A. Olson, N.E. West, J.C. Mosely, M.A. Schroeder, T.D. Whitson, R.F. Miller, M.A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management. 57:2-19.

Crawley, M. J. 2005. Statistics: An Introduction using R. John Wiley & Sons Ltd., England.

Dahlgren, D.K. 2009. Greater sage-grouse ecology, chick survival, and population dynamics, parker mountain, Utah. Dissertation, Utah State University, Logan, UT, USA.

Dalke, P.D., D.B. Pyrah, D.C. Stanton, J.E. Crawford, and E.F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. Journal of Wildlife Management. 27:811-841.

Elbin, S.B., and J. Burger. 1994. Implantable microchips for individual identification in wild and captive populations. Wildlife Society Bulletin 22:677-683.

Ellis, K.L. 1984. Behavior of lekking sage grouse in response to a perched Golden Eagle. Western Birds 15:37-38.

Fischer, R. A., A. D. Apa, W. L. Wakkinen, K. P. Reese, and J. W. Connelly. 1993. Nesting-area fidelity of sage-grouse in southeastern Idaho. Condor 95: 1038-1041.

Giesen, K.M., T.J. Schoenberg, and C.E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224-231.

Gregg, M.A., J.A. Crawford, M.S. Drut, and A.K. Delong. 1994. Vegetational cover and predation of sage grouse nests in Oregon. Journal of Wildlife Management 58:162-166.

Hall, F., and E. Haney. 1997. Distribution and trend of sage grouse (*Centrocercus urophasianus*) in relation to overhead transmission lines in Northeastern California. California Department of Fish and Game. Unpublished Report.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69: 638-649.

Jehle, G., A. A. Yackel Adams, J. A. Savidge, and S. K. Skagen. 2004. Nest survival estimation: A review of alternatives to the Mayfield estimator. Condor 106: 472-484.

Kaiser, R. C. 2006. Recruitment by greater sage-grouse in association with natural gas development in Western Wyoming. M.S. thesis. University of Wyoming, Larimie, WY.

Kendall, W. L., and J. D. Nichols. 1995. On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. Journal of Applied Statistics 22:751-762.

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration and breeding proportions using capture-recapture data with Pollock's robust design. Ecology 78:563-578.

Nevada Sage Grouse Project. 2001. Nevada sage-grouse conservation strategy. Governor's Sage-Grouse Conservation Team. Nevada Division of Wildlife, Reno, Nevada.

Paruelo, J. M. and W. K. Lauenroth. 1995. Regional patterns of normalized difference vegetation index in North American shrublands and grasslands. Ecology 76:1888-1898.

Rotella, J. J., M. L. Taper, and A. J. Hansen. 2000. Correcting nesting-success estimates for observer effects: maximum-likelihood estimates of daily survival rates with reduced bias. Auk 117:92-109.

Schroeder, M.A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in North-Central Washington. Condor 99:933-941.

Schroeder, M.A., and C.E. Braun. 1991. Walk-In traps for capturing Greater Prairie-Chickens on leks. Journal of Field Ornithology 62:378-385.

Sedinger, J.S. 2007. Improving understanding and assessment of greater sage-grouse populations. University of Idaho College of Natural Resources Experiment Station Bulletin 88: 43-56.

Sveum, C. M., Edge, D.W. and Crawford, J.A. 1998. Nesting habitat selection by sage grouse in south-central Washington. Journal of Range Management 51:265-269.

Wakkinen, W.L., K.P. Reese, J.W. Connelly, and R.A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin, 20:425-426.

Walker, B.L. 2008. Greater sage-grouse response to coal-bed natural gas development and West

Nile virus in the Powder River Basin, Montana and Wyoming, USA. Dissertation. The University of Montana. Missoula, MT, USA. 218 pp.

Wallestad, R., and D.P. Pyrah. 1974. Movement and nesting of sage grouse hens in Central Montana. Journal of Wildlife Management 38:630-633.

Wallestad, R., J.G. Peterson, and R.L. Eng. 1975. Foods of adult sage grouse in central Montana. Journal of Wildlife Management 39:628-630.

Walsh, D.P. 2002. Population estimation techniques for greater sage-grouse. Thesis, Colorado State University, Fort Collins, Colorado, USA.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (suppl):120-139.

Wik, P. A. 2002. Ecology of greater sage-grouse in south-central Owyhee County, Idaho. M.S. thesis, University of Idaho, Moscow, ID.

Table 1. Number of males captured, recaptured, and resighted during spring trapping. Number of unique individuals is shown in parentheses.

| Year | New Captures | Recaptures | Resights | Collared Males |
|---|---|---|---|---|
| 2003 | 146 | 26(20) | 12(11) | 7 |
| 2004 | 106 | 43(36) | 41(26) | 5 |
| 2005 | 104 | 55(48) | 37(25) | 1 |
| 2006 | 134 | 37(35) | 56(35) | 1 |
| 2007 | 113 | 37(30) | 34(12) | 4 |
| 2008 | 62 | 30(26) | 91(45) | 14 |
| 2009 | 46 | 50(34) | 59(23) | 9 |
| 2010 | 50 | 35(31) | 109(33) | 22 |
| 2011 | 63 | 44(30) | 107(42) | 23 |
| Total | 824 | 357(227) | 546(181*) | 61* |

* Does not account for unique individuals monitored across study years.

Table 2. Highest single day lek attendance for each lek by sex and year.

**Males**

| Lek | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 |
|---|---|---|---|---|---|---|---|---|---|
| Big Pole | 13 | 16 | 20 | 19 | 11 | 21 | 22 | 25 | 13 |
| Buckhorn | 23 | 39 | 40 | 48 | 21 | 10 | 11 | 7 | 3 |
| Camp | 8 | 12 | 9 | 9 | 7 | 5 | 4 | 0 | 0 |
| Dome House | 15 | 17 | 28 | 47 | 22 | 23 | 12 | 17 | 9 |
| Gable Canyon | 18 | 21 | 30 | 23 | 12 | 19 | 19 | 7 | 12 |
| Horse Creek | 43 | 61 | 40 | 31 | 17 | 15 | 4 | 8 | 8 |
| Henderson Pass | | | | | | 27 | 16 | 7 | 8 |
| Kobeh | 14 | 10 | 12 | 54 | 6 | 7 | 6 | 9 | 14 |
| Lone Mountain | 32 | 33 | 50 | 63 | 56 | 34 | 22 | 17 | 30 |
| Modarelli Mine | 11 | 9 | 23 | 47 | 17 | 23 | 16 | 19 | 28 |
| Pinefield | 36 | 37 | 49 | 67 | 34 | 27 | 22 | 29 | 30 |
| Pony Express | 14 | 11 | 15 | 15 | 10 | 6 | 8 | 0 | 11 |
| Quartz Road | | | | 34 | 11 | 22 | 20 | 36 | 27 |
| **Total** | **227** | **266** | **316** | **423*** | **224** | **212*** | **182** | **181** | **193** |

**Females**

| Lek | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 |
|---|---|---|---|---|---|---|---|---|---|
| Big Pole | 2 | 6 | 2 | 6 | 0 | 5 | 0 | 0 | 4 |
| Buckhorn | 12 | 3 | 5 | 24 | 6 | 7 | 6 | 4 | 2 |
| Camp | 0 | 0 | 1 | 4 | 3 | 2 | 1 | 1 | 0 |
| Dome House | 1 | 5 | 4 | 5 | 3 | 8 | 5 | 1 | 2 |
| Gable Canyon | 3 | 6 | 2 | 3 | 1 | 2 | 2 | 1 | 1 |
| Horse Creek | 22 | 28 | 4 | 4 | 1 | 6 | 2 | 1 | 0 |
| Henderson Pass | | | | | | 8 | 6 | 3 | 3 |
| Kobeh | 5 | 3 | 2 | 4 | 1 | 1 | 2 | 7 | 1 |
| Lone Mountain | 3 | 7 | 17 | 11 | 14 | 12 | 6 | 2 | 10 |
| Modarelli Mine | 1 | 8 | 2 | 2 | 4 | 9 | 3 | 3 | 5 |
| Pinefield | 5 | 7 | 13 | 18 | 8 | 8 | 2 | 3 | 3 |
| Pony Express | 1 | 1 | 1 | 6 | 3 | 1 | 0 | 0 | 2 |
| Quartz Road | | | | 2 | 2 | 2 | 3 | 8 | 18 |
| **Total** | **55** | **74** | **53** | **87*** | **46** | **69*** | **38** | **34** | **51** |

*Does not include increase associated with the addition of new study leks

Table 3. Average number per point of the most common raptor and corvid species seen across all three transects combined, during the months of March, April, and May.

| Species | **2003** | **2004** | **2005** | **2006** | **2007** | **2008** | **2009** | **2010** | **2011** |
|---|---|---|---|---|---|---|---|---|---|
| Common Raven | 0.87 | 0.41 | 1.03 | 1.93 | 2.7 | 0.79 | 1.32 | 1.49 | 2.52 |
| American Kestrel | 0.1 | 0.17 | 0.1 | 0.19 | 0.03 | 0.14 | 0.21 | 0.08 | 0.1 |
| Golden Eagle | 0.12 | 0.05 | 0.02 | 0.07 | 0.14 | 0.03 | 0.07 | 0.08 | 0.05 |
| Ferruginous Hawk | 0.05 | 0.01 | 0.03 | 0.05 | 0.02 | 0.03 | 0.07 | 0 | 0.03 |
| Red-tailed Hawk | 0.05 | 0.02 | 0.04 | 0.06 | 0.02 | 0.08 | 0.1 | 0.06 | 0.18 |
| Swainson's Hawk | 0.04 | 0 | 0.01 | 0.03 | 0 | 0.01 | 0 | 0 | 0 |
| Northern Harrier | 0.03 | 0.01 | 0.04 | 0.03 | 0 | 0.01 | 0.06 | 0.01 | 0.05 |
| Prairie Falcon | 0 | 0 | 0.01 | 0.01 | 0 | 0.01 | 0.02 | 0 | 0 |
| Rough-legged Hawk | 0.01 | 0.01 | 0 | 0.01 | 0.05 | 0 | 0.05 | 0.01 | 0 |
| Total Points Surveyed | 201 | 329 | 144 | 159 | 88 | 185 | 161 | 152 | 110 |

Table 4. Number of radioed females and female reproductive statistics by year.

| | **2003** | **2004** | **2005** | **2006** | **2007** | **2008** | **2009** | **2010** | **2011** |
|---|---|---|---|---|---|---|---|---|---|
| # of Radioed Hens | 15 | 21 | 32 | 61 | 71 | 45 | 66 | 75 | 67 |
| # of Hens Nested | 11 | 16 | 30 | 45 | 30 | 32 | 51 | 61 | 51 |
| # of Hens Failed 1st | 6 | 9 | 22 | 25 | 21 | 26 | 15 | 46 | 35 |
| # of Hens Renest | 1 | 4 | 8 | 1 | 1 | 8 | 17 | 18 | 9 |
| # Hatch | 5 | 7 | 12 | 20 | 10 | 7 | 20 | 20 | 18 |
| # With Brood at 45 Days | | | 9 | 11 | 3 | 5 | 9 | 10 | 10 |

Table 5. Performance of known-fate models of female sage-grouse monthly survival in Eureka County, NV.

| Model[a] | Δ AICc | wi | No Param | Deviance |
|---|---|---|---|---|
| $\Phi$ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_B$ + $NDVI_{SF}$ | 0.000 | 0.374 | 10 | 1271.273 |
| $\Phi$ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_B$ | 0.025 | 0.369 | 9 | 1273.311 |
| $\Phi$ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_{SF}$ | 4.878 | 0.033 | 9 | 1278.164 |
| $\Phi$ Season + $Nest_S$ + $Brood_F$ * Age | 4.975 | 0.031 | 8 | 1280.274 |
| $\Phi$ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_F$ | 5.287 | 0.027 | 9 | 1278.573 |
| . | . | . | . | . |
| . | . | . | . | . |
| . | . | . | . | . |
| $\Phi$ Year | 38.862 | 0.000 | 8 | 1314.16 |

[a] Model selection notation follows Burnham and Anderson (2002). Capture-mark-recapture notation follows Lebreton et al. (1992). NDVI = standardized estimates of annual Normalized Difference Vegetation Indices measured in sagebrush habitats; Brood = female associated with ≥ 1 chick at 45 days of brood age; Nest = female successfully hatched nest in year *t*; Age = minimum known age since initial capture. Season = monthly survivals constrained to be the same based on season of the year. Covariate effects were applied to specific seasons, as indicated by subscripts: B = Breeding (March-May); S=Summer (June-July); F=Fall (August-October); W=Winter (November-February).

Table 6. Combined model weights ($\sum w_i$) indicating relative support for competing model structures of apparent survival (Φ) and per-capita recruitment (*f*) of male greater sage-grouse in Eureka County, NV. Φ was estimated using robust design models, and *f* was estimated using Pradel models, in Program MARK.

| Vital Rate | Parameter structure[a] | Models Considered[b] | # Models $w_i > 0.01$ | $\sum w_i$ |
|---|---|---|---|---|
| Survival | Φ (NDVI + Exotic + NDVI*Exotic) | 5 | 4 | 0.60 |
| | Φ (NDVI + Exotic) | 4 | 4 | 0.21 |
| | Φ (Exotic) | 7 | 4 | 0.18 |
| | Φ (Year + Exotic) | 4 | 0 | 0.01 |
| | Φ (Year) | 4 | 0 | 0.00 |
| | Φ (NDVI) | 4 | 0 | 0.01 |
| | Φ (.) | 5 | 0 | 0.00 |
| Recruitment | *f* (NDVI + Exotic + NDVI*Exotic) | 1 | 1 | 1.00 |
| | *f* (NDVI + Exotic) | 1 | 0 | 0.00 |
| | *f* (Year + Exotic) | 1 | 0 | 0.00 |
| | *f* (Exotic) | 1 | 0 | 0.00 |
| | *f* (NDVI) | 1 | 0 | 0.00 |
| | *f* (Year) | 2 | 0 | 0.00 |
| | *f* (.) | 1 | 0 | 0.00 |

[a] NDVI = standardized estimates of annual Normalized Difference Vegetation Indices measured in sagebrush habitats; Exotic = total impact of exotic grassland invasion within 5.0 km of study leks; Year = full time variation among study years; . = Parameter held constant across study years.

[b] Indicates the total number of models with a given structure included in the analysis. Equivalent values indicate equal consideration.

Table 7. Annual estimates of survival (Φ), per-capita recruitment (*f*), and abundance (N) of male sage-grouse in Eureka County, Nevada. All estimates were generated using male capture-mark-recapture data in Program MARK.

| Year | Φ[a] (SE) | *f* [b] (SE) | N (SE) |
|---|---|---|---|
| 2003 | 0.57 (0.03) | 0.21 (0.04) | 574 (62) |
| 2004 | 0.64 (0.06) | 0.48 (0.07) | 532 (58) |
| 2005 | 0.66 (0.08) | 0.77 (0.18) | 612 (65) |
| 2006 | 0.56 (0.04) | 0.19 (0.04) | 603 (64) |
| 2007 | 0.48 (0.06) | 0.09 (0.03) | 486 (55) |
| 2008 | 0.48 (0.05) | 0.08 (0.03) | 230 (32) |
| 2009 | 0.53 (0.04) | 0.15 (0.04) | 230 (32) |
| 2010 | - | - | 172 (27) |

[a] Survival of males from year *t* to year *t+1*.

[b] Per-capita recruitment of males from year *t* into the year *t+1* breeding population.

Table 8. Performance of Robust Design capture-mark-recapture modeling impacts of radio-collars on male greater sage-grouse survival or behavior in Eureka Co., NV, from 2003-2011. γ was modeled assuming random temporary emigration (γ"= γ')(Kendal and Nichols 1995).

| Model[a] | Δ AICc | wi | No Param | Deviance |
|---|---|---|---|---|
| {Φ(NDVI) γ(Density+Radio) Detection (Year+Secondary+Radio) Recapture (Year+Secondary+Radio+Beta)} | 0 | 0.668 | 18 | 3609.839 |
| {Φ(NDVI+Radio) γ(Density+Radio) Detection(Year+Secondary+Radio) Recapture(Year+Secondary+Radio+Beta)} | 1.774 | 0.275 | 19 | 3609.558 |
| {Φ(NDVI) γ(Density) Detection(Year+Secondary+Radio) Recapture(Year+Secondary+Radio+Beta)} | 6.018 | 0.033 | 17 | 3617.908 |
| {Φ(.) γ(Radio) Detection(Year+Secondary+Radio) Recapture(Year+Secondary+Radio+Beta)} | 8.28 | 0.011 | 16 | 3622.218 |
| . | . | . | . | . |
| . | . | . | . | . |
| . | . | . | . | . |
| {Φ(.) γ(.) Detection(Year) Recapture(Quadratic trend} | 100.121 | 0 | 14 | 3718.147 |

[a] Model selection notation follows Burnham and Anderson (2002). Capture-mark-recapture notation follows Lebreton et al. (1992). NDVI = standardized estimates of annual Normalized Difference Vegetation Indices measured in sagebrush habitats.

Density = autoregressed counts of males observed displaying on study leks during the previous breeding season. Beta = structural parameter differentiating between probabilities of initially detecting and repeated detections of an individual. Radio = parameter differentiating between individuals with radio-collars and individuals with bands-only.

Table 9. Performance of Robust Design capture-mark-recapture models of male greater sage-grouse temporary emigration (γ) in Eureka Co., NV, from 2003-2010. Structure for survival (Φ), capture probability (*p*) and recapture probability (*c*) were held constant across models as: Φ = NDVI + Exotic + NDVI*Exotic; *p* = Year ; *c* = *p*(Year) + occasion (Blomberg et al. *in review*). γ was modeled assuming random temporary emigration (γ"= γ')(Kendal and Nichols 1995).

| Model[a] | $\Delta QAIC_c$ | $w_i$ | No. Param. | QDeviance |
|---|---|---|---|---|
| γ (Density + Exotic ) | 0.00 | 0.19 | 16 | 1828.12 |
| γ (Density$^2$ + Exotic ) | 0.16 | 0.18 | 17 | 1826.22 |
| γ (Density + Exotic + Age) | 1.23 | 0.10 | 17 | 1827.29 |
| γ (Density$^2$ + Exotic + Age) | 1.41 | 0.10 | 18 | 1825.40 |
| γ (Density$^2$ + Exotic + Condition) | 1.86 | 0.08 | 18 | 1825.86 |
| γ (Density + Exotic + Condition) | 1.92 | 0.07 | 17 | 1827.98 |
| γ (Exotic ) | 3.78 | 0.03 | 15 | 1833.96 |
| γ (Trajectory * NDVI + Exotic ) | 3.90 | 0.03 | 18 | 1827.90 |
| γ (Trajectory + NDVI + Exotic ) | 3.95 | 0.03 | 17 | 1830.01 |
| γ (Density) | 4.35 | 0.02 | 15 | 1834.53 |
| γ (Trajectory + Exotic ) | 4.66 | 0.02 | 16 | 1832.78 |
| γ (Condition + Exotic ) | 4.91 | 0.02 | 16 | 1833.03 |
| γ (Trajectory * NDVI + Exotic + Age) | 5.00 | 0.02 | 19 | 1826.93 |
| γ (Trajectory * NDVI + Exotic + Condition) | 5.08 | 0.02 | 19 | 1827.01 |
| γ (Density$^2$) | 5.09 | 0.02 | 16 | 1833.21 |
| γ (NDVI + Exotic ) | 5.80 | 0.01 | 16 | 1833.93 |
| γ (Trajectory + Exotic + Age) | 5.96 | 0.01 | 17 | 1832.02 |
| γ (Condition + Exotic + Age) | 6.04 | 0.01 | 17 | 1832.10 |
| γ (Year + Exotic ) | 6.11 | 0.01 | 21 | 1823.89 |
| γ (Trajectory, + Year + Exotic ) | 6.11 | 0.01 | 21 | 1823.89 |
| γ (Density + NDVI ) | 6.15 | 0.01 | 16 | 1834.28 |
| γ (Trajectory + Condition + Exotic ) | 6.37 | 0.01 | 17 | 1832.43 |
| γ (Density$^2$ + Condition ) | 6.84 | 0.01 | 17 | 1832.91 |
| γ (Density$^2$ + NDVI ) | 6.96 | 0.01 | 17 | 1833.02 |
| γ (Year + Exotic + Age) | 7.52 | 0.00 | 22 | 1823.22 |
| γ (.) | 8.34 | 0.00 | 14 | 1840.57 |
| γ (Age) | 8.64 | 0.00 | 15 | 1838.82 |
| γ (Trajectory) | 8.88 | 0.00 | 15 | 1839.06 |
| γ (Condition) | 9.49 | 0.00 | 15 | 1839.67 |
| γ (Condition + Age) | 11.74 | 0.00 | 17 | 1837.80 |
| γ (Year) | 12.16 | 0.00 | 20 | 1832.02 |
| γ (Year + Age) | 13.02 | 0.00 | 21 | 1830.80 |

[a] Model selection notation follows Burnham and Anderson (2002). Capture-mark-recapture notation follows Lebreton et al. (1992). NDVI = standardized estimates of annual Normalized Difference Vegetation Indices measured in sagebrush habitats. Exotic = proportion of exotic grassland invasion within 5.0 km of study leks. Trajectory = general population trajectory (increase versus decline) as indicated by field surveys. Density = autoregressed counts of males observed displaying on study leks during the previous breeding season. Condition = average body condition of all adult males captured in a given year. Age = subadult (first breeding season) or adult (second or later breeding season).

Table 10. Performance of Pradel capture-mark-recapture models of male greater sage-grouse realized population change ($\lambda_R$) in Eureka Co., NV, from 2003-2010. Structure for survival ($\Phi$), capture probability (*p*) and recapture probability (*c*) were held constant across models as: $\Phi$ = Year; *p* = Year + secondary occasion; *c* = *p* (Blomberg et al ).

| Model[a] | $\Delta AIC_c$ | $w_i$ | No. Param. | Deviance |
|---|---|---|---|---|
| $\lambda_R$ (NDVI) | 0.00 | 0.79 | 18 | 5023.76 |
| $\lambda_R$ (Trend) | 3.70 | 0.12 | 18 | 5027.46 |
| $\lambda_R$ (Trend$^2$) | 4.65 | 0.08 | 19 | 5026.32 |
| $\lambda_R$ (Year) | 9.96 | 0.01 | 23 | 5023.22 |
| $\lambda_R$ (.) | 17.15 | 0.00 | 17 | 5043.00 |

[a] Model selection notation follows Burnham and Anderson (2002). Capture-mark-recapture notation follows Lebreton et al. (1992). NDVI = standardized estimates of annual normalized difference vegetation indices. Trend = linear trend in annual $\lambda_R$. Trend$^2$ = quadratic trend in annual $\lambda_R$. Year = full annual variation. . = $\lambda_R$ constant across years.

Table 11. Performance of known-fate models of female sage-grouse monthly survival in Eureka County, NV.

| Model[a] | Δ AICc | wi | No Param | Deviance |
|---|---|---|---|---|
| $\Phi$ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_B$ + $NDVI_{SF}$ | 0.000 | 0.374 | 10 | 1271.273 |
| $\Phi$ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_B$ | 0.025 | 0.369 | 9 | 1273.311 |
| $\Phi$ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_{SF}$ | 4.878 | 0.033 | 9 | 1278.164 |
| $\Phi$ Season + $Nest_S$ + $Brood_F$ * Age | 4.975 | 0.031 | 8 | 1280.274 |
| $\Phi$ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_F$ | 5.287 | 0.027 | 9 | 1278.573 |
| . | . | . | . | . |
| . | . | . | . | . |
| . | . | . | . | . |
| $\Phi$ Year | 38.862 | 0.000 | 8 | 1314.16 |

[a] Model selection notation follows Burnham and Anderson (2002). Capture-mark-recapture notation follows Lebreton et al. (1992). NDVI = standardized estimates of annual Normalized Difference Vegetation Indices measured in sagebrush habitats; Brood = female associated with ≥ 1 chick at 45 days of brood age; Nest = female successfully hatched nest in year *t*; Age = minimum known age since initial capture. Season = monthly survivals constrained to be the same based on season of the year. Covariate effects were applied to specific seasons, as indicated by subscripts: B = Breeding (March-May); S=Summer (June-July); F=Fall (August-October); W=Winter (November-February).

Table 12. Performance of multistate models of female sage-grouse reproductive success in Eureka County, NV. Model structures for survival and recapture probability were held constant across models as: Φ (State + Age); p (.).

| Model[a] | $\Delta AIC_c$ | $w_i$ | No. Param. | Deviance |
|---|---|---|---|---|
| Ψ (NDVI- Dirrect + State) | 0.000 | 0.437 | 7 | 540.973 |
| Ψ (NDVI - Direct * State) | 2.050 | 0.157 | 8 | 540.916 |
| Ψ (State) | 2.964 | 0.099 | 6 | 546.029 |
| Ψ (NDVI - Carry Over + State) | 3.041 | 0.096 | 7 | 544.013 |
| Ψ (State * Age) | 4.036 | 0.058 | 8 | 542.903 |
| Ψ (NDVI - Carry Over * State) | 4.827 | 0.039 | 8 | 543.694 |
| Ψ (State + Age) | 4.921 | 0.037 | 7 | 545.893 |
| Ψ (NDVI) | 5.332 | 0.030 | 6 | 548.397 |
| Ψ (State + Year) | 6.156 | 0.020 | 10 | 540.769 |
| Ψ (.) | 6.302 | 0.019 | 5 | 551.446 |
| Ψ (Year) | 8.254 | 0.007 | 9 | 545.001 |
| Ψ (State + Year) | 34.106 | 0.000 | 9 | 570.852 |

[a] Model selection notation follows Burnham and Anderson (2002). Capture-mark-recapture notation follows Lebreton et al. (1992). NDVI = standardized estimates of annual Normalized Difference Vegetation Indices measured in sagebrush habitats; NDVI was modeled as either a direct (effect of $NDVI_t$ on $\Psi_t$) or carry over (effect of $NDVI_{t-1}$ on $\Psi_t$) effect. Age = minimum known age since initial capture. State = reproductive state (Success = raised ≥ 1 chick to 45 days; Fail = unsuccessful in reproduction) in year *t-1*.

# The impacts of noise on greater sage-grouse: A discussion of current management strategies in Wyoming with recommendations for further research and interim protections

Prepared for:
The Bureau of Land Management, Lander Field Office and Wyoming State Office, Cheyenne and Wyoming Game and Fish Department

Dr. Gail L. Patricelli, Associate Professor
Jessica L. Blickley, PhD Candidate in Ecology
Dr. Stacie L. Hooper, Postdoctoral Researcher

Department of Evolution and Ecology, University of California, Davis, CA 95616
email: GPatricelli@ucdavis.edu

# EXECUTIVE SUMMARY

Recent research has demonstrated that noise from natural gas development negatively impacts sage-grouse abundance, stress levels and behaviors (Blickley et al. 2012; Blickley & Patricelli 2012; Blickley et al. In review). Other types of anthropogenic noise sources (e.g. infrastructure from oil, geothermal, mining and wind development, off-road vehicles, highways and urbanization) are similar to gas-development noise and thus the response by sage-grouse is likely to be similar. These results suggest that effective management of the natural soundscape is critical to the conservation and protection of sage-grouse. The goals of this report are to (I) discuss current approaches in the management of new and existing noise sources within and outside sage-grouse core areas of Wyoming, (II) recommend research priorities for establishing effective noise management strategies, and (III) provide managers and policy makers with recommendations for the interim protection of sage-grouse from known or expected impacts of increased noise levels using the best available science to date.

**I. Current Management Strategies in Wyoming**

In this report, we detail some concerns with current management strategies for noise. Management objectives for noise are typically established relative to ambient noise levels, stating that noise levels measured at lek edge should not exceed 10 dB over ambient. The choice of ambient value thus has large consequences, setting the upper limit of allowable noise. Outside core areas, 39 dB is typically used as a default measure of ambient; however, this value is much higher than ambient measures from undisturbed habitats. Inside core areas, Wyoming Executive Order 2011-5 stipulates measurement of ambient values at the perimeter of each lek to establish a baseline. While this will typically lead to more realistic ambient values than 39 dB, the complexity of measurement protocols and variable weather conditions make it impractical to accurately measure ambient levels at each lek. Even accurate ambient measures will include noise from existing sources, which may allow more than 10 dB of noise above an undisturbed ambient. In addition, there is little scientific basis for the "10 dB over ambient" threshold. Further research may find this threshold insufficient to protect sage-grouse—or too stringent. Further, these stipulations apply only within the lek perimeter, potentially allowing disturbance to foraging, nesting and brood-rearing habitat. Finally, this stipulation alone allows a great deal of traffic noise, which has a much more detrimental impact on sage-grouse than more continuous noise (Blickley et al. 2012). In response to these concerns, we offer the following recommendations for consideration during revision and implementation of Resource Management Plans.

**II. Recommendations for research priorities**

We recommend the following research priorities to inform the development of effective management strategies for noise in sage-grouse habitats. (1) We recommend an effort to map baseline pre-development ambient noise levels across the state by combining measurement of existing noise levels by trained personnel with predictive modeling. (2) Once ambient noise values are established, we recommend evaluating whether the current threshold of 10 dB above ambient is appropriate to protect sage-grouse. We recommend that the most feasible way to do so is by using habitat-selection models to analyze changes in sage-grouse population measures relative to variation in noise levels in disturbed areas. This method would also allow assessment of noise impacts outside of the breeding season. (3) Similarly, to establish more effective strategies for managing traffic noise, we recommend that researchers include noise from traffic in habitat-selection models. Doing so would help to establish whether the impacts from traffic noise are better mitigated by setting objectives for noise exposure levels or by restricting the siting and traffic volume of roads directly.

## III. Recommendations for interim protections

Since the needed research will take time to complete, we provide managers and policy makers with the following recommendations for interim management strategies using the best available science to date. We emphasize that protections based on these interim recommendations may need to be revised upon completion of ongoing and future research.

1. Experimental evidence indicates that sage-grouse do not habituate to the impacts of noise over time (Blickley et al. 2012), therefore the combined impact of all anthropogenic noise sources should be considered when assessing disturbance to sage-grouse habitat. Therefore, we recommend that interim noise-management objectives should be set relative to typical ambient noise levels in sage-grouse habitat pre-development. Based on the best available measurements in undisturbed areas (discussed in detail in parts I.1. and III.1. of this report), we recommend an ambient value 20-22 dBA. This new default ambient would replace the previous default of 39 dBA or replace empirical measurements of ambient noise at lek edge.

2. We recommend continuing to allow an increase in noise levels of 10 dB above ambient. As discussed above, we do not yet know whether this level is appropriate to protect sage-grouse. However, this threshold is based on the best available science to date and is therefore reasonable when combined with realistic measures of ambient (i.e. 20-22 dBA).

   Establishing a protocol for the measurement of noise levels would facilitate accurate and repeatable assessment of compliance with noise-exposure objectives. We recommend using an A-weighted $L_{50}$ as a measure of median noise exposure. The most relevant measurements would be those collected during times when noise exposure is most likely to affect greater sage-grouse—nights and mornings (i.e. 6 pm – 9 am). Accuracy would be improved by collection of measurements at multiple (3-4) locations between each noise source and the edge of the protected area. Measurements should be taken with a Type-1 sound level meter (ANSI S1.4-1983; or a method with similar accuracy) for ≥1 hour at each site, ideally over multiple days with suitable climactic conditions.

3. Current stipulations for sage-grouse core areas (WY Executive Order 2011-5) limit noise within the perimeter of the lek. However, in this report we review the evidence that noise will also disturb sage-grouse during off-lek activities critical to reproduction. Therefore we recommend that management strategies aim to protect the soundscape in areas critical for mating, foraging, nesting and brood-rearing activities, rather than protecting the lek alone. Thus we recommend that noise exceeding 10 dB over ambient be managed as a "disruptive activity" throughout sage-grouse nesting and brood-rearing habitat (e.g. BLM Instruction Memorandum WY-2012-019).

4. Given the difficulty of measuring intermittent traffic noise, we recommend that interim management strategies focus not on limiting traffic noise levels, but rather on the siting of roads or the limitation of traffic volumes during crucial times of the day (6 pm to 9 am) and/or season (i.e. breeding season). We estimate that noise levels will typically drop to 30 dBA at 1.3 km (0.8 mi) and to 32 dBA at 1.1 km (0.7 mi) from the road (these levels represent 10 dB over ambient using 20 or 22 dBA ambient respectively). Therefore to avoid disruptive activity in areas crucial to mating, nesting and brood-rearing activities, we recommend that roads should be sited (or traffic should be seasonally limited) within 0.7-0.8 miles from the edge of these areas. We emphasize that we are not recommending the siting of roads 0.7-0.8 miles from the edge of the lek perimeter, but rather 0.7-0.8 miles from the edge of crucial lekking, nesting and early brood-rearing areas.

## BACKGROUND

Greater sage-grouse (*Centrocercus urophasianus*) populations have declined throughout their range, leading to their designation as a candidate for listing under the Endangered Species Act. Among the factors identified as a threat to sage-grouse is the expansion of energy development across much of the remaining sage-grouse habitat (e.g. Aldridge & Boyce 2007; Doherty et al. 2010; Doherty et al. 2008; Holloran et al. 2010; Holloran 2005; Kaiser 2006; Naugle et al. 2011; Walker et al. 2007). One potential means by which energy development and other human activities might impact sage-grouse populations is through the production of noise (Blickley & Patricelli 2010; Braun 1986; Braun 1998; Connelly et al. 2004; Holloran 2005; Rogers 1964).

Acoustic communication is very important in the reproductive behaviors of sage-grouse, and energy exploration and development activities generate substantial noise; it is therefore important to determine whether noise produced from energy development affects sage-grouse breeding biology. Female sage-grouse use male vocalizations to find leks within the habitat (Gibson 1989), and after their arrival at a lek, females assess male vocalizations (and other aspects of male display) when choosing a mate (Dantzker et al. 1999; Gibson 1996; Gibson & Bradbury 1985; Patricelli & Krakauer 2010; Wiley 1973). Noise from natural gas development is primarily produced by drilling rigs, compressors, generators and traffic on access roads. All of these noise sources are loudest below 2 kHz (Blickley & Patricelli 2012). Male sage-grouse produce acoustic signals between 0.2-2 kHz, so the potential exists for industrial noise to mask sage-grouse communication and thus interfere with the ability of females to find and choose mates (Blickley & Patricelli 2012). For a prey species such as sage-grouse, noise may also increase predation risk by masking the sounds of approaching predators, and/or increase stress levels by increasing the perception of predation risk (Quinn et al. 2006; Rabin et al. 2006). In other vertebrate species, noise has been found to impact individuals directly, for example, by causing startling behaviors, increased heart rate or increased annoyance; all of these factors may interfere with normal foraging, resting and breeding behaviors and contribute to higher stress levels and/or reduced fitness (reviewed in Barber et al. 2009; Kight & Swaddle 2011).

Holloran (2005) found observational evidence suggesting that noise may be at least partly responsible for impacts of natural gas development on sage-grouse populations in the Pinedale Anticline Project Area (PAPA), Wyoming. He found that juvenile males avoid recruitment to leks located near natural-gas drilling sites, even if these leks previously had high male attendance; these effects are more pronounced downwind of the drilling sites where noise levels are higher, indicating that noise may contribute substantially to these declines (Holloran 2005).

To investigate potential impacts from noise on greater sage-grouse lekking activity, we experimentally introduced noise from natural gas drilling rigs and access traffic on roads at eight leks and compared lek attendance to eight paired control leks near Hudson, Wyoming between 2006 and 2008[1]. We found immediate and sustained declines in male attendance on noise leks (29% declines on

[1] We began playback of drilling noise at two leks and traffic noise at two leks in 2006 and began monitoring their paired controls. In 2007 and 2008, we expanded the sample size to include four drilling-noise leks and four traffic-noise leks and their paired controls. Noise was played 24-hours a day beginning in mid-February to early March and continuing through the end of April of each year. Noise was recorded from drilling sites and main haul roads on the PAPA and played back using rock-shaped outdoor speakers placed in a line along one edge of the lek; this created a gradient in noise levels, decreasing with distance from the speakers. On leks with traffic noise playback, recordings of big rig trucks and pickup trucks were combined with 30- and 60-second files of silence at a ratio reflecting the average number of trucks expected to drive on a main energy field access road; these files were then played using the "random shuffle" feature on an MP3 player. On leks with drilling noise, a 14-minute recording of a drilling rig was played on continuous loop. Drilling noise recordings were broadcast on experimental leks at an $L_{eq}$ of 71.4 ± 1.7 dBF (56.1 ± 0.5 dBA) as measured at 16 meters; on traffic noise leks, where the amplitude of the noise varied with the simulated passing of vehicles, noise was broadcast at an $L_{max}$ (maximum RMS amplitude) of 67.6 ± 2.0 dBF (51.7 ± 0.8 dBA). These playback levels approximate the noise level at 0.25 mile (402 m) from a

drilling noise leks and 73% declines on traffic noise leks relative to paired control leks) and evidence of similar declines in female attendance; these results suggest strong noise avoidance in male and possibly female sage-grouse (Blickley et al. 2012). In addition, we found elevated stress hormone levels in fecal samples collected from noise leks compared to control leks, suggesting that even males who do not abandon noisy leks suffer a physiological impact (Blickley et al. In review). Further, our analyses of behaviors on leks with traffic noise playback suggest that males alter the timing of their vocalizations in response to noise—most males wait out noisy periods without strutting (during the sounds of trucks passing), but males who do not wait out the noise, strut at a higher rate (Blickley et al. in prep). These results are consistent with males avoiding the impacts of masking noise on their ability to attract females; other types of disturbance, such as startling or learned aversion to vehicular noise may also contribute to this response. Other types of anthropogenic noise sources (e.g. infrastructure from oil, geothermal, mining and wind development, off-road vehicles, highways and urbanization) are similar to the noise used in this experiment, and thus response by sage-grouse to other noise sources is likely to be similar. These results suggest that effective management of the natural soundscape is critical to the conservation and protection of sage-grouse.

The goals of this report are to (I) discuss current approaches in the management of new and existing noise sources within and outside sage-grouse core areas of Wyoming, (II) recommend research priorities for establishing effective noise management strategies, and (III) provide managers and policy makers with recommendations for the interim protection of sage-grouse from known or expected impacts of increased noise levels using the best available science to date.

# I. CURRENT NOISE MANAGEMENT STRATEGIES IN WYOMING

Noise management strategies in greater sage-grouse habitat typically share three common components: (1) the management objective for noise is established relative to ambient levels, (2) noise is limited to 10 dB over these ambient levels, and (3), compliance with this objective is measured at lek edge. In light of the research reviewed above, here we discuss potential issues with these three components of noise management strategies, both in terms of whether they are practical to implement and in terms of their likely efficacy in reducing disturbance to sage-grouse populations. In addition, we discuss special issues related to management of noise from traffic.

### *1. Ambient noise levels*

Management strategies on Wyoming public lands outside of the core areas (and before the core area strategy was implemented) typically allow for noise exposure on leks up to 10 dB over the ambient level; the ambient level is typically defined as 39 dBA[2], which thus sets the limit of exposure at 49 dBA (e.g. BLM 1999; BLM 2003; BLM 2008). However, there is evidence that 39 dBA is not an appropriate estimate of ambient levels in sagebrush habitat. This value originated in a 1971 EPA report; it is a measurement from a single farm in Camarillo, CA, on an afternoon. The farm is described in the report as follows:

> Rural agricultural near tomato field; 50 yards to the trees around the yard and dwelling area; 160 yds to Walnut Ave., a lightly travelled surface road; 0.6 mi to State Hwy 118, a 2-lane moderately travelled highway; 0.6 mi to LeLeror Ave. and 0.75 mi to La Vista Ave, both lightly travelled surface roads; 3.5 mi to Santa Paula Freeway; 3.6 mi to the Ventura Freeway; 4.5 mi to Camarillo. The major intruding

typical drilling site. To control for visual disturbance of the speaker system and researcher presence, control leks had dummy speakers placed in the same arrangement and were also visited to simulate the periodic battery changes on noise leks.

[2] All dB values presented here are measures of Sound Pressure Level (SPL) and thus relative to the threshold of human hearing (20μPa).

> events were created by jet propeller aircraft flyovers and dogs barking. Other intruding events were background traffic noise. Trucks on distant freeways could be heard distinctly but did not raise the noise level above its residual value. The residual noise level during the evening hours was dominated by crickets. During the day an orchard pruner in the distance controlled the minimum noise level. (EPA 1971)(available here)

Based on this description, it is clear that this farm is very different from undisturbed sage-grouse habitat. This EPA report presented this value as an example of an afternoon noise level in an active rural area; the value was not recommended as a default level for undisturbed landscapes. Further this value is median noise level ($L_{50}$)[3], which in a busy area such as this, will include some noise from the anthropogenic sources listed in the description above, as well as birds, insects, wind gusts, etc. A more appropriate measure is the $L_{90}$—the level exceeded 90% of the time. The $L_{90}$ is accepted by the American National Standards Institute (ANSI S12.9Part1) as a measure of background or "residual noise level"[4]. Indeed, the same EPA report found residual noise levels of 30-34 dBA on rural farms and 16-22 dBA in wilderness areas—whereas 39 dBA residual values were more typical of residential areas in Los Angeles, Detroit and Boston. Further, this 39 dBA measurement was collected during an afternoon, when noise levels are typically higher[5]. Since calm nights and morning are when sound is most critical for communication in sage-grouse, as well as detection of the sounds of approaching predators, this is the most important window of time for noise measurement. Afternoons in much of the habitat of the sage-grouse are windy, making noise measurements difficult and impeding communication and predator detection by sage-grouse and other wildlife[6].

Reports and noise levels measured in disturbed and undisturbed areas in Wyoming further suggest that 39 dB is inappropriate as an ambient value for most sage-grouse habitat. KC Harvey (2009) recently measured noise exposure on leks on the PAPA and found that most leks—even those with multiple active drilling rigs nearby—had residual ($L_{90}$) and median ($L_{50}$) levels much less than the "ambient" of 39 dBA (**Table 1**), demonstrating that this value is unrealistically high. Our measurements of leks in the PAPA and Powder River Basin lead to the same conclusion[7].

---

[3] The $L_{50}$ is the median noise level—the level that was exceeded 50% of the time (see **Figure 1**). This measure is collected over some time period (e.g. 1 hour, or from 6 pm to 9 am) with this period being broken down into much smaller intervals (typically 1 second); an $L_{50}$ of 30 dBA would mean that half of the intervals measured were less than 30 dBA and half of them were greater than 30 dBA. This metric is preferable to using a measure of average noise over a longer interval, like $L_{eq}$ or $L_{avg}$, since these average metrics are more heavily influenced by occasional loud events, such as those caused by a songbirds, insects, aircraft, wind gusts, etc. These intruding sounds will have no impact on the $L_{50}$, unless they are present more than 50% of the time.

[4] The $L_{90}$ is the residual or background noise level. As with the $L_{50}$, the $L_{90}$ is collected over some time period (e.g. 1 hour, or from 6 pm to 9 am) with this period being broken down into much smaller intervals (typically 1 second); an $L_{90}$ of 20 dBA would mean that 10% of the intervals measured were less than 20 dBA and 90% of them were greater than 20 dBA (see **Figure 1**). Residual noise levels reflect background noise level at a site, since they exclude most intruding noise from birds, insects, wind gusts and sporadic anthropogenic noises (passing vehicles or aircraft) that raise the average (e.g. $L_{eq}$ or $L_{avg}$) and peak values (e.g. $L_{peak}$, $L_{max}$, $L_{10}$) over a measurement period. This metric is the most suited for estimating ambient values to set the baseline for management objectives. Note that in an area with anthropogenic noise sources producing continuous noise (like most energy development infrastructure), the $L_{90}$ measurement will not represent pre-development ambient values since the continuous noise source will contribute to the residual levels. To estimate predevelopment ambient for a disturbed site, measurements must be collected in a similar but undisturbed area, or estimated through modeling.

[5] $L_{50}$ measurements at the same Camarillo farm were 32-34 dBA at night and in the early morning; the $L_{90}$ levels at this time were < 30 dBA (US EPA 1971).

[6] This is not to say that daytime noise levels are irrelevant, rather that noise disturbance during this time is less likely to have an impact on breeding, since anthropogenic noise will often be masked by wind noise. Further, since measurements in the afternoon are more difficult and results are more variable, it is less practical to use afternoon measures for ambient or exceedance values. Ideally, however, anthropogenic contributions to noise levels throughout the day would be kept as close to nighttime/morning target levels as possible.

[7] In the Powder River Basin 2007, we measured three leks finding an average $L_{eq}$ of 34.6 dBA, a minimum of 33.4 dBA and a maximum of 36.3 dBA. In the Pinedale Anticline between 2007 and 2009, we measured 14 leks finding an average of 39.1 dBA, a minimum of 31.4 dBA and a maximum of 47.4 dBA. Unfortunately, $L_{90}$ and $L_{50}$ values in dBA were not collected.

Which ambient value would be more appropriate? Based on our review of reports and empirical measurements collected in Wyoming, we estimate that true ambient values pre-development in nights and calm morning in sagebrush habitat are closer to 20-22 dBA (justification for these values is presented in part **III.1.**). If 22 dBA is the true ambient value, then a 49 dBA noise source would exceed ambient by 27 dB—this is a 22-fold increase in the noise level, which would be perceived by humans as at least 6 and a half times louder than ambient; such a sound would dominate the soundscape and cause significant disruption[8].

Indeed, results from our experiments indicate that 49 dBA is too loud to avoid significant impacts on sage-grouse. Our noise-playback leks (described above, Blickley et al. 2012) experienced levels that were in compliance these recommendations, i.e. less than 49 dBA across most of the lek area, except the area within ~20 meters of the speakers. Yet we found large declines in attendance, increases in stress levels and altered display behaviors across the lek (Blickley et al. in review, in prep). Therefore, the available scientific evidence shows that 39 dBA is inappropriate for use as a default ambient value for sage-grouse habitat, and suggests that allowing 49 dBA of noise exposure on leks and other sensitive areas will cause significant disturbance to greater sage-grouse populations.

In 2010, stipulations for sage-grouse core areas in Wyoming were created by Executive Order 2010-4. These stipulations used measured ambient values, rather than using 39 dBA as a default ambient value. A more recent executive order affirms this approach, stating:

> New noise levels, at the perimeter of a lek, should not exceed 10 dBA above ambient noise (existing activity included) from 6:00 p.m. to 8:00 am during the initiation of breeding (March 1 May 15). Ambient noise levels should be determined by measurements taken at the perimeter of a lek at sunrise. (Wyoming Executive Order 2011-5).

Since measured ambient noise levels are likely to be less than 39 dBA in most places, the core area stipulations will typically limit noise to levels lower than 49 dBA and thus offer greater protection for sage-grouse. But since existing activity is explicitly included in measurements of ambient noise, there may be some areas where the core stipulations allow more than 49 dBA, when existing sources lead to ambient measures greater than 39 dBA. Further, each new development may add 10 dB to existing noise levels, potentially causing an incremental increase in noise over time. Such increasing noise would likely cause increasing impacts, since sage-grouse do not appear to habituate to anthropogenic noise over time. The declines we observed on our noise playback leks were immediate and sustained throughout the three-year experiment (Blickley et al. 2012) and elevated stress hormones were observed through the second and third years of the experiment (Blickley et al. In review), indicating that sage-grouse do not adapt to increased noise levels over time. Therefore, the combined impact of all anthropogenic noise sources should be considered when assessing disturbance to sage-grouse habitat. To do so, management objectives would be set relative to the undisturbed soundscape, capping the total noise exposure at or near 10 dB above a "pre-development" ambient value[9].

---

[8] For reference, it is helpful to remember a rule of thumb from physics: every 6 dB increase in noise levels is a doubling in amplitude (measured as changes in air pressure). One often hears the rule of thumb that a 10 dB increase in noise is subjectively *perceived* by humans as a doubling in loudness. However, this perception depends on the frequencies (i.e. pitch) of the sounds and can vary with amplitude. Indeed, in humans a 6 dBA increase in noise level leads to an approximate doubling in the number of noise complaints (ANSI S12.9/Part 4 Table F.1), suggesting that humans are more sensitive than this 10 dB rule of thumb implies. Since we do not know if sage-grouse or other non-human animals perceive sounds similarly to humans, the non-subjective "6 dB doubling" rule of thumb is preferable. An online calculator to determine how decibel values relate to loudness ratios can be found here. OSHA examples of noise levels of common sources can be found here.

[9] Such a cap would not preclude further development at sites which already have sources that exceed ambient by nearly 10 dB. This is due to the complex way that multiple sound sources combine to determine overall noise levels (see formulas and explanation here). A new source would need to be 9 dB less than the existing source at the measurement site (edge of the protected area) to add only 0.5 dB to the total noise exposure. A new source 6 dB quieter than the existing source would lead to a 1 dB increase in total noise level.

In addition, collecting measurements of ambient noise levels in quiet areas is extremely challenging and requires expensive, specialized equipment; this makes the requirement to collect ambient values at each lek difficult to implement. Unfortunately, non-ideal weather (especially wind, even at low levels) and almost all errors by the person deploying the noise meter (e.g. poor placement of the meter for long-term deployment, rustling from clothing, crunching leaves underfoot and even breathing close to the meter when handheld) will inflate ambient measures. Even professional measurements on Type-1 sound level meters will typically overestimate ambient levels in quiet areas (<27 dBA). This is because A-weighting[10] boosts the amplitudes of the mid-frequencies, which in very quiet areas includes noise from the pre-amplifier on the sound-level meter[11]. All of these sources of measurement inaccuracy will inflate ambient values and therefore allow more noise exposure at leks.

In summary, establishing an appropriate ambient value for sage-grouse habitat is a complex task. Further research is needed to establish pre-development ambient noise values, and in the interim, using a realistic estimate of pre-development ambient would offer more protection to sage-grouse than either an unrealistic default value (39 dBA) or ambient values measured at lek edge.

### *2. The 10 dB threshold*

Once an ambient noise value (or values) is established, most current noise management strategies limit new noise levels to 10 dB above this ambient value. This 10 dB threshold is used commonly inside and outside of Wyoming core areas and in other states; however, we do not yet know whether this threshold is sufficient to protect greater sage-grouse. This threshold is based on only a handful of studies on songbirds (Wyoming Bird Conservation Plan, 2003; Dooling & Popper 2007), and there is no scientific basis for assuming that sage-grouse will respond to noise in a manner similar to songbirds. In fact, their low-frequency vocalizations might make them more vulnerable to masking by anthropogenic noise than many songbirds (Blickley & Patricelli 2012). Recent studies of songbirds have found that species with larger body size and lower-frequency vocalizations are more prone to population declines in response to noise (Francis et al. 2009; Hu & Cardoso 2009).

Furthermore, 10 dB is a significant increase in the amount of noise. For an animal vocalizing to communicate with potential mates or offspring, a 10 dB increase in noise levels corresponds to up to a tenfold decrease in the active space of the vocalization—the "listening area" over which it can be detected by receivers (Barber et al. 2009; Brenowitz 1982)[12]. This same increase in noise will lead to

---

[10] A-weighting (ANS S1.42-2001) is used to account for changes in level sensitivity as a function of frequency. In an effort to simulate the relative response of the human ear, A-weighting de-emphasizes the high (>6.3 kHz) and low (<1 kHz) frequencies, and emphasizes the frequencies in between. Unfortunately, there is no weighting specific to sage-grouse or other wildlife. Most birds, besides owls, have hearing capabilities similar or slightly worse than humans; therefore, some experts recommend that A-weighting may be a suitable if not ideal metric for studies of birds (Dooling and Popper 2007).

[11] Most Type-1 (ANSI S1.4-1983) precision sound level meters (SLM) have a "noise floor" of ~17 dB, meaning that they cannot measure quieter sounds, since these sounds will be masked by the noise from the SLM itself. Some SLM noise is typically detected up to 10 dB above the noise floor (i.e. 27 dB), especially when using A-weighting, as discussed in the text. This is not a problem when measuring louder sounds (i.e. many noise sources associated with development) which overwhelm any contribution of the noise from the SLM (as well as noise from a slight breeze or other incidental sounds). Measurements of quiet sounds are thus particularly challenging. Type-2 SLMs are more affordable (often ~$400 rather than ~$9,000 for Type-1) but can have noise floors of ~35 dB and should therefore never be used to measure ambient noise or quiet sound sources (expected to be <35-40 dBA); some more expensive Type-2 meters have noise floors approaching 22 dBA and would therefore be more useful for measuring quiet sounds, but not ambient levels. Within a few decibels above the noise floor, the accuracy of Type-2 meters is typically only slightly lower than Type-1 meters. Type-3 SLMs have higher noise floors and lower accuracy and should not be used for measuring ambient or assessing compliance.

[12] Barber et al. (2009) offered simple formulas for estimating the reduction in detection distance and listening area resulting from an increase in background noise. The formula for calculating how the detection distance changes with an increase in noise is: detection distance=$10^{(-\text{(dB change in noise)}/20)}$. This shows a halving of detection distance for each 6 dB increase in noise, therefore a more than three-fold decrease (69% decrease) in detection distance with a 10 dB increase in noise and a tenfold reduction in detection distance (90% decrease) with a 20 dB increase in noise. When one is concerned with the total area over which a sound can be detected, rather than the distance between the sound source and receiver, then the appropriate measure is listening area. The area of a circle (i.e. listening area

up to a three-fold decrease in the detection distance between two receivers (Barber et al. 2009)[12]—meaning that receiver must be three times closer to hear a vocalization in noise than in quiet conditions, and perhaps more critically, a predator would be able to approach three times closer in noise before it was detected by a sage-grouse. Indeed, the night-time capture of sage-grouse by spotlighting is greatly improved by a noise source to mask the sound of footsteps from approaching biologists (Connelly et al. 2003); predators likely gain a similar advantage in noise. Masking of vocalizations and the sounds of predator approach is only one source of impacts from noise—animals may also suffer from behavioral disruptions, elevated hearth rate, interrupted rest and increased stress levels (reviewed in Barber et al. 2009; Kight & Swaddle 2011). These impacts may have significant consequences; a recent study in humans found a 12% increase in the risk of a heart attack with every 10 dB increase in exposure to chronic traffic noise (Sørensen et al. 2012). Many of these behavioral and physiological impacts may occur at or below the 10 dB threshold. Alternatively, further study may reveal that the 10 dB threshold is sufficient or even too conservative. Therefore, research is needed to determine whether the 10 dB threshold is appropriate for sage-grouse.

### *3. Where measurements are collected*

Inside and outside of the core areas, current management strategies that limit noise to 10 dB over ambient levels typically specify that measurements should be collected at lek edge to assess compliance (e.g. WY Executive Order 2011-5; BLM 1999, 2003, 2008). This introduces two potential problems, which are discussed in turn below.

First, the presence of sage-grouse on the lek will influence sound level measurements. On the edge of a lek with many birds vocalizing, one could find "ambient" noise measures of 50-60 dBA $L_{eq}$[13], which would thus allow up to 60-70 dBA of anthropogenic noise. Even after an ambient value is established, determining whether a development complies with stipulated noise levels would require measuring noise exposure again at lek edge. One can imagine a scenario where increasing development noise causes declines in lek attendance, which causes noise level readings to decrease over time as fewer birds contribute to the sounds of the lek. Clearly, these data would tell us little about the actual noise levels of anthropogenic sources and could be very misleading. There are methods available to reduce this problem, such as using appropriate noise metrics (such as $L_{50}$ and $L_{90}$; see part **I.1.**) and collecting measurements before birds arrive on the lek or after birds are flushed. But this issue makes the current stipulations more difficult, disruptive and ambiguous to implement.

Second, and much more importantly, if noise levels drop down to stipulated levels at the edge of the lek, then much of the area surrounding the lek will be exposed to higher noise levels (see **Figures 3** & **4**). This management strategy therefore protects only a fraction of sage-grouse activities during the breeding season—mate assessment and copulation on the lek—leaving unprotected other critical activities in areas around the lek, such as foraging, roosting, nesting and brood rearing. Our experimental design allowed us to examine only impacts of noise on the lek, since creating noise over a larger area would require noise sources much larger than battery-powered speakers (i.e. actual industrial infrastructure). Thus we cannot provide direct evidence that off-lek noise will impact sage-grouse populations. However, there is indirect evidence of such impacts.

---

around the vocalizing animal) decreases with the square of the radius (i.e. detection distance between the vocalizing animal and the receiver), so here the formula is: listening area = $10^{(-(\text{dB change in noise})/10)}$. This leads to a halving of listening area with every 3 dB increase in noise and tenfold reduction with every 10 dB. These decreases in active space and detection distance are less extreme when environmental attenuation of noise is considered, but are nonetheless very large (Blickley and Patricelli 2012).

[13] $L_{eq}$ (also called $L_{avg}$) is the equivalent noise level (see Figure 1). This can be thought of as the average noise level across the sample period; more precisely, it is the level of a constant sound over a specific time period that has the same sound energy as the actual (variable) sound.

Evidence suggests that male display and copulation activities on the lek may be affected by noise occurring around the lek area, even if the lek area itself meets management objectives for noise. In order to sustain their costly display behaviors, males must forage off lek, potentially exposing them to higher noise disturbance levels (**Figures 3** & **4**). Vehrencamp et al. (1989) found that males on the lek who are in good condition and are successful in mating forage further from the lek during the day, compared to unsuccessful, poor-condition males (range 200-750 meters, or 0.12-0.46 miles, off lek). Other studies have found males travelling an average of 0.6 miles (max 1.5 miles) to forage off lek (e.g. Schoenberg 1982; Wallestad & Schladweiler 1974). If foraging in noisy areas increases male stress levels or predation risk, or decreases foraging efficiency (as has been found in other vertebrate species; Quinn et al. 2006; Rabin et al. 2006), then these noise impacts may affect subsequent male display behaviors on the lek. More importantly, there is evidence that females and juvenile males use the sounds created by males on the lek to locate leks in the landscape (Gibson 1989). Blickley and Patricelli (2012) found that industrial noise masks these sounds, which will make it more difficult for females and juvenile males in noisy areas surrounding a lek to find the lek itself. Reduced female visitation would decrease copulation activities on the lek, and reduced juvenile male recruitment would lead to male attendance declines over time. For these reasons, the protection of lekking activities may require protection of more than just the lek surface alone.

Additionally, other critical components of successful breeding occur off lek, potentially in areas with higher noise levels **(Figures 3** & **4**). Since 64% of females nest within a 5 km (3.1 mile) radius of the lek and 74-80% of females nest within a 6.4 km (4 mile) radius of the lek (Holloran & Anderson 2005; Moynahan 2004), many of these nesting females will experience noise levels exceeding management objectives for the lek. Most vocalizations used between hens and chicks are much quieter than sounds produced by males on leks (Schroeder et al. 1999), and therefore much more prone to masking (Blickley & Patricelli 2012). Additionally, predation rates can be high for chicks and females on nests in disturbed habitats (Hagen 2011), and females likely rely mainly on acoustic rather than visual cues to predator approach at night. Thus when noise masks the sounds of predator approach, females and chicks may be more at risk in noisy areas than males on the lek. Further, breeding females may suffer detrimental health impacts from elevated stress, at a time when stress levels are already elevated (Jankowski 2007). While we do not have direct evidence for an impact of noise on these off-lek activities, there is evidence that proximity to roads and infrastructure (which raises noise levels) affects nest placement, nest initiation rates, chick survival and brood-rearing activities (Aldridge & Boyce 2007; Holloran et al. 2010; Holloran & Anderson 2005; Lyon & Anderson 2003).

Other types of disruptive activities in sage-grouse habitat are managed throughout areas critical for lekking, nesting and early brood rearing (e.g. BLM Instruction Memorandum WY-2012-019; Wyoming Executive Order 2011-5); there is no scientific basis for focusing the monitoring and management of noise on the lek area alone, without including these other critical areas.

### *4. Traffic Noise*

There is evidence that noise from traffic is has a significant impact on sage-grouse. Blickley et al. (2012) found 73% decline in male attendance on traffic-noise leks compared to their paired controls, more than twice the decline observed on drilling-noise leks (29%). Traffic noise was also found to cause an increase in stress hormone levels (Blickley et al. In review) and a disruption of strutting patterns on the lek (Blickley et al. in prep). Further evidence comes from other studies not focused on noise alone. Lyon and Anderson (2003) found that even light vehicular traffic (1–12 vehicles per day) substantially reduced nest initiation rates and increased the distance of nests from lek sites. Holloran (2005) found that traffic on roads within 0.8 miles of the lek during the early morning while males are

strutting is related to declines in male attendance. These results suggest that effective management strategies should include efforts to minimize traffic near areas critical for sage-grouse reproduction.

However, management strategies that allow up to 10 dB of noise above ambient are not sufficient to protect sage-grouse from the impacts of traffic noise. Since traffic noise in sage-grouse habitat is typically intermittent and interspersed with periods of quiet, a great deal of traffic would be needed to raise overall noise levels by 10 dBA. In general, a tenfold increase in traffic is associated with a 10 dB increase in average noise levels, so an increase from 2 to 20 vehicles or from 200 to 2,000 vehicles over a given time interval. A tenfold increase in traffic would likely have a major impact on sage-grouse, yet may not exceed current noise management objectives inside and outside of core areas. This suggests that approaches for the management of more continuous noise sources, such as noise from compressors stations, drilling rigs and other permanent or temporary infrastructure, may not be suitable for the management of traffic noise.

# II. RECOMMENDATIONS FOR RESEARCH PRIORITIES

While our understanding of noise impacts on sage-grouse has improved over the last few years, there is still much to learn. Below, we outline recommendations for research that would help to develop more effective management strategies for anthropogenic noise.

### *1. Establishing ambient values*

As discussed in part **I.1.**, management objectives for noise are typically established relative to ambient noise levels, stating that noise measured at lek edge should not exceed 10 dB over ambient. The choice of ambient value thus has large consequences, setting the upper limit of allowable noise. In order for such management strategies to protect vulnerable species, it is therefore critical to establish accurate ambient values.

Due to the previously discussed difficulty of measuring ambient values at quiet locations, we suggest that it is not feasible or practical to establish baseline noise levels by having agency personnel or consultants with little specialized training measure ambient at each lek prior to development. Further, experimental evidence indicates that ambient values should represent the pre-development ambient levels, such that new developments do not further impact already impacted soundscapes (see part **I.1.**). One approach to establish ambient noise levels is to commission the measurement of ambient levels by professionals with experience in environmental acoustics. Such professionals would need to measure ambient values for each site prior to development (or if there are already noise sources in an area, they could choose a similar but undisturbed area to estimate natural ambient levels). Alternatively these professionals could sample noise levels at representative undisturbed areas across the state, using such measurements to establish ambient values by region or habitat type. Measurements should be collected using a Type-1 precision sound level meter (ANSI S1.4-1983)[11] enclosed in environmental housing for long-term deployment at each site[14]. Alternative methods, such as carefully calibrated audio recording units that can be used to calculate appropriate metrics[14] would also be appropriate (Lynch et al. 2011; Patricelli et al. 2007).

[14] The meter should log A-weighted 1/3-octave spectra of noise at 1-sec intervals. The following metrics (at a minimum) should be collected: Leq, Lmax, Lpeak, $L_{10}$, $L_{50}$, $L_{90}$ (see Figure 1). Each metric should be collected as A-weighted values, and if possible, as dBF (i.e. dB-flat or unweighted) and C-weighted. With a logging SLM, one can save the time history, showing how noise levels change over time in the sampling period. This can be very useful in isolating the causes of change in noise levels. One can also calculate each metric hourly or over the entire sampling period. Hourly metrics are useful when focusing on a critical time window (e.g. 6pm to 9 am). The meter (or a nearby station) should also log wind speed, so that measurements can be excluded when wind likely to contributed to noise levels.

We recommend that a better approach would be to combine such empirical sampling of noise levels with modeling, to create a map of natural ambient noise across the state. This would lead to broader coverage of the state, since collecting empirical measurements at each key site would be time consuming and interpolating levels between these sites would be inaccurate without a model. The National Parks Service (NPS) Natural Sounds and Night Skies Division is currently developing a model to predict ambient noise levels with and without existing developments. The model uses a machine-learning algorithm to improve predictions using publically-available input variables related to location, climate, land cover, hydrology, and degree of human development. The algorithm improves its accuracy (i.e. learns to improve its estimates) with each new empirical measurement. Output from such a model would be available to any parties interested in evaluating the natural noise levels at a current or proposed development site in the state. These measurements are not grouse specific, thus this data would be useful for multiple public and private agencies interested in tracking noise exposure.

### *2. Determining an appropriate threshold*

Once an ambient value is determined, we must then determine whether the current threshold of 10 dB above ambient is sufficient to protect sage grouse. The ideal method to determine the appropriate threshold would be a dose-response experiment, where noise is played back at different levels to different leks, to determine the maximum noise level before an impact occurs. However, such an experiment is logistically infeasible for multiple reasons, including the necessity to impact a very large sample of leks (multiple leks at each playback level, with many playback levels) and large expense. A more feasible way to determine the threshold level at which sage-grouse are impacted by noise is by analyzing nesting success, lek attendance and other population variables relative to existing variation in noise levels in a spatially-explicit manner using habitat-selection modeling. This method examines the impact of "natural" variation in noise exposure across a disturbed landscape, while statistically controlling for other possible contributors, and allows estimation of the slope of the relationship between noise and measures of population change. This relationship can then be used to determine the threshold level at which a minimal (or acceptable) level of impact on sage-grouse occurs. We are currently collaborating with Dr. Matt Holloran to develop noise layers for use in habitat-selection models of the Pinedale Anticline during development (beginning in 1998). We encourage researchers to consider including noise layers in habitat-selection models for other regions. Such an approach would also be useful for examining noise impacts outside of the breeding season, especially in winter, where changes in habitat quality and availability can lead to significant impacts on population health (Beck 1977; Doherty et al. 2008; Swenson et al. 1987).

### *3. Measuring traffic noise*

Evidence shows that traffic noise causes impacts on sage-grouse, as discussed in part **I.4.**; however, limiting traffic noise by setting noise-exposure objectives will be difficult. This is because intermittent traffic, such as the traffic in most sage-grouse habitat, causes short periods of loud noise interspersed with longer periods of quiet. With a variable noise source such as this, is it difficult to choose which metric to use in setting management objectives. This is especially true since we do not know whether it is the total noise exposure through the day (or in a critical time period, such as nights and/or mornings) or the maximum noise level as a vehicle passes that best predicts impacts on grouse. Given that Lyon and Anderson (2003) found that nesting activities can be disturbed by only 1-12 vehicles per day, the chosen metric would need to be sensitive to infrequent sounds. A measure of "average" amplitude (e.g. $L_{eq}$) would be problematic, since the occasional noise events would be averaged with much longer quiet periods, having little effect on measured values (see part **I.4.**). Similarly, the sounds of vehicles passing would have little to no influence on median noise level ($L_{50}$), unless traffic noise is detectable

50% of the time or more. Even measures of maximum noise levels (such as the $L_{max}$, a measure of the maximum RMS amplitude during the sample period; see **Figure 1**) can be problematic, since other sound sources besides vehicles can affect these measures. This is especially problematic during long-term deployment of meters for monitoring, since a single meadowlark perched near (or on) the meter could lead to extremely high $L_{max}$ measurements. Excluding these events would require that they be identified in synchronized audio recordings; alternatively, the 1/3-octave band frequency profile of the noise may be useful for these exclusions. A protocol could be developed to do this, but different methods would need to be tested. Even with such a protocol in place, $L_{max}$ values may be more informative when combined with a measure of exposure, such as $L_{eq}$ or axle counts.

To establish more effective management strategies for traffic noise, more information is needed about which noise metrics best predict traffic impacts on sage-grouse. Such information could be gathered by including traffic noise in habitat-selection models. This approach will allow estimation of the relationships between demographic variables (e.g. lek attendance, nest location, nest success) and traffic variables (distance, traffic level and noise level). This would help to establish whether the impacts from traffic noise are better mitigated through setting noise objectives or by managing the siting and traffic levels of roads directly. If informative metrics are identified for measurement of traffic noise, then protocols should be established for accurate and repeatable measurements in the field, given the challenges discussed. The noise layers we are currently developing for the Pinedale Anticline area will include traffic noise and allow us to begin addressing this issue. We encourage researchers to consider including traffic-noise layers in habitat-selection models for other regions.

# III. RECOMMENDATIONS FOR INTERIM PROTECTIONS

The research described above, however, will take time. Below, we provide managers and policy makers with recommendations for the interim protection of sage-grouse from known or expected impacts of increased noise levels using the best available science to date. We emphasize that protections based on these interim recommendations may need to be revised upon completion of ongoing and future research.

### *1. Setting an ambient value*

Based on our review of reports and empirical measurements collected in Wyoming, we have concluded that true ambient values pre-development in nights and calm morning in sagebrush habitat are likely to be 16-22 dBA. The first source for this conclusion is the 1971 EPA report from which the original 39 dBA ambient value was drawn (US EPA 1971). This report finds residual noise levels ($L_{90}$)[4] in wilderness areas of 16-22 dBA[15], measured during day and nighttime at a campsite on the north rim of the Grand Canyon National Park; the report concludes that "these increases in (residual) noise level, from wilderness to farm and to city, are the result of man's activities and his use of machines". Lynch et al. (2011) more recently measured noise exposure at 189 sites in 43 U.S. National Parks, finding an average 24-hour residual noise level of 21.6 dBA[16].

[15] 16 dBA was the daytime residual level (7am to 7pm) and ~22 dBA was the night time residual level (10pm-7am). In most places, nighttime residual levels will be lower than daytime due to environmental conditions (temperature, humidity, breeze, etc.) However, these values are reversed due to crickets which were active early in the night. Evening readings of ~28 dBA (7pm to 10 pm) were dominated by crickets and are not included here since insect noise is minimal during the sage-grouse breeding season due to low temperatures.

[16] These measures include only the 1/3 octave bands from 12.5 Hz to 800 Hz, so they are not directly comparable to the full-spectrum measures from other sources given in the text (these narrower-spectrum measures will be lower than the full-spectrum measures). However, these frequencies span most anthropogenic noise and residual noise in undisturbed areas, so this measure provides an appropriate estimate of ambient noise levels at these sites (Lynch et al. 2011).

In addition, we have analyzed the detailed data from long-term deployment of a sound level meter by KC Harvey consulting on the Pinedale Anticline Project Area (KC Harvey 2009)[17]. The median $L_{90}$ among these 12 leks was 27.2 dBA and the minimum lek was 22.2 dBA (**Table 1**, **Figure 2**). Given that all of these leks experienced some noise from natural gas infrastructure and highways (and that this Type-2 sound level meter[11] had a noise floor of 20-22 dBA), these are conservative (i.e. slightly high) estimates of pre-development ambient. Other recent measurements in areas with low levels of disturbance have found similar residual levels[18].

Since 16 dBA is at or below the limit of measurement on most Type-1 sound level meters[11], it would be a difficult to implement protections based on this ambient value without an immediate shift in methods for measurement and/or data-processing. Further, it is clear that residual ambient values even in undisturbed areas are sometimes higher. Therefore, we recommend that an ambient value of 20-22 dBA should be used for interim protections in sage-grouse habitat. In revised management strategies, this new default ambient would replace the previous default of 39 dBA or replace empirical measurements of ambient at lek edge.

### *2. Setting a threshold above ambient*

As discussed in part **I.2.**, we do not yet know whether limiting noise to 10 dB above ambient is appropriate for protecting sage-grouse. However, we recommend continuing to use the 10 dB threshold as an interim measure, combined with appropriate measures of ambient (i.e. 20-22 dBA). This threshold value is based on the best available science to date, but should be revised as needed when better information becomes available. Using 20 dBA as the ambient value, this would allow up to 30 dBA of noise exposure; using 22 dBA as ambient, this would allow up to 32 dBA of noise exposure.

How should compliance with this management objective be measured? Noise can be variable over time, space and frequency spectrum, so no single metric can capture this complexity. However, using multiple metrics to assess compliance may be complicated to implement, at least in the interim. Therefore, we recommend using the A-weighted $L_{50}$ as a measure of median noise exposure[3]. This metric is useful because it is less influenced by the brief intruding sounds (e.g. birds, insects and airplanes) that can dominate other metrics. This metric may also exclude some types of noise produced by the development being monitored, including vehicles (unless traffic is very heavy). For that reason, it will typically not be effective at reflecting impact caused by traffic noise. Despite this concern, the $L_{50}$ is recommended because otherwise birds, insects and other indicators of a healthy habitat may be counted against compliance (unless audio recordings are produced, allowing monitors to exclude time periods with such activity; this may be a preferable solution in the long run, but it will require time to develop such a protocol).

We recommend that measurements are made during times when noise exposure is most likely to affect greater sage-grouse: nights and mornings (i.e. 6 pm – 9 am). Further, we recommend using the average of $L_{50}$ values at multiple (3-4) locations between each noise source and the edge of the protected area. Since noise values can change with topography and local ground cover, this will reduce the impact of aberrant measurements (high or low) at particular locations. Measurements should be

---

[17] Available here.

[18] A recent EIS (DOE EA-1849) for a geothermal development in sage-grouse habitat near Elko, NV, found an ambient noise level of 25 dBA (measured from 12-5am on 6/17/11). This area is described as follows: "Existing noise at the power plant site is dominated by ambient sources including wind, ranch vehicles, livestock, irregular mineral exploration, and recreational uses such as all-terrain vehicles, on BLM land to the west of the site". We also collected brief ambient noise values with a handheld Type-1 noise meter on Preacher Lek near Hudson, WY. This lek is on relatively-undisturbed federal land, but noise from nearby Highway 789 was clearly audible when readings were being collected. Six males were present on the lek, but ambient measures were collected when birds were not vocalizing. The $L_{90}$ for these measurements was 25.4 dBA. These two measures are slightly higher than the 22 dB given as the upper end of the range of pre-development ambient values, which is appropriate since both sites have anthropogenic noise sources nearby.

taken with a Type-1 sound level meter[11] (or a method with similar accuracy and a noise floor <25 dBA). We recommend making measurements of at least 1 hour at each site, ideally over multiple days and climactic conditions, since weather (temperature [especially temperature inversions], humidity and wind) can affect noise levels. We recommend collecting additional metrics whenever possible, for research and long-term monitoring[14].

It should be noted that based on the measurements presented in **Table 1**, four of the 12 monitored leks on the Pinedale Anticline are in compliance with the noise management objectives recommended here based on a 20 dBA ambient value (i.e. they do not exceed an $L_{50}$ of 30 dBA). Two of the other leks are within 0.5 dB of compliance with recommended objectives based on an ambient of 22 dBA. Given that these leks are in a heavily developed area, which has experienced declines in sage-grouse populations (Holloran et al. 2010; Holloran 2005), this suggests (1) that these recommended protections are not as onerous as they may initially seem, even using an ambient value of 20 dBA, and (2) that even these stricter recommendations may not suffice to avoid population declines if noise levels are measured at lek edge (as in Table 1), rather than across nesting and brood-rearing habitats, as discussed below.

### *3. Redefining the protected area*

Current noise management strategies typically recommend noise measurements at the edge of the lek to assess compliance (e.g. WY Executive Order 2011-5; BLM 1999, 2003, 2008). This approach manages noise levels the lek area itself, and not the surrounding habitat critical to support lekking activities and successful reproduction. In part **I.3.**, we review the evidence that this off-lek noise will affect on-lek activities and successful reproduction. Therefore we recommend that interim and longer-term management strategies aim to protect the soundscape in areas critical for mating, foraging, nesting and brood-rearing activities. Thus we recommend that noise exceeding 10 dB over ambient be managed as a "disruptive activity" throughout sage-grouse nesting and brood-rearing habitat (e.g. BLM Instruction Memorandum WY-2012-019). To accomplish this, we recommend measuring compliance with noise objectives at the edge of nesting/brood-rearing habitats, rather than at the ledge of the lek.

### *4. Limiting traffic noise*

Given the difficulty of measuring intermittent traffic noise and the uncertainty about which metrics are informative (see part **II.3.**), we recommend that interim protections focus not on setting objectives for traffic noise levels, but rather on the siting of roads or the limitation of traffic during critical times of the day (6pm to 9 am) and/or year (breeding season).

To develop interim recommendations for the siting of roads, we estimated the distance from a road at which noise levels ($L_{max}$ as a single vehicle passes) will drop down to 10 dB over ambient. Using an ambient of 20 dBA, we calculate that vehicle noise will diminish to 30 dB at ~1.3 km (0.8 miles) from the road. Using an ambient of 22 dB, we calculate that vehicle noise will diminish to 32 dBA at ~1.1 km (0.7 miles) from the road[19]. Therefore to avoid disruptive activity in areas crucial to

[19] To calculate this estimate of impact distances from roads, we used 2006 measurements of noise levels from 17 vehicles (flatbed trucks and big rigs) on the Luman Road and 8 vehicles on the North Jonah Road on the Jonah Field in Sublette County, WY. All measurements were made at ¼ mile from the road. A-weighted $L_{max}$ values were averaged for each road and the average of the two roads was 45.47 dBA (S.E. = 1.3 dBA; range 37 - 58.7 dBA); we similarly calculated average A-weighted levels for each octave from 16-16,000 Hz. In each octave band, we calculated propagation using the assumption of spherical spreading (see formula here) and octave-specific excess attenuation values from the Pinedale Anticline Noise Analysis report prepared by the BLM with assistance from the Army Corps of Engineers and US Forest Service (BLM, 1999). Using these methods, we extrapolated noise propagation beyond our ¼-mile levels until levels reached 32, 30, 22 and 20 dBA; the distances at which those levels were reached are presented above. These estimates are based on the maximum noise levels as a single vehicle passes, however, on roads with sufficient traffic to create a steady stream of vehicles, noise

mating, nesting and brood-rearing activities, we recommend that managers consider siting roads (or seasonally limiting traffic) within 0.7-0.8 miles from the edge of these areas. We emphasize that we are recommending restrictions within 0.7-0.8 miles of the edge of sage-grouse nesting and brood-rearing habitat (e.g. BLM Instruction Memorandum WY-2012-019), not the lek edge. Further, note that noise from traffic will be audible at least until levels drop down to ambient values, which will occur 1.5-1.7 miles from the road[19]. These distances may be much farther during temperature inversions, which are common during the lekking hours in sage-grouse habitat (for an ambient of 20 dB and 22 dB respectively, traffic noise in a temperature inversion would reach 10 dB over ambient at 1.1 and 1.4 miles from the road, and this noise would reach ambient at 2.8 and 3.3 miles from the road). Therefore, adopting these recommendations will not eliminate traffic noise in critical areas, but should reduce its impact.

Given that traffic noise was found to have more than twice the impact of continuous noise on lek attendance (Blickley et al. 2012), minimizing traffic noise as a disruptive activity in all areas critical for successful reproduction should be a priority in any revised noise management strategy. In areas where implementing recommended limits on siting or traffic is not possible, other measures may reduce traffic noise impacts. One possibility would be to adjust timing of the shift change in development areas to avoid causing an increase in traffic during critical times. Avoiding shift changes between 6 pm and 9 am would be ideal, but if this is not possible, then avoiding 12 am to 9 am would likely be a significant improvement.

---

drops off more slowly and these distances would be up to *twice as far* (levels would follow predictions of cylindrical spreading, dropping only 3 dB with every doubling of distance, rather than 6 dB, as assumed here). Similarly, noise levels drop off according to predictions of cylindrical spreading during temperature inversions, which are common in sage-grouse habitat during the early morning. For these reasons, the distances presented above may be conservative estimates (i.e. underestimates) of the distance that sound will propagate from a road. The same calculations were used to estimate propagation distances around a hypothetical noise source in Figure 3 and a drilling rig in Figure 4. For Fig 4, we used an example drilling rig measured in the PAPA in 2006 at an $L_{eq}$ of 66.7 dBA at 216 feet. This drilling rig measurement is from a single example rig and is not meant to be representative of all drilling rigs. The hypothetical source in Fig 3 uses the same octave spectrum as the drilling rig, which is typical of industrial noise sources, but is scaled to an overall dBA level of 65 dBA at 1000 feet.

## AUTHORS

**Dr. Gail L. Patricelli** is an Associate Professor of Evolution and Ecology at the University of California, Davis. Dr. Patricelli studies bioacoustics, breeding behaviors and noise impacts in sage-grouse and songbirds. For the last seven years, Dr. Patricelli has been investigating the impacts of noise from natural gas development activities on greater sage-grouse lek attendance, stress levels and behaviors with graduate student Jessica Blickley and postdoctoral scholars Dr. Diane Blackwood, Dr. Stacie Hooper, and Dr. Alan Krakauer. Dr. Patricelli has published multiple peer-reviewed papers on noise impacts on wildlife and has served on Expert Panels to establish noise measurement protocols for the National Parks Service.

**Jessica Blickley** is a graduate student completing her Ph.D. in Ecology in the Patricelli Lab at the University of California, Davis. Ms. Blickley has been studying noise impacts on sage-grouse for 6 years. Ms. Blickley has published multiple peer-reviewed papers on noise impacts on wildlife, and has served on Expert Panels to establish noise measurement protocols for the National Parks Service. She recently co-edited an Ornithological Monograph on the impacts of anthropogenic noise on birds and bird studies (available here).

**Dr. Stacie Hooper** is a postdoctoral researcher in the Patricelli Lab in the Department of Evolution and Ecology at the University of California, Davis. Dr. Hooper has published multiple peer-reviewed papers on noise impacts on wildlife; her dissertation research addressed noise impacts on ground squirrels in Yosemite National Park. Dr. Hooper also works for the California Department of Fish and Game as the California Wildlife Habitat Relationships (CWHR) program coordinator, maintaining and updating species range data and habitat suitability models to predict species occurrence across the state. She is also part of the California contingent of the Western Governor's Association's Crucial Habitat Assessment Tool (CHAT) team.

**Figure 1. Some common metrics used to measure noise levels.** The gray line represents the noise level (RMS amplitude over a short sample period, typically one second) as it changes over time through the sampling period (the time history).

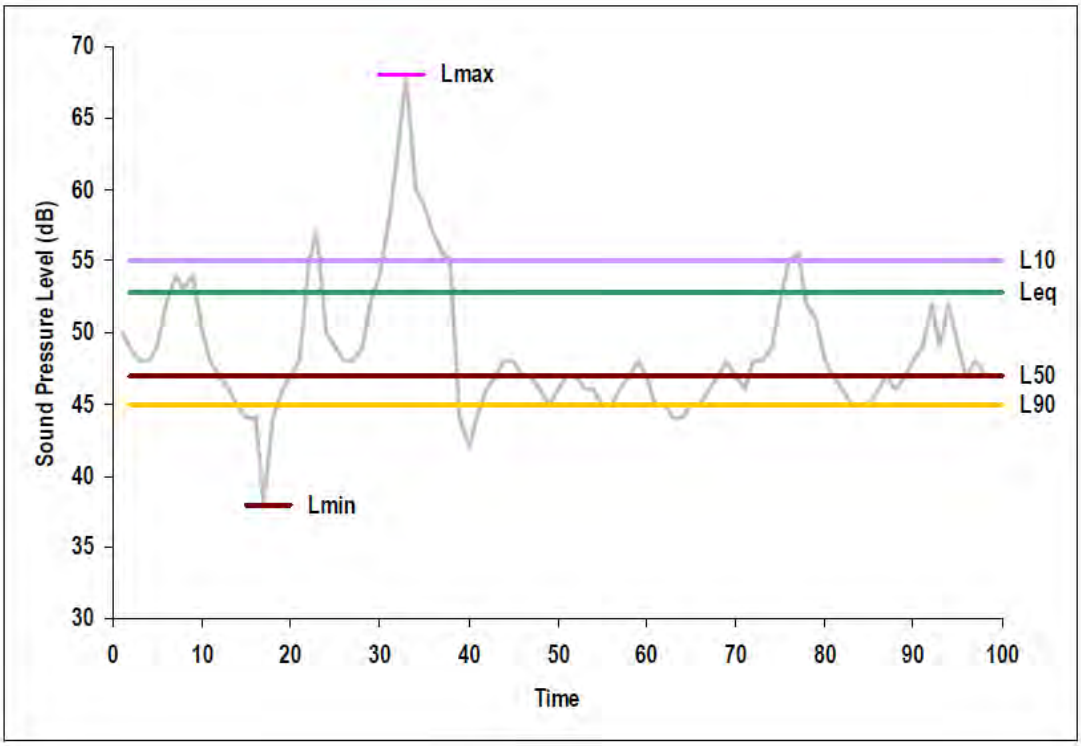


**Table 1. Spring 2009 noise levels on leks in the Pinedale Anticline Project Area.** Data were collected by KC Harvey Consultants (KC Harvey 2009) from multi-day deployments of four Type-2 sound level meters (Quest - SoundPRO-DL-2-1/3-10; noise floor 20-22 dB). All measures are presented in dBA. Weather data are not available and windy periods were not excluded, so these values likely include substantial energy from wind. All leks are close enough to development sites, access roads and/or highways to experience anthropogenic noise (see Figure 2); it is not clear from the report whether noise levels may also reflect sounds from males displaying on the leks (displaying males on these relatively-small leks are unlikely to significantly impact $L_{50}$ or $L_{90}$ measures, but may affect other metrics). Measurements are from the full 24 hrs/day, so they are not focused on the night and morning periods likely critical to greater sage-grouse (6 pm to 9 am).

| Lek Name | Dates | Duration (hrs) | $L_{90}$ | $L_{50}$ | $L_{10}$ | $L_{avg}$ ($L_{eq}$) | $L_{max}$ | $L_{min}$ | $L_{peak}$ |
|---|---|---|---|---|---|---|---|---|---|
| Alkali Draw | April 2 & 6 | 121 | 23.6 | 28.8 | 41.2 | 44.1 | 92.6 | 19.6 | 114.0 |
| Big Fred | April 12, 16 & May 12 | 123 | 27.6 | 33.9 | 44.0 | 42.4 | 80.2 | 22.0 | 100.5 |
| Bloom Reservoir | April 22 & 27 | 120 | 22.2 | 29.2 | 44.7 | 41.9 | 83.9 | 19.4 | 103.4 |
| Cat | May 2 & 7 | 120.3 | 22.8 | 28.1 | 44.1 | 44.3 | 86.9 | 19.6 | 106.0 |
| Little Fred | April 12, 16 & May 7 | 85.5 | 32.7 | 36.7 | 45.5 | 44.2 | 80.8 | 31.8 | 101.9 |
| Lovatt West | April 22, 23 & May 12 | 127 | 30.4 | 33.7 | 48.3 | 47.4 | 84.5 | 28.2 | 106.8 |
| Lower Sand Springs Draw | May 7 | 111.3 | 25.9 | 29.8 | 41.5 | 39.7 | 73.4 | 23.6 | 88.6 |
| Mesa Road 3 | May 12 | 141.3 | 31.9 | 32.1 | 33.1 | 32.5 | 53.4 | 31.7 | 88.5 |
| Oil Fork Road | April 17, 22 & 27 | 120.4 | 24.5 | 33.0 | 46.7 | 42.8 | 78.0 | 22.8 | 88.6 |
| The Rocks | April 6 | 147.5 | 32.1 | 33.1 | 46.8 | 44.4 | 95.3 | 31.7 | 107.7 |
| Shelter Cabin Reservoir | April 6, 12 & May 27 | 99.1 | 27.1 | 32.4 | 41.9 | 40.5 | 78.0 | 23.3 | 88.6 |
| South Rocks | May 2 | 121 | 27.4 | 33.3 | 46.2 | 42.7 | 73.7 | 23.8 | 88.6 |
| MEAN | | 119.8 | 27.4 | 32.0 | 43.7 | 42.2 | 80.1 | 24.8 | 98.6 |
| MEDIAN | | 120.7 | 27.2 | 32.7 | 44.4 | 42.8 | 80.5 | 23.4 | 101.2 |
| S.D. | | 16.4 | 3.7 | 2.5 | 4.0 | 3.7 | 10.8 | 4.8 | 9.4 |
| S.E. | | 3.3 | 0.7 | 0.5 | 0.8 | 0.7 | 2.2 | 1.0 | 1.9 |
| MAX | | 147.5 | 32.7 | 36.7 | 48.3 | 47.4 | 95.3 | 31.8 | 114.0 |
| MIN | | 85.5 | 22.2 | 28.1 | 33.1 | 32.5 | 53.4 | 19.4 | 88.5 |

**Figure 2. Locations of leks presented in Table 1.** This is figure 1 from the report by KC Harvey showing locations where noise measurements were collected (KC Harvey 2009).

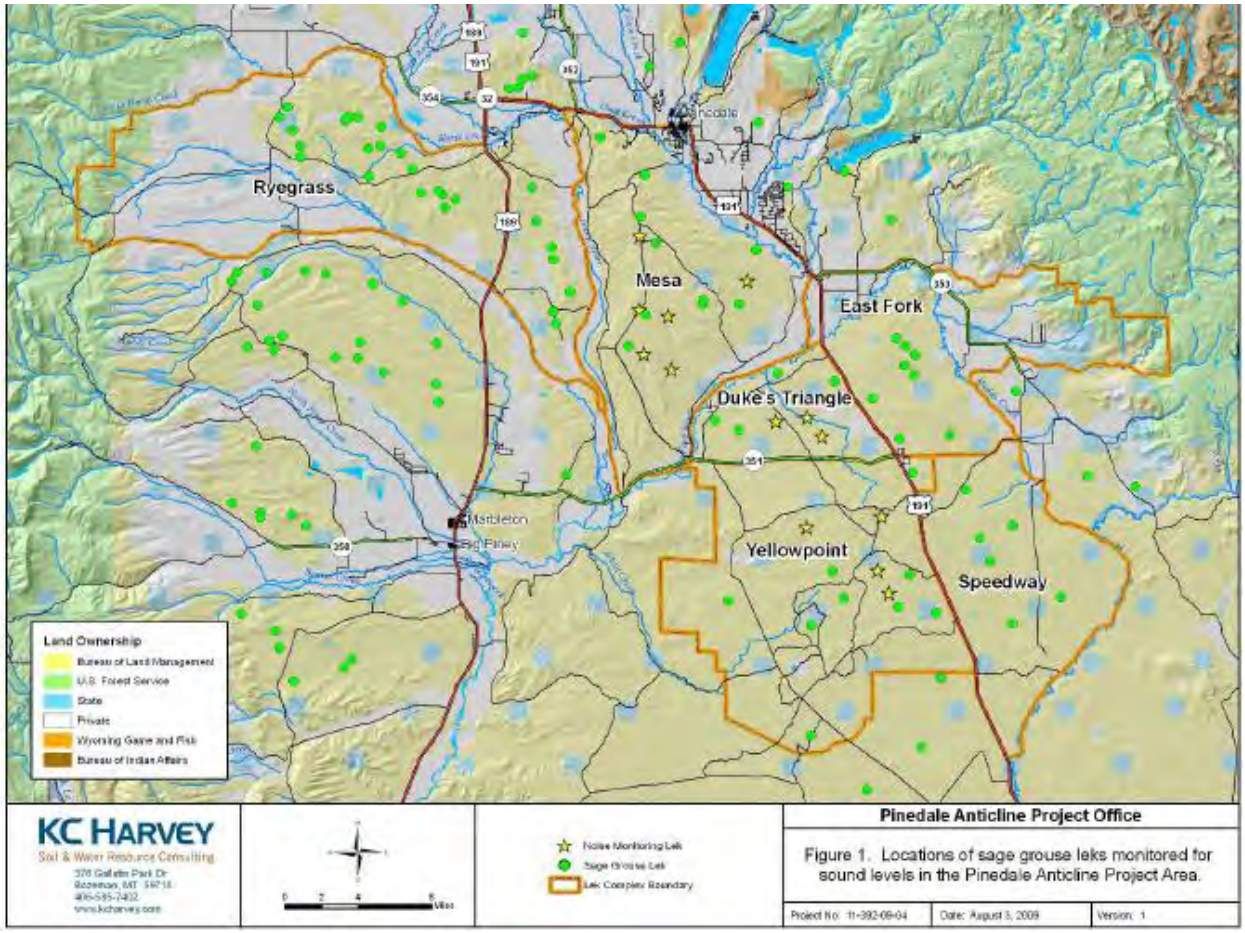


**Figure 3. An illustration of noise levels surrounding a lek.** This illustration shows a lek in the center, surrounded by a 0.6 mile buffer, a 1.9 mile buffer encompassing ~45% of nests, and a 4-mile buffer encompassing 74-80% of nests (Holloran & Anderson 2005; Moynahan 2004). Noise propagation is shown from a hypothetical loud noise source or combination of sources measuring 65 dBA at 1000 feet (with the same frequency spectrum as drilling noise[19]) located at the edge of the 1.9 mile buffer. Noise is predicted to exceed 10 dBA over ambient (20 dBA) for a radius of approximately 1.9 miles (darker blue), and to be audible above ambient for at least 3.4 miles (lighter blue)[19]. This figure demonstrates that even when the lek area is within recommended noise levels, much of the surrounding area critical for foraging, nesting and brood-rearing may be exposed to higher levels of noise. Distances are approximately to scale and calculations assume no temperature inversions, which nearly double sound propagation distances, and no topographical or ground effects[19].

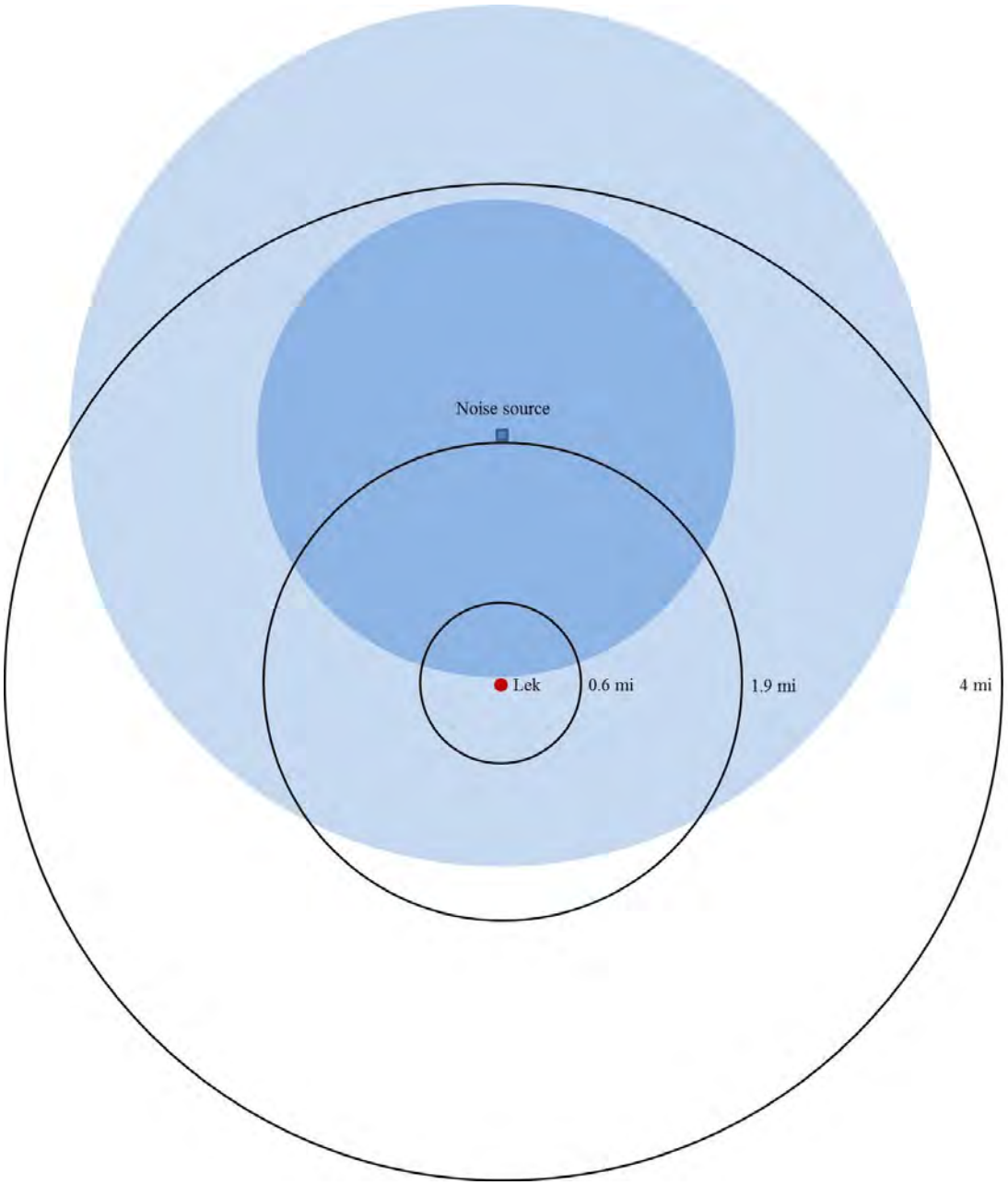
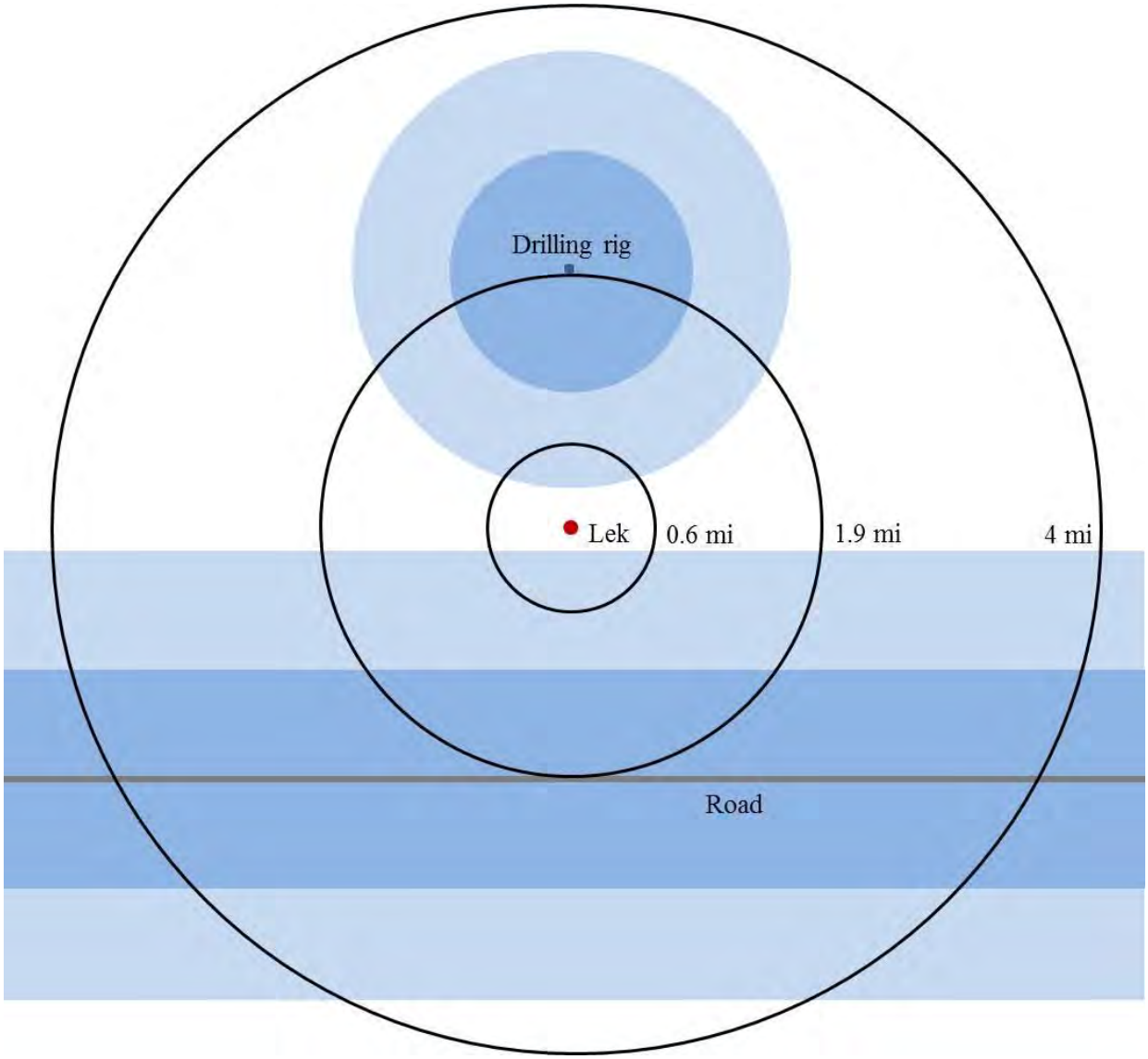


**Figure 4. Traffic and drilling noise surrounding a lek.** This illustration shows a lek in the center, surrounded by a 0.6 mile buffer, a 1.9 mile buffer encompassing ~45% of nests, and a 4-mile buffer encompassing 74-80% of nests (Holloran & Anderson 2005; Moynahan 2004). Noise from an example natural gas drilling rig at the edge of the 1.9 mile buffer exceeds 10 dBA over ambient (20 dBA) for a radius of approximately 0.9 miles (darker blue), and is audible above ambient for at least 1.65 miles (lighter blue)[19]. An average road at the lower edge of the 1.9 mile buffer will have noise levels ($L_{max}$) exceeding ambient by 10 dBA for a distance of 0.8 miles and will be audible above ambient for at least 1.7 miles with each passing vehicle[19]. With both sound sources, the lek area is within recommended noise levels, but much of the surrounding area critical for foraging, nesting and brood-rearing is exposed to higher levels of noise. Distances are approximately to scale and calculations assume no temperature inversions, which nearly double sound propagation distances, and no topographical or ground effects[19].



**REFERENCES CITED**


Aldridge, C. L. & Boyce, M. S. 2007 Linking occurrence and fitness to persistence: Habitat-based approach for endangered Greater Sage-Grouse. *Ecological Applications* **17**, 508-526.

Barber, J. R., Crooks, K. R. & Fristrup, K. M. 2009 The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution* **25**, 180-189.

Beck, T. D. I. 1977 Sage Grouse Flock Characteristics and Habitat Selection in Winter. *The Journal of Wildlife Management* **41**, 18-26.

Blickley, J. L., Blackwood, D. & Patricelli, G. L. 2012 Experimental Evidence for the Effects of Chronic Anthropogenic Noise on Abundance of Greater Sage-Grouse at Leks. *Conservation Biology* **26**, 461-471.

Blickley, J. L., Blackwood, D. L., Hardy, E. L. & Patricelli, G. L. in prep Temporal flexibility in greater sage-grouse (Centrocercus urophasianus) signaling behavior in response to chronic industrial noise playback.

Blickley, J. L. & Patricelli, G. L. 2010 Impacts of Anthropogenic Noise on Wildlife: Research Priorities for the Development of Standards and Mitigation. *Journal of International Wildlife Law and Policy* **13**, 274-292.

Blickley, J. L. & Patricelli, G. L. 2012 Potential acoustic masking of greater sage-grouse display components by chronic industrial noise. *Ornithological Monographs* **74**, 23-35.

Blickley, J. L., Word, K. R., Krakauer, A. H., Phillips, J. L., Sells, S. N., Wingfield, J. C. & Patricelli, G. L. In review Experimental chronic noise exposure is related to elevated fecal corticosteroid metabolites in lekking male greater sage-grouse (*Centrocercus urophasianus*). *PloS ONE*.

BLM. 1999 Noise Analysis for the Pinedale Anticline Oil and Gas Exploration and Development Project, Sublette Co. WY: Bureau of Land Managment Pinedale Field Office.

BLM. 2003 Final Environmental Impact Statement and Proposed Plan Amendment for the Powder River Basin Oil and Gas Project, vol. 3 (ed. B. F. office).

BLM. 2008 Record of Decision for the Supplemental Environmental Impact Statement Pinedale Anticline Oil and Gas Exploration and Development Project (ed. B. P. F. O. US Department of the Interior).

Braun, C. E. 1986 Changes in Sage Grouse lek counts with advent of surface coal mining. *Proc. Issues and Tech. in the Manage. of Impacted West. Wildl.* **2**, 227-231.

Braun, C. E. 1998 Sage grouse declines in western North America: what are the problems? *Proc. West. Assoc. State Fish & Wildl. Agencies* **78**, 139-156.

Brenowitz, E. A. 1982 The active space of red-winged blackbird song. *The Journal of Comparative Physiology* **147**, 511-522.

Connelly, J. W., Knick, S. T., Schroeder, M. A. & Stiver, S. J. 2004 Conservation Assessment of Greater Sage-grouse and Sagebrush Habitats, pp. 610. Cheyenne, WY: West. Assn. Fish and Wildlife Agencies.

Connelly, J. W., Reese, K. P. & Schroeder, M. A. 2003 *Monitoring of greater sage-grouse habitats and populations*. College of Natural Resources Experiment Station Bulletin 80: University of Idaho, Moscow, ID.

Dantzker, M. S., Deane, G. B. & Bradbury, J. W. 1999 Directional acoustic radiation in the strut display of male sage grouse *Centrocercus urophasianus*. *The Journal of Experimental Biology* **202**, 2893-2909.

Doherty, K. E., Naugle, D. E. & Walker, B. L. 2010 Greater Sage-Grouse Nesting Habitat: The Importance of Managing at Multiple Scales. *Journal Of Wildlife Management* **74**, 1544-1553.

Doherty, K. E., Naugle, D. E., Walker, B. L. & Graham, J. M. 2008 Greater sage-grouse winter habitat selection and energy development. *Journal Of Wildlife Management* **72**, 187-195.

Dooling, R. J. & Popper, A. N. 2007 The Effects of Highway Noise on Birds, pp. 74. Sacramento, CA: The California Department of Transportation Division of Environmental Analysis.
EPA. 1971 Community Noise (ed. EPA).
Francis, C. D., Ortega, C. P. & Cruz, A. 2009 Noise Pollution Changes Avian Communities and Species Interactions. *Current Biology* **19**, 1415-1419.
Gibson, R. M. 1989 Field playback of male display attracts females in lek breeding sage grouse. *Behavioral Ecology and Sociobiology* **24**, 439-443.
Gibson, R. M. 1996 Female choice in sage grouse: the roles of attraction and active comparison. *Behavioral Ecology and Sociobiology* **39**, 55-59.
Gibson, R. M. & Bradbury, J. W. 1985 Sexual selection in lekking grouse: phenotypic correlates of male strutting success. *Behavioral Ecology and Sociobiology* **18**, 117-123.
Hagen, C. A. 2011 Predation on Greater Sage-Grouse: Facts, Process, and Effects. In *Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats*, vol. 38 (ed. S. T. Knick & J. W. Connelly). Berkeley, CA.: University of California Press.
Harvey, K. 2009 Pinedale Anticline Project Area Sage Grouse Monitoring: Noise Monitoring Report (ed. P. A. P. Office).
Holloran, M., Kaiser, R. & Hubert, W. 2010 Yearling greater sage-grouse response to energy development in Wyoming. *Journal of Wildlife Management* **74**, 65-72.
Holloran, M. J. 2005 Greater Sage-Grouse (*Centrocercuc urophasianus*) Population Response to Natural Gas Field Development in Western Wyoming. In *Department of Zoology and Physiology*, pp. 114. Laramie: University of Wyoming.
Holloran, M. R. J. & Anderson, S. H. 2005 Spatial distribution of Greater Sage-Grouse nests in relatively contiguous sagebrush habitats. *Condor* **107**, 742-752.
Hu, Y. & Cardoso, G. C. 2009 Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? *Behavioral Ecology* **20**, 1268-1273.
Jankowski, M. D. 2007 The influence of habitat disturbance and synergized resmethrin on avian immunocompetence, vol. Ph.D.: The University of Wisconsin, Madison.
Kaiser, R. 2006 Recruitment by greater sage-grouse in association with natural gas development in western Wyoming. In *Department of Zoology and Physiology*, vol. M.S. Laramie, WY: University of Wyoming.
Kight, C. R. & Swaddle, J. P. 2011 How and why environmental noise impacts animals: an integrative, mechanistic review. *Ecology Letters* **14**, 1052-1061.
Lynch, E., Joyce, D. & Fristrup, K. 2011 An assessment of noise audibility and sound levels in U.S. National Parks. *Landscape Ecology* **26**, 1297-1309.
Lyon, A. G. & Anderson, S. H. 2003 Potential gas development impacts on sage grouse nest initiation and movement. *Wildlife Society Bulletin* **31**, 486-491.
Moynahan, B. J. 2004 Landscape-scale factors affecting population dynamics of Greater Sage-Grouse (Centrocercus urophasianus) in north-central Montana, vol. Ph.D. Missoula, MT: University of Montana.
Naugle, D. E., Doherty, K. E., Walker, B. E., Holloran, M. J. & Copeland, H. J. 2011 Energy development and Greater Sage-Grouse. In *Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats*, vol. 38 (ed. S. T. Knick & J. W. Connelly). Berkeley, CA.: University of California Press.
Patricelli, G. L., Dantzker, M. S. & Bradbury, J. W. 2007 Differences in acoustic directionality among vocalizations of the male red-winged blackbird (Agelaius phoeniceus) are related to function in communication. *Behavioral Ecology and Sociobiology* **61**, 1099-1110.
Patricelli, G. L. & Krakauer, A. H. 2010 Tactical allocation of effort among multiple signals in sage grouse: an experiment with a robotic female. *Behavioral Ecology* **21**, 97-106.

Quinn, L., Whittingham, J., Butler, J. & Cresswell, W. 2006 Noise, predation risk compensation and vigilance in the chaffinch Fringilla coelebs. *Journal of Avian Biology* **37**, 601-608.
Rabin, L. A., Coss, R. G. & Owings, D. H. 2006 The effects of wind turbines on antipredator behavior in California ground squirrels (Spermophilus beecheyi). *Biological Conservation* **131**, 410-420.
Rogers, G. E. 1964 Sage Grouse investigations in Colorado, vol. 16. Technical Publication No. 16, Colorado Game, Fish and Parks Department, Denver.
Schoenberg, T. J. 1982 Sage grouse movements and habitat selection in North Park, Colorado: Colorado State University, Fort Collins, CO.
Schroeder, M. A., Young, J. R. & Braun, C. E. 1999 Sage Grouse: *Centrocerus urophasianus*. *Birds of North America* **425**, 1-28.
Sørensen, M., Andersen, Z. J., Nordsborg, R. B., Jensen, S. S., Lillelund, K. G., Beelen, R., Schmidt, E. B., Tjønneland, A., Overvad, K. & Raaschou-Nielsen, O. 2012 Road Traffic Noise and Incident Myocardial Infarction: A Prospective Cohort Study. *PLoS ONE* **7**, e39283.
Swenson, J. E., Simmons, C. A. & D. Eustace, C. 1987 Decrease of sage grouse Centrocerus urophasianus after ploughing of sagebrush steppe. *Biological Conservation* **41**, 125-132.
Vehrencamp, S. L., Bradbury, J. W. & Gibson, R. M. 1989 The Energetic Cost Of Display In Male Sage Grouse. *Animal Behaviour* **38**, 885-896.
Walker, B. L., Naugle, D. E. & Doherty, K. E. 2007 Greater Sage-Grouse Population Response to Energy Development and Habitat Loss. *Journal of Wildlife Management* **71**, 2644-2654.
Wallestad, R. O. & Schladweiler, P. 1974 Breeding season movements and habitat selection of male sage grouse. *Journal of Wildlife Management* **38**, 634-637.
Wiley, R. H. 1973 Territoriality and non-random mating in sage grouse (*Centrocercus urophasianus*). *Animal Behaviour Monographs* **6**, 85-169.

Received: 6 July 2017 | Revised: 2 October 2017 | Accepted: 8 November 2017

DOI: 10.1002/ece3.3679

ORIGINAL RESEARCH

WILEY Ecology and Evolution Open Access

# Phenology largely explains taller grass at successful nests in greater sage-grouse

Joseph T. Smith[1] | Jason D. Tack[2] | Kevin E. Doherty[3] | Brady W. Allred[4] | Jeremy D. Maestas[5] | Lorelle I. Berkeley[6] | Seth J. Dettenmaier[7] | Terry A. Messmer[7] | David E. Naugle[1]

[1]Wildlife Biology Program, University of Montana, Missoula, MT, USA

[2]US Fish & Wildlife Service, Habitat and Population Evaluation Team, Missoula, MT, USA

[3]US Fish & Wildlife Service, Lakewood, CO, USA

[4]W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, USA

[5]USDA Natural Resources Conservation Service, West National Technology Support Center, Portland, OR, USA

[6]Montana Department of Fish, Wildlife & Parks, Helena, MT, USA

[7]Department of Wildland Resources, Jack H. Berryman Institute, Utah State University, Logan, UT, USA

**Correspondence**
Joseph T. Smith, Wildlife Biology Program, University of Montana, Missoula, MT, USA.
Email: joe.smith@umontana.edu

**Funding information**
USDA Natural Resources Conservation Service Sage Grouse Initiative

## Abstract

Much interest lies in the identification of manageable habitat variables that affect key vital rates for species of concern. For ground-nesting birds, vegetation surrounding the nest may play an important role in mediating nest success by providing concealment from predators. Height of grasses surrounding the nest is thought to be a driver of nest survival in greater sage-grouse (*Centrocercus urophasianus*; sage-grouse), a species that has experienced widespread population declines throughout their range. However, a growing body of the literature has found that widely used field methods can produce misleading inference on the relationship between grass height and nest success. Specifically, it has been demonstrated that measuring concealment following nest fate (failure or hatch) introduces a temporal bias whereby successful nests are measured later in the season, on average, than failed nests. This sampling bias can produce inference suggesting a positive effect of grass height on nest survival, though the relationship arises due to the confounding effect of plant phenology, not an effect on predation risk. To test the generality of this finding for sage-grouse, we reanalyzed existing datasets comprising >800 sage-grouse nests from three independent studies across the range where there was a positive relationship found between grass height and nest survival, including two using methods now known to be biased. Correcting for phenology produced equivocal relationships between grass height and sage-grouse nest survival. Viewed in total, evidence for a ubiquitous biological effect of grass height on sage-grouse nest success across time and space is lacking. In light of these findings, a reevaluation of land management guidelines emphasizing specific grass height targets to promote nest success may be merited.

KEYWORDS

*Centrocercus urophasianus*, concealment, greater sage-grouse, nest survival, phenology

## 1 | INTRODUCTION

Environmental factors affecting influential demographic parameters are appropriate targets of management to promote habitat quality for species of conservation concern (Mills, 2007). For many birds, characteristics of nest sites that influence nest predation are of interest, as nest success is a key driver of population growth and predation is the primary cause of nest failure (Martin, 1993; Ricklefs, 1969). According

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2017 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

to the nest concealment hypothesis, nests surrounded by dense vegetation should be more successful because they are more difficult for predators to detect or access (Martin, 1992; Martin & Roper, 1988). Furthermore, vegetative concealment may represent an attractive target for conservation action because it can often be managed, for example, through manipulation of herbivory by livestock.

Support for the nest concealment hypothesis is mixed. In a recent review and comparative analysis, 26% of 114 reviewed studies in open-cup-nesting songbirds supported an effect (Borgmann & Conway, 2015). Effects of concealment on nest survival may be difficult to detect if strong selection for concealed nest sites canalizes variation among nests such that most occur in "adaptive peaks" providing adequate concealment (Latif, Heath, & Rotenberry, 2012; Remeš, 2005). However, even studies employing experimental removal of vegetation have returned mixed support for the nest concealment hypothesis (e.g., Bengtson, 1972; Howlett & Stutchbury, 1996; Latif et al., 2012; Peak, 2003). Numerous intrinsic and extrinsic factors may influence the effect of concealment on nest success. For example, birds with more brightly colored plumage appear more dependent on vegetation to conceal the nest from predators (Borgmann & Conway, 2015), and the benefits of visual concealment may depend on the composition of the local predator community (Clark & Nudds, 1991; Colombelli-Negrel & Kleindorfer, 2009; Dion, Hobson, & Lariviere, 2000). More problematic, however, are methodological aspects of studies that produce biased inference with regard to effects of concealment on nest survival (Borgmann & Conway, 2015; Burhans & Thompson, 1998; Gibson, Blomberg, & Sedinger, 2016; McConnell, Monroe, Burger, & Martin, 2017). Here, we focus on a recently highlighted methodological bias pervasive in research regarding habitat–fitness relationships in greater sage-grouse (*Centrocercus urophasianus*).

The greater sage-grouse (hereafter, sage-grouse) is a precocial, ground-nesting species of conservation concern inhabiting sagebrush ecosystems of western North America. Although sage-grouse nest beneath shrubs—primarily sagebrush—perennial grasses and forbs in the interspaces between shrubs have long been thought to provide critical concealment of nests from potential predators (Connelly, Schroeder, Sands, & Braun, 2000). This hypothesis is supported by studies reporting positive associations between height and/or cover of herbaceous vegetation surrounding nest sites and nest survival (Coates & Delehanty, 2008; DeLong, Crawford, & DeLong, 1995; Doherty et al., 2014; Gregg, Crawford, Drut, & DeLong, 1994; Sveum, Edge, & Crawford, 1998). Consequently, sage-grouse conservation efforts and land management policy have focused on increasing herbaceous hiding cover in suitable nesting habitat throughout the range of the species. Although direct links between livestock grazing and sage-grouse demography are lacking, studies indicating positive effects of herbaceous vegetation height and/or cover on nest survival provide a plausible mechanism linking livestock grazing and nest success (Connelly & Braun, 1997; Connelly et al., 2000), a key demographic rate for sage-grouse (Taylor, Walker, Naugle, & Mills, 2012). Thus, the validity of inference about the importance of herbaceous hiding cover for sage-grouse nest success has major implications for the management of sagebrush ecosystems, where livestock grazing is a ubiquitous land use (Knick et al., 2003).

Recent evidence has demonstrated that the positive association between grass height, a commonly used metric of herbaceous concealing cover among sage-grouse nesting studies, and nest survival may be indicative of biased methods rather than a causal relationship (Gibson, Blomberg, et al., 2016; McConnell et al., 2017). Using both empirical and simulation approaches, it has been shown that measuring grass height at nests following nest fate (i.e., hatch or failure) produces inflated or even spurious statistical relationships between grass height and nest survival. Because successful nests persist and are therefore measured later in the season than failed nests, measured concealment is greater at successful nests due to concurrent plant growth rather than a presumed reduction in predation. Despite knowledge of this sampling issue dating back decades (e.g., Burhans & Thompson, 1998), this sampling bias remains pervasive in sage-grouse and other ground-nesting bird literature, with a majority of sage-grouse studies sampling vegetation following nest fate (Gibson, Blomberg, et al., 2016).

Given the far-reaching implications derived from inference about grass height and sage-grouse demography, we were interested in exploring the generality of recent findings reported by Gibson, Blomberg, et al. (2016), and McConnell et al. (2017). Using field data from four geographically distinct study sites representative of the diversity of vegetation communities, predator communities, precipitation regimes, and evolutionary history of grazing found across the range of sage-grouse, we tested the hypothesis that studies using biased field methods that had previously supported a positive association between grass height measured around the nest and nest survival would fail to support such an association after accounting for phenology.

## 2 | METHODS

We employed the model-based methods presented in Gibson, Blomberg, et al. (2016) to correct for phenology in a reanalysis of three datasets from Montana, Utah, and Wyoming (Table 1). In a dataset from Eureka County, Nevada, analyzed by Gibson, Blomberg, et al. (2016), vegetation measurements were made at predicted hatch date and a linear regression relating vegetation height to the date of measurement was used to predict vegetation height at fate date, thereby demonstrating the potential bias arising from such a sampling scheme. We employed this concept in reverse fashion, that is, we regressed vegetation height on date of measurement to predict grass height at hatch date, as although it had been sampled using unbiased methods.

### 2.1 | Datasets

Reanalyzed datasets included a previously published study that found a significant positive influence of live grass height on sage-grouse nest survival across two study areas in the Powder River Basin (PRB) in southeast Montana (hereafter PRB North, $n$ = 209) and northeast

**TABLE 1** We used predictions from five studies across the range of greater sage-grouse, representing $n$ = 1204 nests over a total of 24 study site-years

| Study area | $n$ | Years | Transect length (m) | Samples per nest | Data source |
|---|---|---|---|---|---|
| Eureka County | 396 | 2004-2012 | 10 | 10 | Gibson, Blomberg, et al. (2016); |
| PRB North | 209 | 2003-2006 | 30 | 20 | Doherty et al. (2014) |
| PRB South | 174 | 2004-2006 | 30 | 20 | Doherty et al. (2014) |
| Roundup | 320 | 2012-2015 | 12 | 8 | J. Smith, Unpublished Data |
| NE Utah | 105 | 2012-2015 | 30 | 20 | S. Dettenmaier, Unpublished Data |
| Total | 1204 | | | | |

Each study sampled grass height similarly, using measurements of the nearest grass height to various points along two intersecting transects centered at the nesting shrub. However, total transect length and the number of samples per nest varied by study.

Wyoming (hereafter PRB South, $n$ = 164; Doherty et al., 2014); preliminary data from an ongoing evaluation of grazing treatments on sage-grouse ecology in central Montana (Joseph Smith, University of Montana, Unpublished Data, $n$ = 320); and the first 4 years of a study comparing sage-grouse demography across two study areas in northern Utah (Seth Dettenmaier, Utah State University, Unpublished Data, $n$ = 105). Including findings from Gibson, Blomberg, et al. (2016), these studies encompassed 1204 sage-grouse nests over 24 study site-years from across the range of sage-grouse (Table 1). Each study used similar methodologies to sample herbaceous vegetation surrounding nest sites by taking multiple measurements of grass height along intersecting transects centered on the nesting shrub and using the mean of replicated measurements to represent grass height-surrounding nests (Table 1).

## 2.2 | Statistical analyses

We assumed hatch date was 27 days after the estimated nest initiation date and applied a correction to measured grass height covariates following Gibson, Blomberg, et al. (2016):

$$\mathrm{GrassHeight}_{\mathrm{Hatch}} = \mathrm{GrassHeight}_{\mathrm{Fate}} - \left(\mathrm{SurveyDate}_{\mathrm{Fate}} - \mathrm{SurveyDate}_{\mathrm{Hatch}}\right) \times \beta_{\mathrm{grass}}$$

where, for each study area and year, we fit a linear regression of measured grass height ($\mathrm{GrassHeight}_{\mathrm{Fate}}$) on day of nesting season ($\mathrm{SurveyDate}_{\mathrm{Fate}}$) to estimate $\beta_{\mathrm{grass}}$. This simple correction provided a standardized measurement for grass height across nests regardless of fate. We estimated the effect of grass height on nest success using both corrected and uncorrected covariate measurements by fitting Bayesian daily nest survival models to each dataset (Schmidt, Walker, Lindberg, Johnson, & Stephens, 2010) with the exception of data from Gibson, Blomberg, et al. (2016), who provided estimates from their published analysis. In this approach, we estimated nest survival ($S$) for each nest ($i$) on each day of the nesting season ($t$) via a logit-linear model, which at minimum included an intercept ($\beta_0$) and coefficient for grass height, while also including coefficients that respective authors deemed supportive in top models. Nest encounter histories consisted of observed nest states ($y$) for each day of observation, where $y_{i,t}$ = 1 if nest $i$ was observed alive on day $t$, $y_{i,t}$ = 0 if nest $i$ was observed to have failed (female absent and some or all eggs destroyed), and $y_{i,t}$ = NA on days when nest state was not observed. Beginning on the first day after the nest was detected,

$$y_{i,t} \sim \mathrm{Bern}(y_{i,t-1} S_{i,t})$$

and

$$\mathrm{logit}\left(S_{i,t}\right) = \beta_0 + x_i' \beta$$

Specifically, Doherty et al. (2014), following the original population analyses in Walker (2008), modeled nest survival using covariates including a main and quadratic effect for nest age, and categorical variables for a particularly harsh spring nesting season with major snow events that caused nest abandonment (2003) and the two study regions (PRB North and PRB South). Although the PRB datasets were collected independently, they were combined in the analysis presented in Doherty et al. (2014), and we combine them here for consistency. Although it appears this study was mistakenly recorded as having used a fate date protocol in Gibson, Blomberg, et al. (2016; Table 1), the investigators did attempt to control for phenology by sampling vegetation near the predicted hatch date regardless of nest fate. Nonetheless, close examination of the dataset revealed that a temporal bias in measurement date existed across all study site-year combinations, such that successful nests were measured from 2 to 10 days later than failed nests, on average. To attempt to correct this persistent bias and maintain consistency among reanalyzed datasets, we corrected grass heights to predicted hatch date in the PRB North and PRB South datasets, but these corrections were generally smaller than corrections in the other reanalyzed datasets. Unpublished data from J. Smith included covariates for the log of distance to major roads and a measure of 4-day cumulative rainfall, as well as a random effect for year. Data from Gibson, Blomberg, et al. (2016), and models fit to Utah data included only an intercept and coefficient for measurements of grass height. Our estimates of daily nest survival and nest success are only reflective of the incubation period, as sage-grouse nests are typically found after the onset of incubation, and thus overestimate true

nest success from initiation to hatch (Blomberg, Gibson, & Sedinger, 2015). Moreover, as monitoring intensity of prenesting females may have varied among datasets, incubation success may be more or less biased relative to true nest success and overall success rates are therefore not directly comparable among studies.

We fit daily nest survival models in JAGS 4.0 (Plummer, 2003) with the package rjags (Plummer 2016) in R 3.3.0 (R Core Team 2016), estimating posterior distributions with a total of 90,000 samples from 3 independent Markov chain Monte Carlo (MCMC) chains (30,000 per chain) after discarding the first 20,000 iterations from each chain for burn-in. We placed vague normal prior distributions on all coefficients ($\mu$=0; $\sigma$=1000). Using coefficient posterior distributions, we generated predictions for the mean influence of grass height on nest success, the product of daily nest survival over a 27-day incubation period, and 95% credible intervals over the range of grass height values observed within each respective dataset. We held additional covariates at their mean value where applicable.

We performed an additional analysis to provide a comprehensive assessment of the influence of grass height on nest survival across datasets, excluding nests from Eureka County for which we only had data on the predicted response. Here, we pooled datasets and used generalized linear mixed models to test whether grass surrounding successful nests was taller than grass surrounding failed nests after accounting for phenology. Under the null hypothesis, grass heights (GH) measured at nests are a linear function of ordinal date of measurement (DAY; days since January 1), with normally distributed errors and no difference between successful and failed nests. Our alternative hypothesis was that grass is taller at successful nests than at failed nests after accounting for the linear function of ordinal date. We first used $AIC_C$ model selection (Burnham & Anderson, 2002) to determine the best structure for a null (i.e., phenology) model. We considered a phenology model with a random intercept for each study area-year (1|STUDY:YEAR) combination to allow for variation in grass height inherent among geographically distant study areas and in different years, and a random intercepts and slopes phenology model (DAY|STUDY:YEAR) to allow for different rates of grass growth among years and study areas. To aid in model convergence, we centered the independent variable DAY by subtracting the median day of measurement from all observations. After we determined the best structure for the phenology model using $AIC_C$, we used a likelihood ratio test to assess support for our alternative hypothesis, which was represented with a model following the structure of the most supported phenology model and including a categorical fixed effect for nest fate (FATE; failed = 0, hatched = 1). Linear mixed models were fit using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) in R. Using these datasets, we also tabulated all corrected grass height measurements at successful and failed nests and performed a one-sided Kolmogorov–Smirnov test to examine if distributions of measurements differed between pooled data sets. A one-sided test was chosen to increase statistical power given our a priori expectation that grass would be taller surrounding successful nests than failed nests.

## 3 | RESULTS

Uncorrected, each of the three reanalyzed datasets revealed a strong, positive association between grass height and daily nest survival (Figure 1; dotted lines). Estimated coefficients for grass height using uncorrected grass heights were 0.063 (95% CI from 0.037 to 0.092) for PRB North and PRB South, 0.099 (95% CI from 0.063 to 0.137) for Roundup, and 0.058 (95% CI from 0.002 to 0.118) for NE Utah. Corrections to measured grass heights averaged −1.32 cm and mean absolute correction (|corrected−uncorrected|) was 2.08 cm, with a standard deviation of 2.31 cm. Following adjustment of measured grass heights to remove temporal bias, we found no association between grass height and nest survival in two of the three datasets (Roundup and NE Utah), and a weakened but persistent association in the PRB dataset (Figure 1; solid lines). Estimated coefficients for grass height

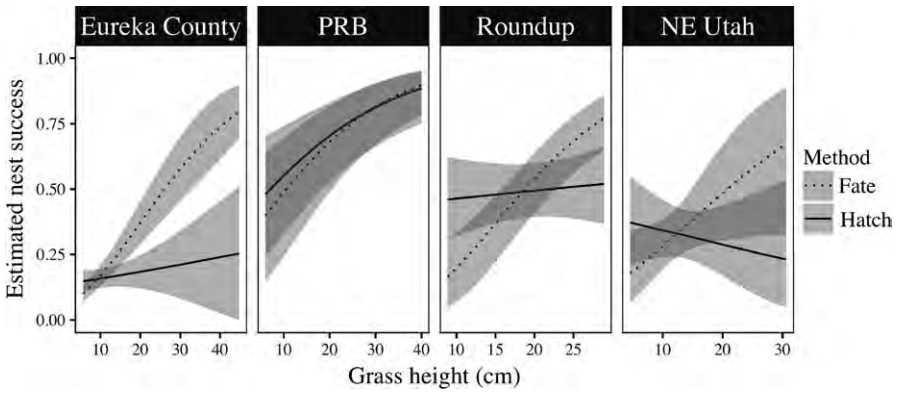



**FIGURE 1** Predicted response of sage-grouse nest success (and 95% CI [Eureka County] or CRI [other studies]) to live grass height using measurements collected with a biased method following determination of nest fate (dotted lines), and those measured or corrected to the predicted hatch date of nests (solid lines). Nest data includes studies from the powder river basin (PRB) in southeastern Montana (PRB North, Doherty et al., 2014, *n* = 209, 2003–2006) and northeast Wyoming (PRB South, Doherty et al., 2014, *n* = 174, 2004–2006); Eureka County, Nevada (Gibson, Blomberg, et al., 2016, *n* = 396, 2004–2012); central Montana near the town of Roundup (J. Smith, University of Montana, unpublished data, *n* = 320, 2012–2015), and northeast Utah (Dettenmaier, Utah State University, unpublished data; *n* = 105, 2012–2015). Note that limits of x-axes change to reflect the range of grass heights observed within respective studies

using corrected grass heights were 0.053 (95% CI from 0.025 to 0.081) for PRB North and PRB South, 0.008 (95% CI from -0.027 to 0.042) for Roundup, and −0.015 (95% CI from −0.060 to 0.032) for NE Utah.

The random intercept and slope phenology model (conditional $R^2$ = 0.51 [Nakagawa & Schielzeth, 2013]) received the most support with an $AIC_C$ score 9.64 units lower than the constant slope model (conditional $R^2$ = .46) and was used as the null model (Figure 2). The alternative hypothesis, that grass height surrounding successful nests was greater than that surrounding failed nests after accounting for phenology, was not supported ($\chi^2$ = 2.74, *df* = 1, *p* = .098). Overall, median height of live grasses, corrected to hatch date, was 15.3 cm at successful nests (*n* = 336) and 15.1 cm at failed nests (*n* = 472; Figure 3). A one-sided Kolmogorov–Smirnov test provided no evidence that the distributions of phenology-corrected grass heights differed between successful and failed nests when pooling across sites and years (*p* = .307).

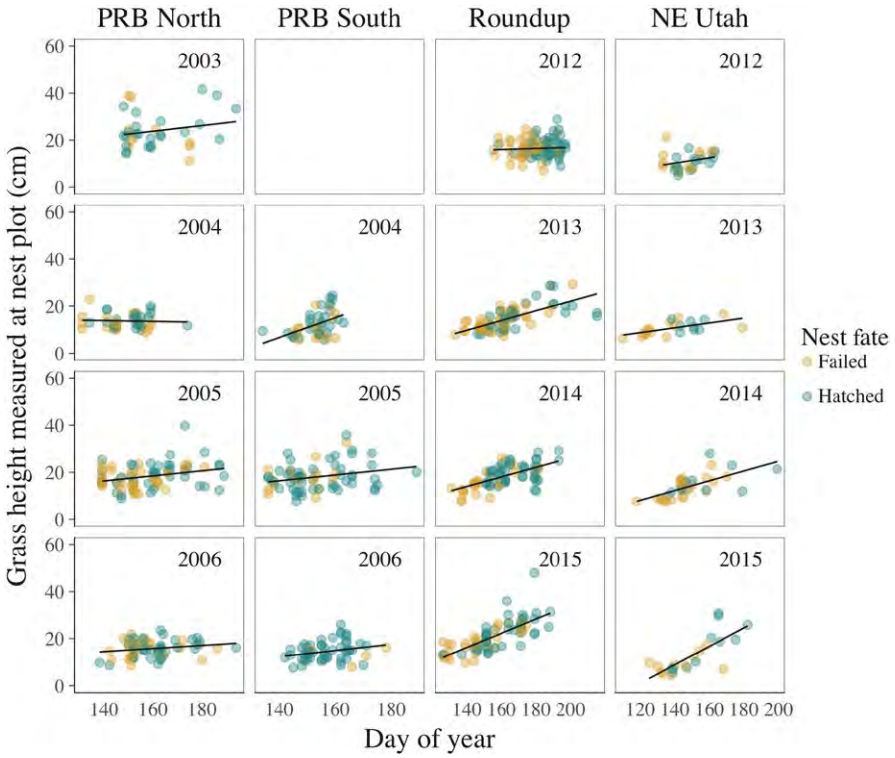



**FIGURE 2** Average grass height surrounding successful and failed sage-grouse nests (*n* = 808) at the ordinal date of measurement by year (rows) and study area (columns). After accounting for phenology, a difference in grass height between successful and failed nests was not supported

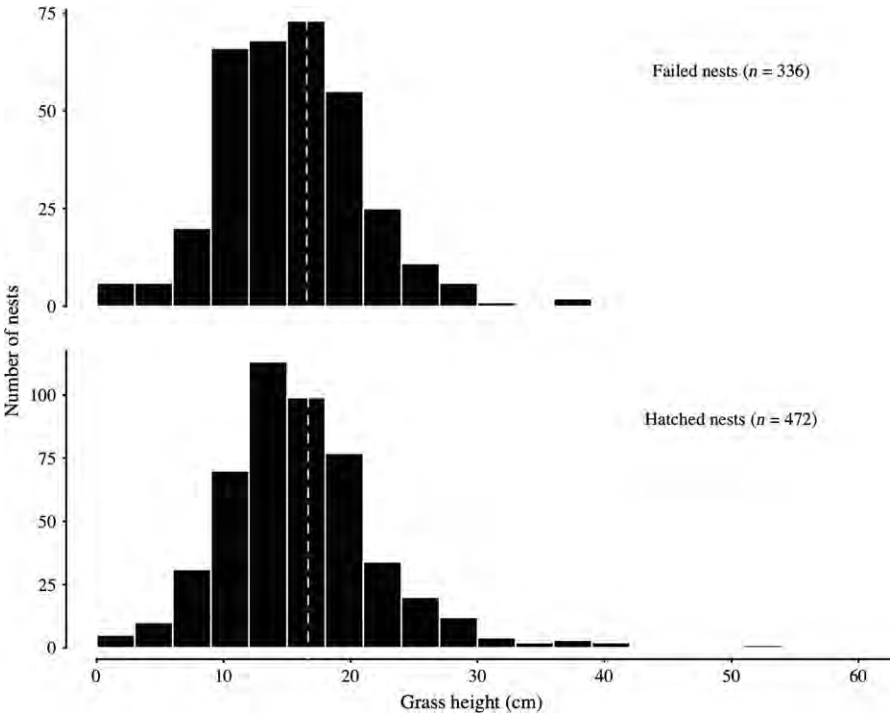



**FIGURE 3** Grass heights surrounding greater sage-grouse nests (*n* = 808) corrected to hatch date. Median height of grass-surrounding nests (dashed vertical lines) was 15.26 cm at successful nests and 15.14 cm at failed nests. A one-sided Kolmogorov–Smirnov test provided no evidence that the distributions of grass heights differed between successful and failed nests (ground-nesting *p* = .307)

## 4 | DISCUSSION

While our analyses revealed mixed support for relationships between grass height and nest survival in sage-grouse, they confirmed recent findings that associations between herbaceous vegetation structure and nest success are frequently byproducts of temporally biased sampling rather than indicative of effect of concealing cover on detectability by predators (Gibson, Blomberg, et al., 2016; McConnell et al., 2017). Sampling vegetation following nest fate, a pervasive practice in studies of sage-grouse and other ground-nesting birds, consistently produces spurious relationships between grass height and nest survival and should, therefore, be avoided. As field crews are rarely able to strictly adhere to a schedule due to weather or other logistic constraints, even studies using field protocols intended to control for phenology may be affected by some degree of temporal bias between failed and successful nests, producing inflated effect sizes (e.g., the PRB dataset reanalyzed here; Doherty et al., 2014).

Taller grass may be associated with reduced nest predation under some conditions, such as in the context of particular predator communities or in years with particularly tall grass. However, grass height does not appear to be a universal indicator of nesting habitat quality for sage-grouse. Including the PRB dataset, we are aware of only three published studies using unbiased methods that support a positive association between grass height and nest survival (Doherty et al., 2014; Gregg et al., 1994; Sveum et al., 1998) among the 11 published studies testing for such an effect (Table 1 in Gibson, Blomberg, et al., 2016). Although the results have generally been interpreted to support the hypothesis that taller grass promotes greater nest survival (Connelly et al., 2000; Crawford et al., 2004), data presented by Sveum et al. (1998; Table 2) merely indicated that cover of short grasses (<18 cm) was lower at successful nests than failed nests in 1 out of 2 years ($n$ = 32 nests), while cover of tall grasses (≥18 cm) did not differ between successful and failed nests in any year, even using a liberal $\alpha$ level of 0.1. Positive relationships between grass height and nest survival may, in fact, be uncommon. It is telling that, when analyzed together, data from the four study areas examined here provided no evidence for a difference in herbaceous vegetation height between successful and failed nests after accounting for plant phenology and timing of sampling (Figures 2 and 3).

The research and management communities must guard against uncritical acceptance of intuitive but untested mechanistic explanations for correlative patterns emerging from observational studies of habitat–fitness relationships. Within the sagebrush ecosystem, the broad acceptance that taller grass causes greater nest success by concealing nests from predators is an example of this type of untested logical connection, as equally plausible alternative hypotheses exist. For example, in multiyear studies, annual variation in precipitation and temperature in the prenesting and nesting periods may simultaneously affect female body condition, incubation behavior, and plant phenology. If conditions favorable to increased body condition or nest attentiveness have coincident positive effects on grass growth, nest success may be positively correlated with grass height absent any causal relationship between the two variables.

An experimental approach involving manipulation of vegetation height-surrounding nests could circumvent these issues, but would be fraught with its own set of difficulties. Sage-grouse females display a propensity toward abandoning reproductive efforts following disturbance by investigators (e.g., Gibson, Blomberg, Atamian, & Sedinger, 2015; Moynahan, Lindberg, Rotella, & Thomas, 2007). Disturbance from experimental manipulation at treatment nests would, therefore, need to be simulated at control nests such that observer-induced abandonment rates would be equal among nests in both groups. This may present an ethical dilemma for a species of conservation concern, or may simply yield sample sizes with inappropriately low statistical power. Furthermore, results of such an experiment would be of questionable relevance to management if manipulations bore little resemblance to defoliation patterns arising via herbivory (France, Ganskopp, & Boyd, 2008). Thus, experimental research is unlikely to provide an easy resolution to the problem. A critical examination of past evidence and careful consideration of alternative mechanistic hypotheses are warranted when considering the observational evidence at hand.

Habitat–fitness relationships are often context-dependent, and therefore variable across a species' range. Effects of concealment on nest survival, for example, may be more likely where cover is sparse. If that were the case, we might expect effects of grass height on nest survival to be more common in study sites characterized by low-shrub cover-surrounding nests. Indeed, the positive association between grass height and nest survival in the PRB study site reanalyzed here occurred in the eastern portion of the range, characterized by high spring precipitation and herbaceous vegetation cover compared to the rest of the sage-grouse range (Doherty, Evans, Coates, Juliusson, & Fedy, 2016). However, there was no relationship between grass height and nest survival in the Roundup study area, which had the lowest average shrub cover (18%) among datasets we considered. Selection of nest sites surrounded by tall grasses (Hagen, Connelly, & Schroeder, 2007) may result in a truncated covariate space such that nests surrounded by very short vegetation are rarely observed, thereby precluding the ability to detect an effect on survival (Chalfoun & Schmidt, 2012; Latif et al., 2012). However, with data from 15 study site-year combinations, we are confident we have surveyed a representative range of conditions chosen by nesting females. The lack of difference in grass height between successful and failed nests across these datasets strongly suggests that height of grasses was not a limiting resource (Figure 3).

The absence of support for an effect of grass height does not imply concealment is wholly unrelated to nest survival in sage-grouse. Selection for larger, taller sagebrush for nest substrates and preference for nesting in areas with greater areal cover of shrubs are well documented (reviewed in Hagen et al., 2007). In preferred sites, grasses and forbs may simply provide little additional visual or olfactory obstruction between a nest and a potential predator beyond that already provided by shrubs (see France, Ganskopp, & Boyd, 2008). Furthermore, while grasses and forbs afford mostly lateral cover, shrubs may provide more effective cover from aerial visual predators such as common ravens (*Corvus corax*), a primary nest predator for sage-grouse (Coates, Connelly, & Delehanty, 2008; Coates & Delehanty, 2008). Previous

research indicates nest site selection in sage-grouse is driven by avian predators at broad scales (Dinkins, Conover, Kirol, & Beck, 2012) and characteristics of nest sites at small scales are more consistent with avoidance of visual (i.e., avian) predators than olfactory (i.e., mammalian) predators (Conover, Borgo, Dritz, Dinkins, & Dahlgren, 2010; Fogarty, Elmore, Fuhlendorf, & Loss, 2017). The lack of association between height of grasses and survival may also indicate a trade-off between nest concealment and the ability of incubating females to detect predators from a distance and alter their behavior in such a way as to reduce detection (Götmark, Blomqvist, Johansson, & Bergkvist, 1995).

Nest success is only one among several influential vital rates affecting sage-grouse population growth, and further research is needed to address how structure of grasses and forbs affects other life stages in sage-grouse. Studies of other grouse suggest vegetation height may be an important driver of brood survival. For example, increased vegetation height and/or greater insect abundance resulting from reduced grazing intensity positively affected production in black grouse (*Tetrao tetrix*) in Britain (Baines, 1996; Calladine, Baines, & Warren, 2002). The positive effect on production was, however, diminished or even reversed when grazing reduction treatments covered larger areas (Calladine et al., 2002), suggesting mosaics of vegetation height may confer greater benefits than uniformly tall vegetation (also see Baines, Richardson, & Warren, 2017; Jahren, Storaas, Willebrand, Moa, & Hagen, 2016). Taller vegetation may also moderate thermal extremes experienced by grouse, a function which may take on increased importance under climate change (Hovick, Elmore, Allred, Fuhlendorf, & Dahlgren, 2014). Although selection of sites with greater visual concealment by brood-rearing sage-grouse has been documented (Kaczor, Herman-Brunson, & Jensen, 2011; Schreiber et al., 2015), studies testing effects of herbaceous vegetation structure on sage-grouse chick survival are few and have produced mixed results (Aldridge, 2005; Gregg & Crawford, 2009). Recently, Gibson, Blomberg, et al. (2016) found survival of sage-grouse chicks to 2 weeks of age was positively associated with height of grasses surrounding the nest, presumably because structure of vegetation at the nest site is assumed to be correlated with structure of vegetation encountered by the precocial chicks during the first weeks of life. Again, however, a causal relationship between grass height and chick survival cannot be inferred. Positive relationships between herbaceous plant height and chick survival could implicate concealment from predators, but it is also plausible that taller grass at the nest is associated with some unmeasured factor—for example, site productivity, precipitation, or soil moisture—which in turn influences factors causally related to chick survival.

While the herbaceous understory is a key component of sagebrush ecosystems and sage-grouse habitat (e.g., Chambers et al., 2014), its role in concealing nests from predators has been overstated in management guidelines and land management documents. For example, the habitat assessment framework (HAF; Stiver et al., 2015), a tool used by the US Bureau of Land Management and US Forest Service to evaluate whether public lands are meeting habitat requirements of sage-grouse, included guidelines for maintaining a minimum height of perennial grasses and forbs in upland nesting habitat (18 cm) based largely on studies suggesting positive effects of vegetation height on nest success. There is, however, little evidence for the existence of the causal relationship between grass height and nest survival on which these guidelines were predicated. While it appears these "fourth order" guidelines may place unwarranted emphasis on the importance of maintaining herbaceous hiding cover for nesting, it should be noted that the HAF appropriately lays out a hierarchical management approach which suggests policies be set at the rangewide and regional scales to limit habitat loss and fragmentation—known causes of population declines among prairie grouse—but emphasizes that significant flexibility should be granted to local managers applying finer scale guidelines (see Chapter 1, Stiver et al., 2015). Persistent, broad-scale threats to sagebrush ecosystems including oil and gas development (Naugle, Doherty, Walker, Holloran, & Copeland, 2011), wildfire and invasive annual grasses (Coates et al., 2016), cropland conversion (Smith et al., 2016), and conifer encroachment (Miller, Naugle, Maestas, Hagen, & Hall, 2017) are well-documented drivers of sage-grouse population declines and should therefore be the highest priority for managers. Maintenance of tall grasses and forbs for nesting cover should not distract managers from addressing these larger threats or preclude the use of management tools that could otherwise improve sage-grouse habitat.

## ACKNOWLEDGMENTS

J. Carlson, V. Dreitz, M. Hebblewhite, P. Lukacs, and T. Martin provided helpful comments on an early draft of the manuscript. This manuscript was improved by comments from D. Gibson and S. Roos. D. Gibson provided data to reproduce findings from the Eureka County dataset shown in Figure 1. Funding for this research was provided by US Department of Agriculture Natural Resources Conservation Service's Conservation Effects Assessment Project and Conservation Innovation Grant Program. Funding for data collected at the Roundup study site was provided by the general sale of hunting and fishing licenses in Montana; Federal Aid in Wildlife Restoration grant W-158-R; Montana Fish, Wildlife & Parks Upland Game Bird Enhancement Program; US Bureau of Land Management Cooperative Agreement L15AC00097; and the Big Sky Upland Bird Association. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

## AUTHOR CONTRIBUTIONS

JTS conceptualized the study, collected field data in central Montana, compiled and quality checked data from all study sites, analyzed data, produced figures, and wrote the manuscript. JDT analyzed data, produced figures, and assisted in writing the manuscript. KED collected field data in PRB and assisted in writing the manuscript. BWA, JDM, and DEN assisted with study conceptualization, interpretation of results, and manuscript writing, and revised several early versions of the manuscript. LIB and TAM contributed field data in central Montana and Northern Utah, respectively, and

critically revised the final manuscript. SJD collected field data in Northern Utah. All authors critically revised and approved the final version of the manuscript.

## ORCID

*Joseph T. Smith* http://orcid.org/0000-0002-5242-2761
*Seth J. Dettenmaier* http://orcid.org/0000-0001-6325-8808

## REFERENCES

Aldridge, C. (2005). Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation, University of Alberta.

Baines, D. (1996). The Implications of grazing and predator management on the habitats and breeding success of black grouse *Tetrao tetrix*. *The Journal of Applied Ecology*, *33*(1), 54–62. https://doi.org/10.2307/2405015

Baines, D., Richardson, M., & Warren, P. (2017). The invertebrate diet of Black Grouse *Tetrao tetrix* chicks: A comparison between northern England and the Scottish Highlands. *Bird Study*, *64*(2), 117–124. https://doi.org/10.1080/00063657.2017.1295018

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48.

Bengtson, S.-A. (1972). Reproduction and fluctuations in the size of duck populations at Lake Mývatn, Iceland. *Oikos*, *23*(1), 35–58. https://doi.org/10.2307/3543925

Blomberg, E. J., Gibson, D., & Sedinger, J. S. (2015). Biases in nest survival associated with choice of exposure period: A case study in North American upland game birds. *The Condor, American Ornithological Society*, *117*(4), 577–588.

Borgmann, K. L., & Conway, C. J. (2015). The nest-concealment hypothesis: New insights from a comparative analysis. *The Wilson Journal of Ornithology*, *127*(4), 646–660. https://doi.org/10.1676/14-162.1

Burhans, D. E., & Thompson, F. R. (1998). Effects of time and nest-site characteristics on concealment of songbird nests. *The Condor*, *100*(4), 663–672. https://doi.org/10.2307/1369747

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information theoretic approach*. New York, NY, USA: Springer-Verlag.

Calladine, J., Baines, D., & Warren, P. (2002). Effects of reduced grazing on population density and breeding success of black grouse in northern England. *The Journal of Applied Ecology*, *39*(5), 772–780. https://doi.org/10.1046/j.1365-2664.2002.00753.x

Chalfoun, A. D., & Schmidt, K. A. (2012). Adaptive breeding-habitat selection: Is it for the birds? *The Auk*, *129*(4), 589–599. https://doi.org/10.1525/auk.2012.129.4.589

Chambers, J. C., Bradley, B. A., Brown, C. S., D'Antonio, C., Germino, M. J., Grace, J. B., … Pyke, D. A.. (2014). Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. Invasion in Cold Desert Shrublands of Western North America. *Ecosystems*, *17*(2), 360–375. https://doi.org/10.1007/s10021-013-9725-5

Clark, R. G., & Nudds, T. D. (1991). Habitat patch size and duck nesting success: The crucial experiments have not been performed. *Wildlife Society Bulletin*, *19*(4), 534–543.

Coates, P. S., Connelly, J. W., & Delehanty, D. J. (2008). Predators of greater sage-grouse nests identified by video monitoring. *Journal of Field Ornithology*, *79*(4), 421–428. https://doi.org/10.1111/j.1557-9263.2008.00189.x

Coates, P. S., & Delehanty, D. J. (2008). Effects of environmental factors on incubation patterns of greater sage-grouse. *The Condor*, *110*(4), 627–638. https://doi.org/10.1525/cond.2008.8579

Coates, P. S., Ricca, M. A., Prochazka, B. G., Brooks, M. L., Doherty, K. E., Kroger, T., … Casazza, M. L. (2016). Wildfire, climate, and invasive grass interactions negatively impact an indicator species by reshaping sagebrush ecosystems. *Proceedings of the National Academy of Sciences*, *113*(45), 12745–12750. https://doi.org/10.1073/pnas.1606898113

Colombelli-Negrel, D., & Kleindorfer, S. (2009). Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). *Ecological Research*, *24*(4), 921–928. https://doi.org/10.1007/s11284-008-0569-y

Connelly, J. W., & Braun, C. E. (1997). Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology*, *3*(3–4), 229–234.

Connelly, J. W., Schroeder, M. A., Sands, A. R., & Braun, C. E. (2000). Guidelines to manage sage grouse populations and their habitats. *Wildlife Society Bulletin*, *28*(4), 967–985.

Conover, M. R., Borgo, J. S., Dritz, R. E., Dinkins, J. B., & Dahlgren, D. K. (2010). Greater sage-grouse select nest sites to avoid visual predators but not olfactory predators. *The Condor*, *112*(2), 331–336. https://doi.org/10.1525/cond.2010.090172

Crawford, J. A., Olson, R. A., West, N. E., Mosley, J. C., Schroeder, M. A., Whitson, T. D., … Boyd, C. S. (2004). Ecology and management of sage-grouse and sage-grouse habitat. *Journal of Range Management*, *57*(1), 2–19. https://doi.org/10.2307/4003949

DeLong, A. K., Crawford, J. A., & DeLong, D. C. (1995). Relationships between vegetational structure and predation of artificial sage grouse nests. *The Journal of Wildlife Management*, *59*(1), 88–92. https://doi.org/10.2307/3809119

Dinkins, J. B., Conover, M. R., Kirol, C. P., & Beck, J. L. (2012). Greater sage-grouse (*Centrocercus urophasianus*) select nest sites and brood sites away from avian predators. *The Auk*, *129*(4), 600–610. https://doi.org/10.1525/auk.2012.12009

Dion, N., Hobson, K. A., & Lariviere, S. (2000). Interactive effects of vegetation and predators on the success of natural and simulated nests of grassland songbirds. *The Condor*, *102*(3), 629–634. https://doi.org/10.1650/0010-5422(2000)102[0629:IEOVAP]2.0.CO;2

Doherty, K. E., Evans, J. S., Coates, P. S., Juliusson, L. M., & Fedy, B. C. (2016). Importance of regional variation in conservation planning: A rangewide example of the Greater Sage-Grouse. *Ecosphere*, *7*(10), e01462. Available from:https://doi.org/10.1002/ecs2.1462

Doherty, K. E., Naugle, D. E., Tack, J. D., Walker, B. L., Graham, J. M., & Beck, J. L. (2014). Linking conservation actions to demography: Grass height explains variation in greater sage-grouse nest survival. *Wildlife Biology*, *20*(6), 320–325. https://doi.org/10.2981/wlb.00004

Fogarty, D. T., Elmore, R. D., Fuhlendorf, S. D., & Loss, S. R. (2017). Influence of olfactory and visual cover on nest site selection and nest success for grassland-nesting birds. *Ecology and Evolution*, *7*, 6247–6258. https://doi.org/10.1002/ece3.3195

France, K. A., Ganskopp, D. C., & Boyd, C. S. (2008). Interspace/undercanopy foraging patterns of beef cattle in sagebrush habitats. *Rangeland Ecology & Management*, *61*(4), 389–393. https://doi.org/10.2111/06-072.1

Gibson, D., Blomberg, E. J., Atamian, M. T., & Sedinger, J. S. (2015). Observer effects strongly influence estimates of daily nest survival probability but do not substantially increase rates of nest failure in Greater Sage-Grouse. *The Auk*, *132*(2), 397–407. https://doi.org/10.1642/AUK-14-197.1

Gibson, D., Blomberg, E. J., Atamian, M. T., & Sedinger, J. S. (2016). Nesting habitat selection influences nest and early offspring survival in Greater Sage-Grouse. *The Condor*, *118*(4), 689–702. https://doi.org/10.1650/CONDOR-16-62.1

Gibson, D., Blomberg, E. J., & Sedinger, J. S. (2016). Evaluating vegetation effects on animal demographics: The role of plant phenology and sampling bias. *Ecology and Evolution*, *6*(11), 3621–3631. Available from:https://doi.org/10.1002/ece3.2148

Götmark, F., Blomqvist, D., Johansson, O. C., & Bergkvist, J. (1995). Nest site selection: A trade-off between concealment and view of the

surroundings? *Journal of Avian Biology*, *26*(4), 305–312. https://doi.org/10.2307/3677045

Gregg, M. A., & Crawford, J. A. (2009). Survival of greater sage-grouse chicks and broods in the Northern Great Basin. *The Journal of Wildlife Management*, *73*(6), 904–913. https://doi.org/10.2193/2007-410

Gregg, M. A., Crawford, J. A., Drut, M. S., & DeLong, A. K. (1994). Vegetational cover and predation of sage grouse nests in Oregon. *The Journal of Wildlife Management*, *58*(1), 162–166. https://doi.org/10.2307/3809563

Hagen, C. A., Connelly, J. W., & Schroeder, M. A. (2007). A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. *Wildlife Biology*, *13*, 42–50. https://doi.org/10.2981/0909-6396(2007)13[42:AMOGSC]2.0.CO;2

Hovick, T. J., Elmore, R. D., Allred, B. W., Fuhlendorf, S. D., & Dahlgren, D. K. (2014). Landscapes as a moderator of thermal extremes: A case study from an imperiled grouse. *Ecosphere*, *5*(3), 1–12.

Howlett, J. S., & Stutchbury, B. J. (1996). Nest concealment and predation in hooded warblers: Experimental removal of nest cover. *The Auk*, *113*(1), 1–9. https://doi.org/10.2307/4088930

Jahren, T., Storaas, T., Willebrand, T., Moa, P. F., & Hagen, B. R. (2016). Declining reproductive output in capercaillie and black grouse – 16 countries and 80 years. *Animal Biology*, *66*(3–4), 363–400. https://doi.org/10.1163/15707563-00002514

Kaczor, N. W., Herman-Brunson, K. M., & Jensen, K. C. (2011). Resource selection during brood-rearing by greater sage-grouse. In B. K. Sandercock, K. Martin, & G. Segelbacher (Eds.), *Ecology, conservation, and management of grouse*, *studies in avian biology* (pp. 169–177). Berkeley, CA, USA: University of California Press.

Knick, S. T., Dobkin, D. S., Rotenberry, J. T., Schroeder, M. A., Vander Haegen, W. M., & Van Riper, C. III (2003). Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats *The Condor*, *105*(4), 611–634. https://doi.org/10.1650/7329

Latif, Q. S., Heath, S. K., & Rotenberry, J. T. (2012). How avian nest site selection responds to predation risk: Testing an 'adaptive peak hypothesis'. *The Journal of Animal Ecology*, *81*(1), 127–138. https://doi.org/10.1111/j.1365-2656.2011.01895.x

Martin, T. E. (1992). Breeding productivity considerations: What are the appropriate habitat features for management? In J. M. Hagan, & D. W. Johnston (Eds.), *Ecology and conservation of neotropical migrant land birds*. Washington, DC, USA: Smithsonian Institute Press.

Martin, T. E. (1993). Nest predation and nest sites - new perspectives on old patterns. *BioScience*, *43*(8), 523–532. https://doi.org/10.2307/1311947

Martin, T. E., & Roper, J. J. (1988). Nest predation and nest-site selection of a western population of the hermit thrush. *The Condor*, *90*(1), 51–57. https://doi.org/10.2307/1368432

McConnell, M. D., Monroe, A. P., Burger, L. W., & Martin, J. A. (2017). Timing of nest vegetation measurement may obscure adaptive significance of nest-site characteristics: A simulation study. *Ecology and Evolution*, *7*(4), 1259–1270. Available from: http://dx.doi.org/10.1002/ece3.2767.

Miller, R. F., Naugle, D. E., Maestas, J. D., Hagen, C. A., & Hall, G. (2017). Special Issue: Targeted Woodland Removal to Recover At-Risk Grouse and Their Sagebrush-Steppe and Prairie Ecosystems. *Rangeland Ecology & Management*, *70*(1), 1–8. https://doi.org/10.1016/j.rama.2016.10.004

Mills, L. S. (2007). *Conservation of wildlife population: Demography, genetics and management*. Malden, MA, USA: Blackwell Publishing.

Moynahan, B. J., Lindberg, M. S., Rotella, J. J., & Thomas, J. W. (2007). Factors affecting nest survival of greater sage-grouse in northcentral montana. *The Journal of Wildlife Management*, *71*(6), 1773–1783. https://doi.org/10.2193/2005-386

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining $R^2$ from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Naugle, D. E., Doherty, K. E., Walker, B. L., Holloran, M. J., & Copeland, H. E. (2011). Energy development and greater sage-grouse. In J. W. Connelly & S. T. Knick (Eds.), *Greater sage-grouse: Ecology and conservation of a landscape species and its habitats*, *studies in avian biology* (pp. 489–503). Berkeley, CA, USA: University of California Press

Peak, R. G. (2003). An experimental test of the concealment hypothesis using American goldfinch nests. *The Wilson Bulletin*, *115*(4), 403–408. https://doi.org/10.1676/03-024

Plummer, M. 2003. JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling. mcmc-jags.sourceforge.net.

Plummer, M. 2016. rjags: Bayesian Graphical Models using MCMC. R package version 4-6. https://CRAN.R-project.org/package=rjags

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Remeš, V. (2005). Birds and rodents destroy different nests: A study of Blackcap *Sylvia atricapilla* using the removal of nest concealment. *Ibis*, *147*(1), 213–216.

Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology*, *9*, 1–48. https://doi.org/10.5479/si.00810282.9

Schmidt, J. H., Walker, J. A., Lindberg, M. S., Johnson, D. S., & Stephens, S. E. (2010). A general Bayesian hierarchical model for estimating survival of nests and young. *The Auk*, *127*(2), 379–386. https://doi.org/10.1525/auk.2009.09015

Schreiber, L. A., Hansen, C. P., Rumble, M. A., Millspaugh, J. J., Gamo, R. S., Kehmeier, J. W., & Wojcik, N. (2015). Microhabitat selection of brood-rearing sites by greater sage-grouse in Carbon County, Wyoming. *Western North American Naturalist*, *75*(3), 348–363. https://doi.org/10.3398/064.075.0312

Smith, J. T., Evans, J. S., Martin, B. H., Baruch-Mordo, S., Kiesecker, J. M., & Naugle, D. E. (2016). Reducing cultivation risk for at-risk species: Predicting outcomes of conservation easements for sage-grouse. *Biological Conservation*, *201*, 10–19. https://doi.org/10.1016/j.biocon.2016.06.006

Stiver, S. J., Rinkes, E. T., Naugle, D. E., Makela, P. D., Nance, D. A., & Karl, J. W. (2015). *Sage-grouse habitat assessment framework: a multiscale assessment tool*. Bureau of Land Management. Retrieved from: https://www.blm.gov/style/medialib/blm/wo/blm_library/tech_refs.Par.34086.File.dat/TR_6710-01.pdf.

Sveum, C. M., Edge, W. D., & Crawford, J. A. (1998). Nesting habitat selection by sage grouse in south-central Washington. *Journal of Range Management*, *51*(3), 265–269. https://doi.org/10.2307/4003409

Taylor, R. L., Walker, B. L., Naugle, D. E., & Mills, L. S. (2012). Managing multiple vital rates to maximize greater sage-grouse population growth. *The Journal of Wildlife Management*, *76*(2), 336–347. https://doi.org/10.1002/jwmg.267

Walker, B. L. 2008. Greater sage-grouse response to coal-bed natural gas development and West Nile virus in the Powder River Basin, Montana and Wyoming, USA. Dissertation, The University of Montana.

**How to cite this article:** Smith JT, Tack JD, Doherty KE, et al. Phenology largely explains taller grass at successful nests in greater sage-grouse. *Ecol Evol*. 2018;8:356–364. https://doi.org/10.1002/ece3.3679

**CSIRO** PUBLISHING

*Wildlife Research*, 2018, **45**, 119–131
https://doi.org/10.1071/WR17123

# Reproductive state leads to intraspecific habitat partitioning and survival differences in greater sage-grouse: implications for conservation

*Kurt T. Smith*[A,B], *Jeffrey L. Beck*[A] *and Christopher P. Kirol*[A]

[A]Department of Ecosystem Science and Management, College of Agriculture and Natural Resources, University of Wyoming, Dept. 3354, 1000 E University Avenue, Laramie, WY 82071, USA.
[B]Corresponding author. Email: ksmith94@uwyo.edu

**Abstract**

***Context.*** Inter- and intraspecific habitat partitioning is widespread across taxa, yet limited information is available on differences in intraspecific habitat selection by same-sex individuals among differing reproductive states. Understanding habitat selection by conspecifics of different reproductive states may help optimise conservation efforts, particularly for gallinaceous bird species such as greater sage-grouse (*Centrocercus urophasianus*), which are long-lived but have only moderate reproductive rates.

***Aims.*** We predicted that habitat use differed between grouse under different reproductive states and that reproductive investment decreased survival of adults in summer.

***Methods.*** We compared habitat characteristics used by brood-rearing and broodless female sage-grouse and evaluated the influence of reproductive investment and habitat use on survival of adult females.

***Key results.*** We found that brood-rearing and broodless female sage-grouse partitioned habitat at micro- and macrohabitat scales. Broodless females were more likely to survive the summer.

***Conclusions.*** Our findings suggest reproductive state variability in habitat selection by female sage-grouse. Broodless females were roosting and foraging in concealed habitats with intermediate visual obstruction and annual vegetation productivity, but less food forb availability compared with early and late brood-rearing females. In contrast, brood-rearing females likely selected more herbaceous understoreys to predictably maximise foraging opportunities and promote growth of their chicks, which appeared to mitigate the influence of reproductive costs on summer survival, particularly during the late brood-rearing period.

***Implications.*** Survival of adult females is critical for population persistence of sage-grouse and other long-lived Galliformes, yet conservation efforts generally focus on habitats used during nesting and brood-rearing. Our results suggest that habitat partitioning is a potential risk-aversion strategy where individuals across different reproductive states likely select habitats to maximise their survival. Conservation efforts should focus on conserving habitats used by both brood-rearing and broodless sage-grouse to ensure population persistence.

**Additional keywords:** behavior, breeding status, reproduction.

Received 12 July 2016, accepted 3 January 2018, published online 19 April 2018

## Introduction

Species that occupy heterogeneous landscapes utilise a spectrum of habitats throughout their life-cycles, potentially making inference about habitat use and identifying important habitats for conservation difficult (Donovan and Thompson 2001). Assessing interspecific and intraspecific habitat partitioning between species and among conspecifics may clarify inferences about habitat selection (e.g. Bañuelos *et al*. 2008; Alves *et al*. 2013); both inter- and intraspecific habitat partitioning are widespread across taxa and between sexes (Burger *et al*. 1977; Werner *et al*. 1977; Cumming *et al*. 1996). Several hypotheses have been proposed to explain sexual habitat segregation including the predation risk hypothesis developed for ungulate species (Bowyer 2004; Ruckstuhl 2007). The predation risk hypothesis proposes that males select riskier habitats that offer higher-quality forage, whereas reproductive females trade off forage quality to enhance offspring survival (Main and Coblentz 1996; Ruckstuhl 2007; Alves *et al*. 2013). Habitat-based segregation (Main and Coblentz 1996; Conradt 1999) may also apply to individuals of the same sex under different reproductive states, which must be accounted for when assessing individual variability of resource use (Bolnick *et al*. 2003). Because habitat choices often influence survival (Wilson and Nussey 2010), accounting for sex-specific or reproductive-state

Journal compilation © CSIRO 2018

variability is necessary for identifying important habitats for conservation.

Reproductive costs imposed on individuals represent tradeoffs between current reproductive effort and future survival under limited energy constraints (Harshman and Zera 2007). These tradeoffs may occur in relatively long-lived species when reproducing individuals balance survival with rearing young to maximise lifetime reproductive success (Erikstad *et al.* 1998). Tradeoffs may also occur following reproductive attempts; the success of reproductive females depends on their own survival as well as offspring survival, whereas unsuccessful females must survive to reproduce in subsequent breeding periods to maximise lifetime reproductive success. Individuals in different reproductive states may utilise various habitats to mitigate these tradeoffs. For example, red deer (*Cervus elaphus*) (Alves *et al.* 2013) and noctule bats (*Nyctalus noctula*) (Mackie and Racey 2007) use different habitats under different reproductive states. In both species, non-reproductive females select different habitats or foraging resources than reproductive females. For species with high maternal parental investment, differences in habitat selection may result as differential responses to risk stimuli under distinct reproductive states (Frid and Dill 2002; Laundre *et al.* 2010). Females with young may be faced with balancing predation risk with foraging opportunities for the adult and dependent young (Main and Coblentz 1996; Ruckstuhl 2007); however, information on habitat partitioning across reproductive states is limited.

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a species of great conservation concern (US Fish and Wildlife Service 2015), currently occupying ~668 000 $km^2$ of sagebrush (*Artemisia* spp.) across <60% of their historic range (Schroeder *et al.* 2004). Sage-grouse face significant threats from range-wide habitat loss and degradation (Connelly *et al.* 2004). Research has repeatedly documented sexual habitat partitioning in sage-grouse during different times of the year (see Connelly *et al.* 2011*a*), but habitat partitioning of females under different reproductive states has received little attention. Sage-grouse, unlike most other gallinaceous species, more closely align with a *K*-selection strategy because they are a relatively long-lived species with only moderate reproductive rates (Pianka 1970; Connelly *et al.* 2011*b*). Growth of sage-grouse populations is particularly sensitive to adult female survival (Johnson and Braun 1999; Schroeder *et al.* 1999; Taylor *et al.* 2012; Dahlgren *et al.* 2016) and range-wide nest success estimates for sage-grouse are generally low as approximately half of the females fail to produce a brood during most years (Schroeder *et al.* 1999; Connelly *et al.* 2011*b*). This is in spite of the fact that nest initiation rates are extremely high (>0.89: Taylor *et al.* 2012). Because adult female survival is critical to sage-grouse persistence, conservation actions that promote adult female survival across all reproductive states may be most beneficial to sage-grouse populations (Taylor *et al.* 2012; Dahlgren *et al.* 2016). Survival of adult female sage-grouse is typically lowest during the breeding season (Moynahan *et al.* 2006; Baxter *et al.* 2013; Blomberg *et al.* 2013) and research has suggested that reproductive investment is negatively correlated with annual adult survival (Blomberg *et al.* 2013).

Identifying habitats used by brood-rearing and females without broods (hereafter broodless) is important when prioritising habitat for sage-grouse; however, most research has focussed on nesting or brood-rearing habitats (e.g. Hagen *et al.* 2007; Connelly *et al.* 2011*a*), leaving a knowledge gap regarding habitat selection by broodless females. Some research suggests that broodless females generally move to mesic sagebrush habitats earlier in the summer than females with broods (Gregg *et al.* 1993). Earlier and longer-distance movements by broodless females compared with brood-rearing females is likely explained by limited mobility of young chicks that are not capable of flight until ~2 weeks after hatch (Wallestad 1971). Because broodless females are more mobile they likely select habitats to minimise predation risk and maximise foraging opportunities and select distinct locations for roosting and diurnal foraging to minimise these risks (Dumroese *et al.* 2015). Reduced movements by adult females with broods may indicate that habitat choice is especially critical during this time to maximise chick growth while simultaneously minimising predation risk (Drut *et al.* 1994; Gregg and Crawford 2007; Huwer *et al.* 2008; Blomberg *et al.* 2012; Guttery *et al.* 2013).

Macrohabitat- (Shepherd *et al.* 2011; Kirol *et al.* 2015) and microhabitat-scale (Gregg *et al.* 1993; Bunnell *et al.* 2004) habitat selection has been assessed for broodless females, but we are unaware of any studies that have evaluated microhabitat selection by brood-rearing and broodless female sage-grouse simultaneously. Differences in selection among brood-rearing and broodless females of other grouse species (e.g. Bañuelos *et al.* 2008) highlights the importance of understanding habitat partitioning across different reproductive states and how this might relate to adult female survival during the same period.

In our study, we compared potential differences in habitat selection by brood-rearing and broodless female sage-grouse roosting locations during the breeding season. We predicted that brood-rearing females would occupy more open sagebrush habitats with greater forb availability to meet the nutritional requirements of dependent chicks. We predicted that broodless females would occupy denser sagebrush habitats for roosting because their increased mobility facilitates movement between distinct roosting and foraging locations. Research has demonstrated that both reproductive costs and habitat use may influence survival of female sage-grouse (Blomberg *et al.* 2013; Kirol *et al.* 2015). Thus, we also evaluated survival of adult females in summer relative to reproductive costs and evaluated whether survival was also associated with habitat use. We predicted that reproductive costs would influence female survival in summer and brood-rearing females occupying more open sagebrush habitats would experience greater mortality risk than broodless females occupying areas with potentially greater concealment cover.

## Materials and methods

### *Study area*

Our study area was located in portions of Fremont and Natrona counties, in central Wyoming, USA (42.63°N, 107.92°W) encompassing ~3098 $km^2$. Elevation ranged from 1644 to 2439 m and included ~81% Federal, 7% State, and 12% privately administered lands. Annual precipitation ranged from ~13.3 to 33.7 cm (NOAA 2016). Vegetation communities in the study

area were dominated by Wyoming big sagebrush (*A. tridentata wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) at higher elevations, with inclusions of basin big sagebrush (*A. t. tridentata*), black sagebrush (*A. nova*), greasewood (*Sarcobatus vermiculatus*), and silver sagebrush (*A. cana*). The major land use in the area was livestock grazing.

### Capture and monitoring

We captured and radio-marked female sage-grouse near leks in spring 2011–13 by spot-lighting and hoop-netting (Giesen *et al*. 1982; Wakkinen *et al*. 1992). We used roosting locations of radio-marked females captured in spring to capture and radio-mark additional females in August each year. We attached radio-transmitters (22 g, Model A4060; Advanced Telemetry Systems Inc., Isanti, MN, USA; <3% body mass) to females with a PVC-covered wire necklace. We began locating female sage-grouse weekly during late April each year with R-1000 hand-held receivers and 3-element antennas (Communication Specialists, Orange, CA, USA). We used fixed-wing aircraft flights to locate individuals not located from ground searches. All sage-grouse were captured, marked, and monitored in accordance with approved protocols (Wyoming Game and Fish Department Chapter 33-801 permit and University of Wyoming Institutional Animal Care and Use Committee protocol 03132011).

We monitored all females weekly irrespective of nesting or brood status from 1 May through 15 August of each year. Consequently, if a female was not documented on a nest or a nesting female was unsuccessful (i.e. failed to hatch at least one egg: Rotella *et al*. 2004), we continued to monitor the female and considered that individual to be broodless unless a renesting attempt was documented. We located nests of radio-marked females by triangulating the signal until the female was spotted or when the location was isolated to a single nest shrub or shrub patch. Once a female was determined to be nesting, we monitored the nest weekly until the female was no longer located in the area to determine nest fate. We monitored nests from a distance of $\geq$30 m and left the area in an erratic pattern to reduce the potential of the researcher to influence nest predation (i.e. leaving a scent trail to the nest: Kirol *et al*. 2012). For successfully hatched nests we determined whether the female was with a brood by visual observations of chicks or brooding behaviour by the female (Kirol *et al*. 2012). If no brooding behaviour was detected during two successive telemetry visits, we estimated the date of brood loss as the midpoint between the last date when the female was determined to be with a brood and the first visit when a brood was not detected. We further assessed brood fate by night-time spotlight counts at ~35 days after hatching and considered broods successful when at least one chick was present with the hen at this time (Walker 2008; Kirol *et al*. 2015).

### Habitat sampling and analysis

We evaluated vegetative and ground cover microhabitat parameters at randomly selected brood-rearing locations (early and late brood-rearing periods), summer broodless female locations, and random locations along two perpendicular 30-m transects centred at each grouse and random location aligned in cardinal directions. We measured microhabitat variables that have been shown to be important predictors of microhabitat selection by sage-grouse in other studies (e.g. Hagen *et al*. 2007; Kirol *et al*. 2012; Dinkins *et al*. 2016) (Table 1), as well as variables that we suspected to be biologically relevant. We defined the early brood-rearing period as the 2-week period following nest hatch (Bergerud and Gratson 1988; Thompson *et al*. 2006), and estimated microhabitat characteristics at two locations during 2011 and one location during 2012 and 2013 for each brood-rearing female during this period. For late brood-rearing (2–5 weeks after hatching), we recorded habitat characteristics at two locations in 2011 and one location in 2012 and 2013 when chicks were estimated to be between 20 and 35 days of age. We sampled no more than two locations for each broodless female during each year. We separated brood-rearing between early and late periods because chicks are not capable of flight until ~2 weeks after hatch (Wallestad 1971), resulting in more restricted movement during that time. Broodless female locations were sampled between late June and July each year. Sampling was conducted as soon as possible after each telemetry visit, but no later than two weeks after the individual was located. We estimated herbaceous and ground cover attributes using the Daubenmire (1959) technique in $20 \times 50$ cm quadrats ($n = 17$ quadrats location$^{-1}$) placed at predetermined locations along both 30-m transects. We recorded shrub canopy cover with the line intercept method and computed percentage cover for each shrub species (Canfield 1941; Wambolt *et al*. 2006). We recorded shrub density by counting shrubs rooted within 1-m belt transects positioned along the right side of each 30-m transect. Visual obstruction was measured using a Robel pole (dm: Robel *et al*. 1970) placed in the centre of each location and measurements were recorded from a distance of 5, 10, and 15 m at 1-m height from each cardinal direction. We measured the droop height of current and residual perennial grasses in each $20 \times 50$ cm quadrat and the height of the tallest leader, excluding inflorescences, for each shrub encountered along each 30-m line transect. We examined microhabitat at paired random locations constrained by a random distance (100–500 m) and direction from each sage-grouse use location (Aldridge and Boyce 2008), during the same day that use locations were sampled.

We were interested in potential differences in selection by sage-grouse under different reproductive states compared with available habitat. We first used multinomial logistic regression models using function ‘multinom’ in package ‘nnet’ in R (Venables and Ripley 2002; R Core Team 2015), where resource use was identified as microhabitat sampling locations for radio-marked early brood-rearing, late brood-rearing, or broodless female sage-grouse, and resource availability was defined as random microhabitat sampling locations. Multinomial logistic regression is useful for modelling habitat selection when there are >2 response categories. This method allowed for simultaneous comparisons of microhabitat selection by early brood-rearing, late brood-rearing and broodless females relative to available habitats in a single model with the same predictor variables across reproductive states. Similar approaches have been used to assess the influence of habitat predictors on nesting and brood-rearing sage-grouse (Dinkins *et al*. 2014) and brood-rearing and broodless capercaillie (*Tetrao urogallus cantabricus*) (Bañuelos *et al*. 2008).

**Table 1. Variables used in model selection to evaluate greater sage-grouse microhabitat selection in central Wyoming, USA, 2011–13**

Ground cover and herbaceous canopy cover were estimated from 17 Daubenmire (0.1 $m^2$) quadrats at each location

| Variable names | Description |
|---|---|
| Ground cover (%) | |
| Bground[A] | Mean bare ground from Daubenmire quadrats |
| Cactus[A] | Mean cactus cover from Daubenmire quadrats |
| Crypto[A] | Mean biological soil crust cover from Daubenmire quadrats |
| Gravel[A] | Mean gravel cover from Daubenmire quadrats |
| Litter | Mean litter from Daubenmire quadrats |
| Height and visual obstruction | |
| BsageH[A,B,C] | Mean big sagebrush height (cm) for each plant along two perpendicular 30-m transects |
| ShrubH[A,B,C] | Mean total shrub height (cm) from each plant along two perpendicular 30-m transects |
| PerGrassH | Averaged maximum perennial grass droop height (cm) from Daubenmire quadrats |
| ResGrassH | Averaged maximum residual grass droop height (cm) from Daubenmire quadrats |
| VO[B] | Visual obstruction estimated from Robel pole (dm) |
| Herbaceous canopy cover (%) | |
| AnGrass[A] | Mean annual grass cover from Daubenmire quadrats |
| PerGrass[A] | Mean perennial grass cover from Daubenmire quadrats |
| ResGrass[A] | Mean residual grass cover from Daubenmire quadrats |
| FoodF[A,C] | Mean food forb cover from Daubenmire quadrats |
| NFoodF | Mean non-food forb cover from Daubenmire quadrats |
| SpeciesR | Mean food forb species richness from Daubenmire quadrats |
| Shrub characteristics | |
| Bsage[A,B,C] | Mean big sagebrush cover (%) measured from two perpendicular 30-m transects |
| BsageD | Big sagebrush density (plants $m^{-2}$) measured along two perpendicular 30-m transects |
| Shrub[B,C] | Mean total shrub cover (%) estimated from two perpendicular 30-m transects |
| ShrubD[1] | Total shrub density (plants $m^{-2}$) measured along two perpendicular 30-m transects |

[A]Variables were not brought forward following initial screening.
[B]Quadratic transformations assessed.
[C]Standard deviation assessed with two perpendicular 30-m transects for cover and height.

Prior to model selection, both non-informative variables with 85% confidence intervals of parameter estimates overlapping 0 (Arnold 2010) and single-variable models that had Akaike's information criterion adjusted for small sample size (AICc: Burnham and Anderson 2004) values higher than the intercept-only model were removed. We computed Pearson's correlation matrix to test for collinearity among predictors and removed the less predictive of two correlated variables based on AICc when correlation coefficients (r) were $\geq|0.6|$. We explored all combinations of the remaining variables that were brought forward following initial variable screening procedures (Burnham and Anderson 2002). The model with the lowest AICc score was identified as being the best fit model; however, models within 4 AICc of the top model were considered competitive (Arnold 2010). After the best model(s) were identified, we used binomial generalised mixed models with package 'lme4' (Bates *et al.* 2015) using predictor variables from competitive multinomial logistic regression models to evaluate reproductive states individually. Resource use was defined as either early brood-rearing, late brood-rearing, or broodless female microhabitat sampling locations and resource availability was defined as random locations. All models included individual as a random intercept term to account for potential differences in microhabitat selection by year and repeated sampling of microhabitat locations for each individual.

We used a second set of binomial generalised mixed models to identify habitat selection across reproductive states using remotely sensed products at the macrohabitat scale. This was necessary to test our predictions that adult female survival was related to both reproductive costs and the habitats used over the entire summer season to match our adult female survival analysis period. Note that we were unable to collect microhabitat information at every female telemetry location across the summer season. We developed a single model for each reproductive state using an integrated normalised difference vegetation index (INDVI; 250-m resolution) generated for each year as the sole predictor variable. INDVI provides a metric of growing season production of vegetation and has been linked to plant nutritional quality and insect abundance (Pettorelli *et al.* 2005, 2011). Normalised difference vegetation index (NDVI) has been positively associated with sage-grouse summer habitat selection and population productivity (Blomberg *et al.* 2012; Dinkins *et al.* 2014). Resource use was identified as early brood-rearing, late brood-rearing, or broodless female locations and resource availability was defined as available locations. Available locations were generated at a rate of five times the number of used locations for each reproductive state and were restricted to a 90% fixed kernel surrounding all summer locations (default bivariate kernel smoothing parameter: Worton 1989; Calenge 2006), representing

a population level design (Type 1 Design *sensu* Thomas and Taylor 2006).

### *Adult female survival*

We evaluated adult female survival relative to reproductive status, total reproductive effort, brooding effort, and distance moved between subsequent relocations. We defined reproductive status as the behaviour (nesting, brood-rearing, roosting) during the previous telemetry visit. Total reproductive effort was defined as the estimated number of weeks spent incubating and brood-rearing, whereas brooding effort was the number of weeks spent brood-rearing following a successful nesting attempt during the previous telemetry visit, respectively. Total reproductive effort and brooding effort represented the cumulative effects of reproductive activities that could not be captured with reproductive status during the previous week. That is, we expected that cumulative effects of nesting and brood rearing activities may better explain mortality risk rather than the reproductive status of an individual during the previous monitoring interval. We truncated total reproductive effort and brooding effort to reflect uncertainty in brood retention following night-time spotlight counts at 35 days (five weeks) after hatching. Chicks often become more visible as they grow; however, brood flocking behaviour makes parental assessment difficult after ~5 weeks (Dalke *et al*. 1963; Dahlgren *et al*. 2010). Therefore, the maximum value of total reproductive effort of ~9 weeks was reflective of the incubation period for successful nests (27 days; 25–29-day incubation period: Schroeder Young and Braun 1999) plus the estimated age when night-time spotlight counts were conducted ($35 \pm 0.3$ (s.e.) days after hatching). Average distance moved was estimated as the linear distance between consecutive relocations. We assessed brood movement because more mobile broods could have increased exposure to predators or experienced greater movements due to insufficient local food resources (Drut *et al*. 1994; Gibson *et al*. 2017).

We used mixed-effects Cox's proportional hazards regression (Cox PH: Cox 1972) using function 'coxme' in package 'coxme' in R (Therneau 2015; R Core Team 2015) to identify relationships between predictor variables and sage-grouse reproductive seasonal survival with the counting process (Andersen and Gill 1982; Therneau and Grambsch 2000). Year was included as a random effect in all models. The counting process accounts for time-dependent and discontinuous hazard intervals, and allows baseline hazards to vary with time (Allison 2010). Cox PH assisted in assessing variables that had the greatest influence on adult survival (Hosmer and Lemeshow 1999). To align with our observation intervals that were ~7 days, we modelled weekly female survival from nesting (1 May) through 15 August during each year for all females (~15-week survival period: Winterstein *et al*. 2001). We used left and right censoring to properly incorporate individuals entering and leaving the study at different times (Winterstein *et al*. 2001). If a female was never located on a nest, we used the average day of nest initiation for each year as the day that individual entered the sample. We estimated mortality dates from the last known telemetry monitoring interval, and used the midpoint between the last two locations (most recent location determined alive and date when located dead) as the estimated mortality date. Individuals that did not die during the study were right censored.

We used AICc (Burnham and Anderson 2002) to evaluate model support for Cox PH models. We assessed correlation between covariates and did not allow variables to compete in the same model when $r \geq |0.6|$. We brought forward variables when single-variable models showed an improvement over the null model and explored all variable combinations of non-correlated variables to evaluate model support. Once we identified the most predictive model explaining female survival relative to reproductive investment, we included INDVI and interaction terms of the main effects to assess model improvement over the reproductive model. We assured that proportional hazards assumptions were met by examining Schoenfeld residuals for each covariate in the top model (Schoenfeld 1982).

## Results

We sampled 233 female sage-grouse plots (68 early brood-rearing, 49 late brood-rearing, 116 broodless female), and 233 random microhabitat plots for 133 radio-marked female sage-grouse from 1 May to 15 August 2011–13. We monitored 32, 80, and 101 individuals during 2011, 2012, and 2013, respectively. Microhabitat plot sampling dates ranged from 14 May to 5 July for early brood, 12 June to 20 July for late brood, and 30 June to 27 July for broodless females. The percentage of broodless females (i.e. females that failed to hatch a nest or lost their chicks before 5 weeks of age) during 2011, 2012, and 2013 breeding seasons ranged from 69.5 to 82.6%. Average weekly movement distance between estimated relocations was $1518 \pm 116$ m (s.e.) for brood-rearing females and $1539 \pm 78$ m (s.e.) for broodless females.

### *Habitat selection*

Eight multinomial logistic regression models, including nine variables, were competitive, explaining microhabitat selection across all sage-grouse reproductive states (Table 2). We used all variables across competitive models to evaluate microhabitat selection for each reproductive state individually. Shrub canopy cover variables included big sagebrush density (individual plants $m^{-2}$) and shrub cover variability. Big sagebrush density was positively associated with early brood-rearing selection, and a marginal predictor of late brood-rearing and broodless female microhabitat selection (Tables 3, 4). Shrub cover variability (%) was positively associated with late brood-rearing, but uninformative for early brood-rearing and broodless female microhabitat selection (Tables 3, 4). The ground cover variable litter (%) was positively correlated with broodless female selection, but was uninformative for early and late brood-rearing selection. Horizontal visual obstruction variables included visual obstruction, perennial grass height, and residual grass height. Visual obstruction as a quadratic term was positively correlated with early brood-rearing and broodless females, but was a marginal predictor for late brood-rearing (Tables 3, 4, Fig. 1*a*). Perennial grass height was positively associated and residual grass height negatively associated with early brood-rearing, but both predictors were uninformative for late brood-rearing and broodless females

**Table 2. Top and competing multinomial logistic regression models and model fit statistics best explaining sage-grouse selection for early-brood, late-brood, and broodless female microhabitat in central Wyoming, USA, 2011–13**

K, number of parameters; ΔAICc, change in Akaike's Information Criterion score from the top model; $w_i$, Akaike weights

| Model | Model fit statistics | | | |
|---|---|---|---|---|
| | K | ΔAICc | $w_i$ | Deviance |
| BsageD + ShrubSD + VO + $VO^2$ + Litter + NFoodF + SpeciesR | 24 | 0.00 | 0.19 | 915.74 |
| BsageD + ShrubSD + VO + $VO^2$ + NFoodF + SpeciesR | 21 | 0.11 | 0.18 | 922.49 |
| ShrubSD + VO + $VO^2$ + Litter + NFoodF + SpeciesR | 21 | 0.30 | 0.16 | 922.68 |
| BsageD + ShrubSD + VO + $VO^2$ + PerGrassH + NFoodF + SpeciesR | 24 | 1.79 | 0.08 | 917.53 |
| ShrubSD + VO + $VO^2$ + NFoodF + SpeciesR | 18 | 2.00 | 0.07 | 930.93 |
| BsageD + ShrubSD + VO + $VO^2$ + PerGrassH + ResGrassH + NFoodF + SpeciesR | 27 | 2.20 | 0.06 | 911.21 |
| BsageD + ShrubSD + VO + $VO^2$ + PerGrassH + ResGrassH + Litter + NFoodF + SpeciesR | 30 | 3.03 | 0.04 | 905.22 |
| BsageD + ShrubSD + VO + $VO^2$ + PerGrassH + Litter + NFoodF + SpeciesR | 27 | 3.33 | 0.04 | 912.33 |
| Null | 3 | 167.71 | 0.00 | 1128.11 |

**Table 3. Parameter estimates with 90% confidence intervals (LCL and UCL) from binomial generalised mixed models evaluating sage-grouse early brood, late brood, and broodless female habitat selection relative to random habitats in central Wyoming, USA, 2011–13**

| Parameter | Early Brood versus Random | | | Late Brood versus Random | | | Broodless versus Random | | |
|---|---|---|---|---|---|---|---|---|---|
| | Estimate | LCL | UCL | Estimate | LCL | UCL | Estimate | LCL | UCL |
| Microhabitat selection | | | | | | | | | |
| Intercept | –5.453 | – | – | –3.363 | – | – | –4.444 | – | – |
| Shrub cover variables | | | | | | | | | |
| BsageD | 0.453 | 0.093 | 0.813[A] | –0.375 | –0.896 | 0.147 | –0.101 | –0.435 | 0.232 |
| ShrubSD | 0.020 | –0.008 | 0.048 | 0.075 | 0.039 | 0.111[A] | 0.002 | –0.029 | 0.033 |
| Ground cover variables | | | | | | | | | |
| Litter | 0.003 | –0.014 | 0.020 | –0.008 | –0.029 | 0.013 | 0.016 | 0.001 | 0.030[A] |
| Horizontal visual obstruction variables | | | | | | | | | |
| VO | 1.841 | 0.752 | 2.929[A] | –0.049 | –0.851 | 0.752 | 1.615 | 1.008 | 2.222[A] |
| $VO^2$ | –0.251 | –0.415 | –0.087[A] | 0.054 | –0.045 | 0.153 | –0.124 | –0.192 | –0.056[A] |
| PerGrassH | 0.095 | 0.020 | 0.170[A] | –0.076 | –0.179 | 0.027 | 0.028 | –0.030 | 0.086 |
| ResGrassH | –0.082 | –0.150 | –0.014[A] | 0.037 | –0.044 | 0.118 | –0.035 | –0.085 | 0.016 |
| Herbaceous canopy cover variables | | | | | | | | | |
| SpeciesR | 0.495 | 0.077 | 0.913[A] | 1.601 | 1.087 | 2.115[A] | –0.360 | –0.778 | 0.057 |
| NfoodF | –0.180 | –0.290 | –0.070[A] | –0.111 | –0.221 | –0.001[A] | 0.033 | –0.021 | 0.087 |
| Macro habitat selection | | | | | | | | | |
| Intercept | –4.673 | – | – | –6.264 | – | – | –2.673 | – | – |
| INDVI | 0.0276 | 0.012 | 0.043[A] | 0.060 | 0.049 | 0.072[A] | 0.030 | 0.023 | 0.036[A] |

[A]90% confidence intervals that do not include zero.

**Table 4. Mean microhabitat characteristics and standard errors (in parentheses) of sage-grouse early brood, late brood, broodless and random locations in central Wyoming, USA, 2011–13**

| Characteristic | Early Brood | Late Brood | Broodless | Random |
|---|---|---|---|---|
| Shrub canopy cover (%) | | | | |
| BsageD | 1.5 (0.1) | 1.1 (0.1) | 1.3 (0.1) | 1.3 (0.1) |
| ShrubSD | 22.1 (1.4) | 30.4 (2.8) | 24.8 (0.9) | 19.8 (0.5) |
| Ground cover (%) | | | | |
| Litter | 42.0 (2.3) | 38.9 (2.8) | 49.1 (1.6) | 36.5 (1.2) |
| Horizontal visual obstruction | | | | |
| VO (dm) | 2.7 (0.1) | 3.6 (0.3) | 3.7 (0.2) | 2.2 (0.1) |
| PerGrassH (cm) | 16.4 (0.5) | 16.6 (0.8) | 17.6 (0.6) | 15.2 (0.3) |
| ResidGrassH (cm) | 13.1 (0.5) | 14.1 (0.9) | 15.4 (0.6) | 14.7 (0.4) |
| Herbaceous canopy cover (%) | | | | |
| SpeciesR | 0.8 (0.1) | 1.1 (0.1) | 0.5 (0.1) | 0.5 (0.0) |
| NFoodF | 1.3 (0.3) | 1.8 (0.4) | 3.6 (0.4) | 2.8 (0.3) |

(Table 3, 4). Herbaceous ground cover variables included species richness and non-food forb cover. Species richness was positively correlated with early brood and late brood, but was marginally correlated with broodless female microhabitat selection (Tables 3, 4, Fig. 1*b*). Early and late brood habitat selection were negatively correlated with non-food forb cover, and marginally correlated with broodless female microhabitat selection (Tables 3, 4, Fig. 1*c*). INDVI was positively correlated with early brood, late brood, and broodless female habitat selection at the macrohabitat scale (Table 3, Fig. 3*a*).

### *Survival*

Initial variable screening indicated that distance moved between relocations had less model support than the null model (Table 5). Total reproductive effort and brood-rearing effort were highly correlated ($r = 0.86$) and were not allowed to compete in the same model. The most predictive reproductive effort model of adult

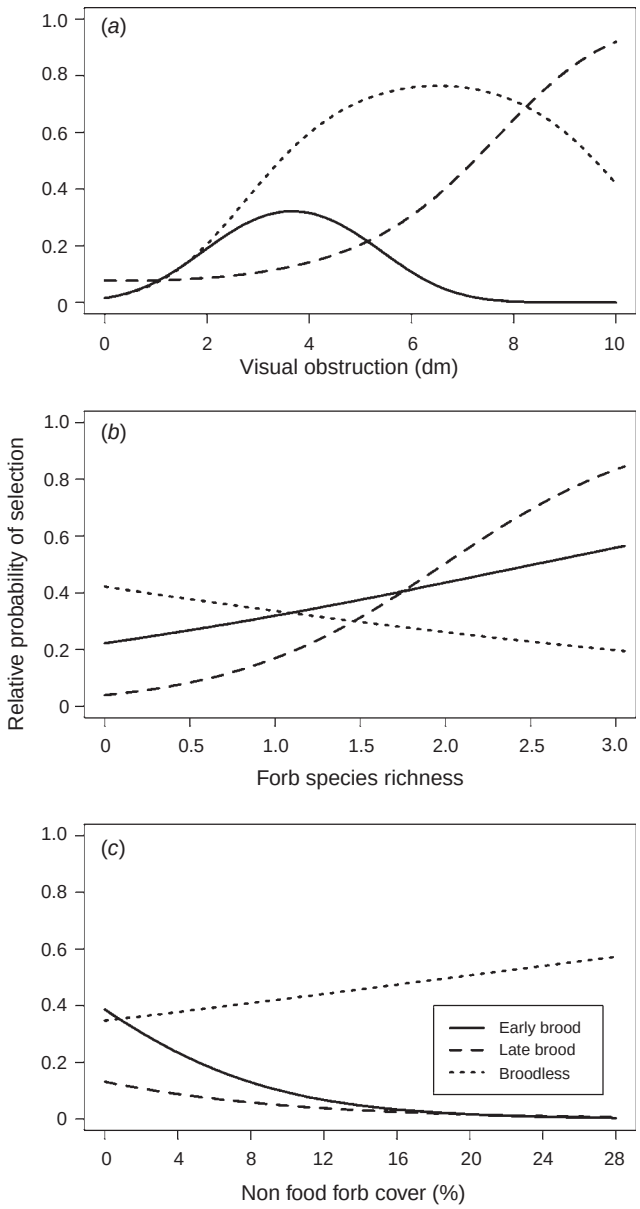



**Fig. 1.** Relative probability of selection of early-brood, late-brood, and broodless female summer habitats as a function of (*a*) visual obstruction, (*b*) forb species richness, and (*c*) non-food forb cover in central Wyoming, USA, 2011–13.

female survival to 15 weeks included the single variable that estimated total reproductive effort (Table 5). For every 1-week increase in reproductive effort, the adult female hazard rate increased by ~20.7% (Fig. 2). Inclusion of INDVI and the interaction between total reproductive effort and INDVI improved model fit relative to the model that only contained total reproductive effort (Table 6). Both total reproductive effort ($\hat{\beta}_1 = 0.089 \pm 0.03$, s.e.) and INDVI ($\hat{\beta}_1 = 0.086 \pm 0.03$, s.e.) were negatively associated with female summer survival. However, the interaction term between total reproductive effort and INDVI ($\hat{\beta}_1 = -0.002 \pm 0.001$, s.e.), indicated that mortality risk associated with INDVI varied with total reproductive effort. For predictions, we partitioned total reproductive effort into reproductive states by averaging the number of days spent in total reproductive activity for each group during the study (early brood = $5.0 \pm 0.06$ weeks, late brood = $8.2 \pm 0.06$ weeks, broodless = $1.2 \pm 0.05$ weeks) (Fig. 3*b*). We used model coefficients to predict mortality risk across the range of INDVI values for each reproductive state. Visual interpretation of prediction plots suggested that INDVI had little influence on survival of early brood-rearing females, late brood-rearing females had lower mortality risk in areas with greater INDVI, and broodless females had greater mortality risk in areas with greater INDVI.

## Discussion

Our study used a relatively long-lived gallinaceous species to assess conspecific habitat partitioning. We evaluated the influence of reproductive state on partitioning of habitat and whether habitat partitioning was consequential to adult female survival. We found that female sage-grouse partitioned habitat across reproductive states at both micro- and macrohabitat scales. During the same period, adult female survival was negatively related to reproductive effort and an index of annual productivity – females that were rearing chicks were ~20.7% more likely to die when brood-rearing for an additional week. Adult female survival was also negatively related to plant productivity; however, we found evidence that survival associated with productivity varied with reproductive investment. Differences in habitat use among individuals in other tetraonid species have been documented (Bañuelos *et al*. 2008; Blanco-Fontao *et al*. 2013) and some macrohabitat-scale research suggests that habitats used by reproductive female sage-grouse differ from those used by non-breeding individuals (Shepherd *et al*. 2011; Kirol *et al*. 2015). However, information identifying differences in microhabitat selection between brood-rearing and broodless female sage-grouse is lacking. Further, survival consequences of habitat partitioning by reproductive and broodless female sage-grouse has not been assessed in the context of different habitat use. Yet, reduced adult female survival relative to reproductive investment has been documented in other sage-grouse populations (Moynahan *et al*. 2006; Sika 2006; Blomberg *et al*. 2013; Dinkins *et al*. 2014). Here we suggest that differences in adult survival under different reproductive states are also partially explained by differences in habitats used by brood-rearing and broodless females.

Early brood-rearing females selected microhabitats with greater density of big sagebrush, intermediate visual obstruction, greater perennial grass height, less residual grass height, greater food forb species richness, and less non-food forb herbaceous cover. The importance of structure, cover, and food for early brood-rearing sage-grouse has been well documented and are consistent with our findings that early brood-rearing females selected areas of intermediate sagebrush cover with greater herbaceous understoreys during nesting and brood rearing (Sveum *et al*. 1998; Connelly *et al*. 2000; Bunnell *et al*. 2004; Hagen *et al*. 2007; Doherty *et al*. 2010; Kirol *et al*. 2012) to meet the nutritional requirements of chicks (Johnson 1987; Johnson and Boyce 1990; Barnett and Crawford 1994; Dumroese *et al*. 2015), while providing structural cover for concealment

**Table 5. Model fit statistics from single variable, reproductive investment, and reproductive investment plus environmental models from the model building procedure used to assess adult female survival to 15 weeks in central Wyoming, USA, 2011–13**

K, number of parameters; ΔAICc, change in Akaike's Information Criterion score from the top model; $w_i$, Akaike weights

| Model | Model fit statistics | | | |
|---|---|---|---|---|
| | K | ΔAICc | $w_i$ | Deviance |
| Single Variables | | | | |
| Total reproductive effort | 2 | 0.00 | 0.73 | –179.07 |
| Brood-rearing effort | 2 | 3.94 | 0.10 | –181.04 |
| Reproductive status | 3 | 4.66 | 0.07 | –180.39 |
| Null | 1 | 4.82 | 0.07 | –182.48 |
| Distance moved | 2 | 6.40 | 0.03 | –182.27 |
| Reproductive Variables | | | | |
| Total reproductive effort | 2 | 0.00 | 0.65 | –179.07 |
| Total reproductive effort + Reproductive status | 4 | 3.61 | 0.11 | –178.87 |
| Brood-rearing effort | 2 | 3.94 | 0.09 | –181.04 |
| Reproductive status | 3 | 4.66 | 0.06 | –180.39 |
| Null | 1 | 4.82 | 0.06 | –182.48 |
| Brood-rearing effort + Reproductive status | 4 | 6.44 | 0.03 | –180.28 |
| Reproductive + Environmental Variables | | | | |
| Total reproductive effort + INDVI + Total reproductive effort × INDVI | 4 | 0.00 | 0.84 | –174.38 |
| Total reproductive effort | 2 | 4.43 | 0.09 | –177.60 |
| Total reproductive effort + INDVI + big sagebrush | 4 | 5.36 | 0.06 | –179.07 |
| Null | 1 | 10.17 | 0.01 | –182.48 |

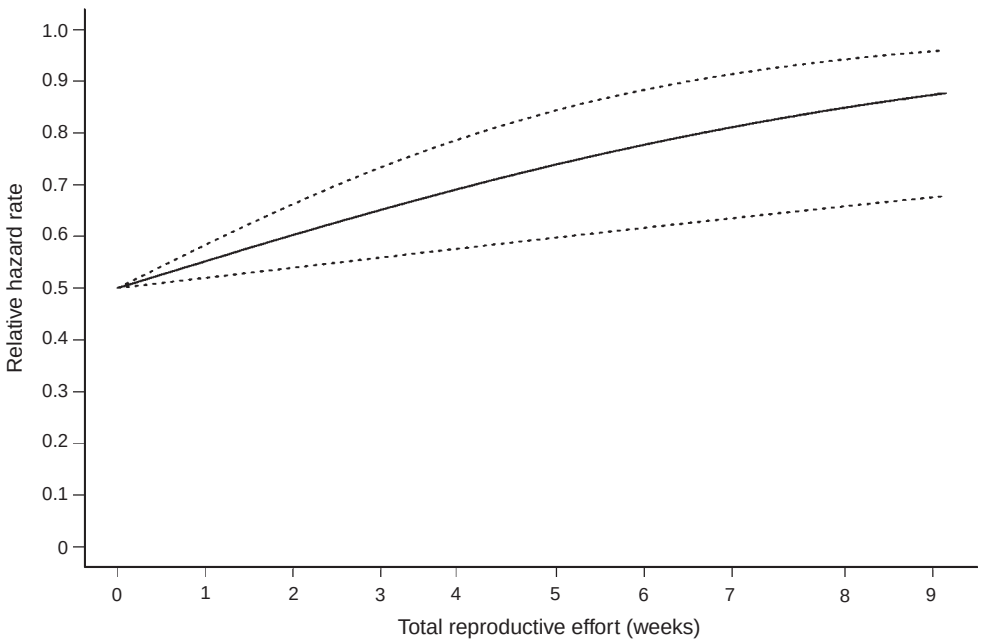



**Fig. 2.** Relative hazard rates for the most-supported model that included total reproductive effort (weeks) predicting adult female sage-grouse survival in central Wyoming, USA, 2011–13. Hazard rates were plotted with 90% confidence intervals (dashed lines).

from predators and thermal protection (Schroeder *et al*. 1999; Gregg and Crawford 2007; Kirol *et al*. 2012). As chicks grow, females with chicks generally move to more mesic habitats (i.e. late brood-rearing habitats) with resource-rich forbs (Wallestad 1971; Atamian *et al*. 2010). In our study, late brood-rearing females selected sagebrush habitats with greater variability in shrub cover, greater food forb species richness, and less non-food forb herbaceous cover when compared with available habitat. Hagen *et al*. (2007) reported that late brood-rearing females select for greater forb and grass cover, and use shrub cover in proportion to its availability, which is generally corroborated by our findings. At the macrohabitat

**Table 6. Parameter estimates, risk ratios, and 90% confidence intervals (LCL and UCL) for variables in the final model used to assess adult female survival to 15 weeks in central Wyoming, USA, 2011–13**

| Parameter | Estimate | s.e. | Risk ratio | LCL | UCL |
|---|---|---|---|---|---|
| Total reproductive effort | 0.089 | 0.026 | 1.093 | 1.047 | 1.140 |
| INDVI | 0.086 | 0.029 | 1.089 | 1.039 | 1.142 |
| Total reproductive effort × INDVI | –0.002 | 0.001 | 0.998 | 0.996 | 0.999 |

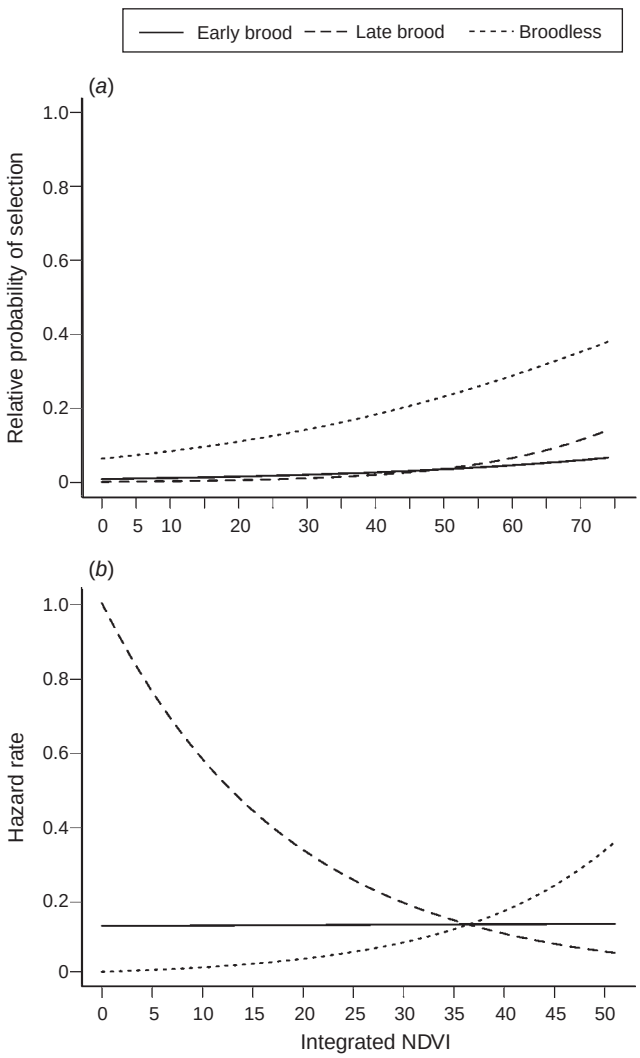



**Fig. 3.** Relative probability of selection of early-brood, late-brood, and broodless female summer habitats as a function of (*a*) INDVI, and (*b*) hazard rates relative to INDVI across reproductive states in central Wyoming, USA, 2011–13. We approximated each reproductive state by partitioning total reproductive effort into the average number of days spent in total reproductive activity for each group (early brood = 5.0 ± 0.06 weeks; late brood = 8.2 ± 0.06 weeks; broodless = 1.2 ± 0.05 weeks).

scale we found that as the brood-rearing period progressed, brooding females selected areas with greater INDVI values. This is also consistent with the findings of others (Dinkins *et al*. 2014).

Habitat partitioning was evident between broodless and brood-rearing females. Broodless females only selected for greater litter and greater horizontal visual obstruction, whereas all other microhabitat features received only moderate support in our models. Broodless females showed contrasting selection patterns for big sagebrush density, food forb species richness, and non-food forb cover compared with early brood-rearing females. Habitat selection trends were more similar between broodless and late brood-rearing females; perhaps the most distinct differences in microhabitat between individuals in these reproductive states were selection for visual obstruction. Visual obstruction estimates total horizontal obstruction and includes all microtopographic and vegetation (e.g. shrub, grass, herbaceous) attributes that provide concealment cover for individuals. Furthermore, visual obstruction is strongly associated with above-ground vegetation biomass (Robel *et al*. 1970). Studies of sage-grouse during the nesting period have documented the importance of visual obstruction (Kirol *et al*. 2012; Dinkins *et al*. 2016). Similarly, early brood-rearing females were likely selecting areas with sufficient nutritional resources in a way that maximised structural concealment cover (i.e. intermediate herbaceous understorey and shrub overstorey cover).

Sage-grouse chicks almost exclusively consume insects and forbs during early brood-rearing, when nutritional requirements are high for growth and survival (Johnson 1987; Johnson and Boyce 1990; Gregg and Crawford 2007). Gallinaceous chicks likely feed throughout the day to meet their nutritional requirements (Maxson 1977), perhaps at a cost of increased predation risk to both adults and chicks. Similar to our study, Sika (2006) found that days spent brood-rearing were negatively associated with adult survival. Because exogenous resources are the dominant nutritional resources associated with sage-grouse reproductive effort and nesting success (Gregg 2006), reproductive costs likely do not influence survival outside of the reproductive season; rather, nutritional quality during the preincubation period may be most predictive of productivity (Barnett and Crawford 1994; Gregg 2006). Our findings support our predictions that adult survival was influenced by both reproductive behaviours and intraspecific habitat partitioning.

While we do not have data on predator communities in our study area, sage-grouse research has demonstrated that habitat selection is a balance between meeting biological or reproductive demands and avoiding predation through concealment or avoidance of riskier habitats (Hagen 2011; Dinkins *et al*. 2012). It reasons that increased conspicuousness during the brood-rearing reproductive state may be at the expense of increased predation risk in selected habitats. Our results suggest that females may be more vulnerable to predation as a function of habitat partitioning when brooding chicks. Brood protection and decreased vigilance during foraging may also partially explain increased female mortality due to predation. However, individuals that selected more productive sites, particularly late brood-rearing females, had greater survival in these more productive areas. We suspect that these areas maximised security cover and foraging opportunities for late brood-rearing females; yet, relationships between structural concealment and herbaceous cover in sagebrush communities

are complex (Sowell *et al.* 2011; Camp *et al.* 2013). Unfortunately, the mismatch between sampling scales of our microhabitat (30 m) and remotely sensed INDVI (250 m) did not allow us to directly link microhabitat use to survival, indicating that further research is necessary to identify the mechanisms associated with this finding.

Nonetheless, previous research on other Galliformes supports our findings. Blanco-Fontao *et al.* (2013) suggested that habitat partitioning in greater prairie chickens (*Tympanuchus cupido*) resulted in females selecting more protein-rich diets in autumn compared with males, which likely selected habitats to reduce predation risk. Bunnell *et al.* (2004) examined microhabitat differences between brood-rearing and adult sage-grouse, but did not differentiate between males and broodless females, so their findings are difficult to compare with ours. Adults selected greater sagebrush height and less forb diversity compared with brood-rearing females (Bunnell *et al.* 2004). Because broodless females were not rearing broods, they were likely roosting and foraging in habitats that maximised concealment from predators (Lima 1985) while meeting their more basic nutritional needs. The same parent–offspring conflict (Trivers 1974) has been demonstrated in other tetraonids, with higher summer mortality of brood-rearing females and habitat partitioning by broodless females that exploit denser cover (Maxson 1978).

Ungulates provide a well documented case of habitat partitioning and suggest that, in some populations, males and females should be effectively managed as separate species (Conradt 1999; Bowyer 2004; Ruckstuhl 2007). Similarly, sufficient differences in habitat selection among tetraonid species (Bañuelos *et al.* 2008; Blanco-Fontao *et al.* 2013), including sage-grouse under different reproductive states, suggests that this principle should be applied when identifying the array of habitats used by both brood-rearing and broodless female sage-grouse. Sage-grouse habitat management generally focuses on nesting and brood-rearing habitats; however, habitat partitioning between brood-rearing and broodless females, as described here, suggests the need to re-evaluate strategies for sage-grouse habitat conservation. The success of reproductive female sage-grouse depends on their survival, to reproduce in subsequent breeding seasons, as well as the survival of their offspring. Therefore, adult survival is a critical component of sage-grouse population persistence. This is particularly true in years of poor population productivity when adult female survival may have the greatest influence on population demography (Taylor *et al.* 2012; Dahlgren *et al.* 2016). While it is evident that reproductive costs are high for sage-grouse, habitats used by individuals under different reproductive strategies may help to ameliorate these costs; conserving habitats used by all females during the breeding season should be a top priority for conservation efforts. In our study, ~3 of every 4 female sage-grouse were broodless, further highlighting the need to provide habitat for this important cohort of sage-grouse populations. Maintaining heterogeneous sagebrush landscapes that provide dense overstorey cover for broodless females interspersed with more open sagebrush habitats with concomitant herbaceous understoreys for foraging and brood-rearing is necessary to maintain the variability and juxtaposition of sage-grouse habitats necessary for all individuals within a population.

## Conflicts of interest

The authors declare no conflicts of interest.

## Acknowledgements

We received logistical support from T. Christiansen and S. Harter from the Wyoming Game and Fish Department, and S. Oberlie and T. Vosburgh from the Bureau of Land Management (Lander Field Office). Our work would not have been possible without the cooperation and help of several landowners and research technicians. This work was supported by the Wyoming Game and Fish Department (grant no. WYGF40415); Wyoming Sage-grouse Conservation Fund of the Wyoming Game and Fish Department from Bates Hole, Big Horn Basin, Southwest, South-central and Wind River/Sweetwater River Local Sage-grouse Working Groups (grant nos 1001401, 1001970, and 1002656); the Margaret and Sam Kelly Ornithological Research Fund (grant no. 170016758); and Wyoming Wildlife and Natural Resource Trust (grant no. 1002157).

## References

Aldridge, C. L., and Boyce, M. S. (2008). Accounting for fitness: combining survival and selection when assessing wildlife–habitat relationships. *Israel Journal of Ecology & Evolution* **54**, 389–419. doi:10.1560/IJEE.54.3-4.389

Allison, P. D. (Ed.) (2010) 'Survival Analysis Using SAS: A Practical Guide.' 2nd edn. (SAS Institute: North Carolina.)

Alves, J. A., Alves da Silva, A., Soares, A. M. V. M., and Fonseca, C. (2013). Sexual segregation in red deer: is social behaviour more important that habitat preferences? *Animal Behaviour* **85**, 501–509. doi:10.1016/j.anbehav.2012.12.018

Andersen, P. K., and Gill, R. D. (1982). Cox's regression model for counting processes: a large sample study. *Annals of Statistics* **10**, 1100–1120. doi:10.1214/aos/1176345976

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* **76**, 391–406.

Atamian, M. T., Sedinger, J. S., Heaton, J. S., and Blomberg, E. J. (2010). Landscape-level assessment of brood rearing habitat for greater sage-grouse in Nevada. *Journal of Wildlife Management* **74**, 1533–1543. doi:10.1111/j.1937-2817.2010.tb01281.x

Bañuelos, M. J., Quevedo, M., and Obeso, J. R. (2008). Habitat partitioning in endangered Cantabrian capercaille *Tetrao urogallus cantabricus*. *Journal of Ornithology* **149**, 245–252. doi:10.1007/s10336-007-0267-5

Barnett, J. K., and Crawford, J. A. (1994). Pre-laying nutrition of sage grouse hens in Oregon. *Journal of Range Management* **47**, 114–118. doi:10.2307/4002817

Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **678**, 1–48.

Baxter, R. J., Larsen, R. T., and Flinders, J. T. (2013). Survival of resident and translocated greater sage-grouse in Strawberry Valley, Utah: a 13-year study. *Journal of Wildlife Management* **77**, 802–811. doi:10.1002/jwmg.520

Bergerud, A. T., and Gratson, M. W. (1988). Survival and breeding strategies of grouse. In 'Adaptive Strategies and Population Ecology of Northern Grouse'. (Eds A. T. Bergerud, and M. W. Gratson.) pp. 473–577. (University of Minnesota Press: Minneapolis, MN.)

Blanco-Fontao, B., Sandercock, B. K., Obeso, J. R., McNew, L. B., and Quevedo, M. (2013). Effects of sexual dimorphism and landscape composition on the trophic behavior of greater prairie chicken. *PLoS One* **8**, e79986. doi:10.1371/journal.pone.0079986

Blomberg, E. J., Sedinger, J. S., Atamian, M. T., and Nonne, D. V. (2012). Characteristics of climate and landscape disturbance influence the dynamic of greater sage-grouse populations. *Ecosphere* **3**. doi:10.1890/ES11-00304.1

Blomberg, E. J., Sedinger, J. S., Nonne, D. V., and Atamian, M. T. (2013). Seasonal reproductive costs contribute to reduced survival of female greater sage-grouse. *Journal of Avian Biology* **44**, 149–158. doi:10.1111/j.1600-048X.2012.00013.x

Bolnick, D. I., Svanback, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., and Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* **161**, 1–28. doi:10.1086/343878

Bowyer, R. T. (2004). Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. *Journal of Mammalogy* **85**, 1039–1052. doi:10.1644/BBL-002.1

Bunnell, K. D., Flinders, J. T., Mitchell, D. C., and Warder, J. H. (2004). Occupied and unoccupied sage grouse habitat in Strawberry Valley, Utah. *Journal of Range Management* **57**, 524–531. doi:10.2307/4003983

Burger, J., Howe, M. A., Hahn, C., and Chase, J. (1977). Effects of tide cycles on habitat selection and habitat partitioning by migrating shorebirds. *The Auk* **94**, 743–758. doi:10.2307/4085271

Burnham, K. P., and Anderson, D. R. (Eds) (2002). 'Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach.' 2nd edn. (Springer Science + Business Media: New York.)

Burnham, K. P., and Anderson, D. R. (2004). Multimodal inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* **33**, 261–304. doi:10.1177/0049124104268644

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**, 516–519. doi:10.1016/j.ecolmodel.2006.03.017

Camp, M. J., Rachlow, J. L., Woods, B. A., Johnson, T. R., and Shipley, L. A. (2013). Examining functional components of cover: the relationship between concealment and visibility in shrub–steppe habitat. *Ecosphere* **42**, 19.

Canfield, R. H. (1941). Application of the line interception method in sampling range vegetation. *Journal of Forestry* **39**, 388–394.

Connelly, J. W., Schroeder, M. A., Sands, A. R., and Braun, C. E. (2000). Guidelines to manage sage grouse populations and their habitats. *Wildlife Society Bulletin* **28**, 967–985.

Connelly, J. W., Knick, S. T., Schroeder, M. A., and Slater, S. J. (2004). Conservation assessment of greater sage-grouse and sagebrush habitats. Unpublished Report. Western Association of Fish and Wildlife Agencies, Cheyenne, WY, USA.

Connelly, J. W., Rinkes, E. T., and Braun, C. E. (2011*a*). Characteristics of greater sage-grouse habitats: a landscape species at the micro and macro scales. In 'Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats'. (Eds S. T. Knick, and J. W. Connelly.) pp. 69–83. Studies in Avian Biology, Volume 38. (University of California Press: California, USA.)

Connelly, J. W., Rinkes, E. T., and Braun, C. E. (2011*b*). Characteristics and dynamics of greater sage-grouse populations. In 'Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats'. (Eds S. T. Knick, and J. W. Connelly.) pp. 53–68. Studies in Avian Biology, Volume 38. (University of California Press: California, USA.)

Conradt, L. (1999). Social segregation is not a consequence of habitat segregation in red deer and feral Soay sheep. *Animal Behaviour* **57**, 1151–1157. doi:10.1006/anbe.1999.1067

Cox, D. R. (1972). Regression models and life-tables. *Journal of the Royal Statistical Society. Series B. Methodological* **34**, 187–220.

Cumming, H. G., Beange, D. B., and Lavoie, G. (1996). Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. *Rangifer* **16**, 81–94. doi:10.7557/2.16.4.1224

Dahlgren, D. K., Messmer, T. A., Thacker, E. T., and Guttery, M. R. (2010). Evaluation of brood detection techniques: recommendations for estimating greater sage-grouse productivity. *Western North American Naturalist* **70**, 233–237. doi:10.3398/064.070.0210

Dahlgren, D. K., Guttery, M. R., Messmer, T. A., Caudill, D., Elmore, R. D., Chi, R., and Koons, D. N. (2016). Evaluating vital rate contributions to greater sage-grouse population dynamics to inform conservation. *Ecosphere* **7**, e01249. doi:10.1002/ecs2.1249

Dalke, P. D., Pyrah, D. B., Stanton, D. C., Crawford, J. E., and Schlatterer, E. F. (1963). Ecology, productivity, and management of sage grouse in Idaho. *Journal of Wildlife Management* **27**, 810–841. doi:10.2307/3798496

Daubenmire, R. (1959). A canopy-coverage method of vegetational analysis. *Northwest Science* **33**, 43–61.

Dinkins, J. B., Conover, M. R., Kirol, C. P., and Beck, J. L. (2012). Greater sage-grouse (*Centrocercus urophasianus*) select nest sites and brood sites away from avian predators. *The Auk* **129**, 600–610. doi:10.1525/auk.2012.12009

Dinkins, J. B., Conover, M. R., Kirol, C. P., Beck, J. L., and Frey, S. N. (2014). Greater sage-grouse (*Centrocercus urophasianus*) select habitat based on avian predators, landscape composition, and anthropogenic features. *The Condor* **116**, 629–642. doi:10.1650/CONDOR-13-163.1

Dinkins, J. B., Smith, K. T., Beck, J. L., Kirol, C. P., Pratt, A. C., and Conover, M. R. (2016). Microhabitat conditions in Wyoming's sage-grouse core areas: effects on nest site selection and survival. *PLoS One* **11**, e0150798. doi:10.1371/journal.pone.0150798

Doherty, K. E., Naugle, D. E., and Walker, B. L. (2010). Greater sage-grouse nesting habitat: the importance of managing at multiple scales. *Journal of Wildlife Management* **74**, 1544–1553. doi:10.1111/j.1937-2817.2010.tb01282.x

Donovan, T. M., and Thompson, F. R. III (2001). Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecological Applications* **11**, 871–882. doi:10.1890/1051-0761(2001)011[0871:MTETHA]2.0.CO;2

Drut, M. S., Crawford, J. A., and Gregg, M. A. (1994). Brood habitat use by sage grouse in Oregon. *The Great Basin Naturalist* **54**, 170–176.

Dumroese, R. K., Luna, T., Richardson, B. A., Kilkenny, F. F., and Runyon, J. B. (2015). Conserving and restoring habitat for greater sage-grouse and other sagebrush-obligate wildlife: the crucial link of forbs and sagebrush diversity. *Native Plants Journal* **16**, 276–299. doi:10.3368/npj.16.3.276

Erikstad, K. E., Fauchald, P., Tveraa, T., and Steen, H. (1998). On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* **79**, 1781–1788. doi:10.1890/0012-9658(1998)079[1781:OTCORI]2.0.CO;2

Frid, A., and Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* **6**. doi:10.5751/ES-00404-060111

Gibson, D., Blomberg, E. J., Atamian, M. T., and Sedinger, J. S. (2017). Weather, habitat composition, and female behavior interact to modify offspring survival in greater sage-grouse. *Ecological Applications* **27**, 168–181. doi:10.1002/eap.1427

Giesen, K. M., Schoenberg, T. L., and Braun, C. E. (1982). Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* **10**, 224–231.

Gregg, M. A. (2006). Greater sage-grouse reproductive ecology: linkages among habitat resources, maternal nutrition, and chick survival. Ph.D. dissertation. Available from ProQuest database (3219759).

Gregg, M. A., and Crawford, J. A. (2007). Survival of greater sage-grouse chicks and broods in the northern Great Basin. *Journal of Wildlife Management* **71**, 646–651. doi:10.2193/2006-353

Gregg, M. A., Crawford, J. A., and Drut, M. S. (1993). Summer habitat use and selection by female sage grouse (*Centrocercus urophasianus*) in Oregon. *The Great Basin Naturalist* **53**, 293–298.

Guttery, M. R., Dahlgren, D. K., Messmer, T. A., Connelly, J. W., Reese, K. P., Terletzky, P. A., Burkepile, N., and Koons, D. N. (2013). Effects of landscape-scale environmental variation on greater sage-grouse chick survival. *PLoS One* **8**, e65582. doi:10.1371/journal.pone.0065582

Hagen, C. A. (2011). Predation on greater sage-grouse: facts, process and effects. In 'Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats'. (Eds S. T. Knick, and J. W. Connelly.) pp. 95–100. Studies in Avian Biology, Volume 38. (University of California Press: California, USA.)

Hagen, C. A., Connelly, J. W., and Schroeder, M. A. (2007). A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. *Wildlife Biology* **13**, 42–50. doi:10.2981/0909-6396(2007)13[42:AMOGSC]2.0.CO;2

Harshman, L. G., and Zera, A. J. (2007). The cost of reproduction: the devil in the details. *Trends in Ecology & Evolution* **22**, 80–86. doi:10.1016/j.tree.2006.10.008

Hosmer, D. W., and Lemeshow, S. (1999). 'Applied Survival Analysis: Regression Modeling of Time to Event Data.' (John Wiley: New Jersey, USA.)

Huwer, S. L., Anderson, D. R., Remington, T. E., and White, G. C. (2008). Using human-imprinted chicks to evaluate the importance of forbs to sage-grouse. *Journal of Wildlife Management* **72**, 1622–1627. doi:10.2193/2004-340

Johnson, G. D. (1987). Effects of rangeland grasshopper control on sage grouse in Wyoming. M.Sc. Thesis. Available from ProQuest database (EP22602).

Johnson, G. D., and Boyce, M. S. (1990). Feeding trials with insects in the diet of sage grouse chicks. *Journal of Wildlife Management* **54**, 89–91. doi:10.2307/3808906

Johnson, K. H., and Braun, C. E. (1999). Viability and conservation of an exploited sage-grouse population. *Conservation Biology* **13**, 77–84. doi:10.1046/j.1523-1739.1999.97284.x

Kirol, C. P., Beck, J. L., Dinkins, J. B., and Conover, M. R. (2012). Microhabitat selection for nesting and brood-rearing greater sage-grouse in xeric big sagebrush. *The Condor* **114**, 75–89. doi:10.1525/cond.2012.110024

Kirol, C. P., Beck, J. L., Huzurbazar, S. V., Holloran, M. J., and Miller, S. N. (2015). Identifying greater sage-grouse source and sink habitats for conservation planning in an energy development landscape. *Ecological Applications* **25**, 968–990. doi:10.1890/13-1152.1

Laundre, J. W., Hernandez, L., and Ripple, W. J. (2010). The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal* **3**, 1–7. doi:10.2174/1874213001003030001

Lima, S. L. (1985). Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia* **66**, 60–67. doi:10.1007/BF00378552

Mackie, I. J., and Racey, P. A. (2007). Habitat use varies with reproductive state in noctule bats (*Nyctalus noctula*): implications for conservation. *Biological Conservation* **140**, 70–77. doi:10.1016/j.biocon.2007.07.031

Main, M. B., and Coblentz, B. E. (1996). Sexual segregation in Rocky Mountain mule deer. *Journal of Wildlife Management* **60**, 497–507. doi:10.2307/3802067

Maxson, S. J. (1977). Activity patterns of female ruffed grouse during the breeding season. *The Wilson Bulletin* **89**, 439–455.

Maxson, S. J. (1978). Spring home range and habitat use by female ruffed grouse. *Journal of Wildlife Management* **42**, 61–71. doi:10.2307/3800690

Moynahan, B. J., Lindberg, M. S., and Thomas, J. W. (2006). Factors contributing to process variance in annual survival of female sage-grouse in Montana. *Ecological Applications* **16**, 1529–1538. doi:10.1890/1051-0761(2006)016[1529:FCTPVI]2.0.CO;2

National Centers for Environmental Information (NOAA) (2016). Annual Climatological Summary for station Lander 1 N, WY US COOP:485392, for 2011 and 2012, Asheville, NC, USA. Available at: http://www1.ncdc.noaa.gov/pub/orders/cdo/672061.pdf.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., and Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution* **20**, 503–510. doi:10.1016/j.tree.2005.05.011

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrejewska, B., Lima, M., and Kausrud, K. (2011). The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. *Climate Research* **46**, 15–27. doi:10.3354/cr00936

Pianka, E. R. (1970). On R and K selection. *American Naturalist* **104**, 592–597. doi:10.1086/282697

R Core Team (2015). R: A Language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/.

Robel, R. J., Briggs, J. N., Dayton, A. D., and Hulbert, L. D. (1970). Relationship between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* **23**, 295–297. doi:10.2307/3896225

Rotella, J. J., Dinsmore, S. J., and Shaffer, T. L. (2004). Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* **27**, 187–205.

Ruckstuhl, K. E. (2007). Sexual segregation in vertebrates: proximate and ultimate causes. *Integrative and Comparative Biology* **47**, 245–257. doi:10.1093/icb/icm030

Schoenfeld, D. (1982). Residuals for the proportional hazards regression model. *Biometrika* **69**, 239–241. doi:10.1093/biomet/69.1.239

Schroeder, M. A., Young, J. R., and Braun, C. E. (1999). Sage grouse (*Centrocercus urophasianus*). In 'The Birds of North America'. (Eds A. Poole, and F. Gill.) pp. 1–28. (The Birds of North America Inc.: New York.)

Schroeder, M. A., Aldridge, C. L., Apa, A. D., Bohne, J. R., Braun, C. E., Bunnell, S. D., Connelly, J. W., Deibert, P. A., Gardner, S. C., Hilliard, M. A., Kobriger, G. D., McAdam, S. M., McCarthy, C. W., McCarthy, J. J., Mitchell, D. L., Rickerson, E. V., and Stiver, S. J. (2004). Distribution of sage-grouse in North America. *The Condor* **106**, 363–376. doi:10.1650/7425

Shepherd, J. F., Reese, K. P., and Connelly, J. W. (2011). Landscape fragmentation and nonbreeding greater sage-grouse. In 'Ecology, Conservation, and Management of Grouse'. (Eds B. K. Sandercock, K. Martin, and G. Segelbacher.) pp. 77–88. Studies in Avian Biology, Volume 39. (University of California Press: California, USA.)

Sika, J. L. (2006). Breeding ecology, survival rates, and causes of mortality of hunted and nonhunted greater sage-grouse in central Montana. M.Sc. Thesis.

Sowell, B. F., Wambolt, C. L., Woodward, J. K., and Lane, V. R. (2011). Relationship of Wyoming big sagebrush cover to herbaceous vegetation. *Natural Resources and Environmental Issues* **16**, 1–4.

Sveum, C. M., Crawford, J. A., and Edge, W. D. (1998). Use and selection of brood-rearing habitat by sage grouse in south central Washington. *The Great Basin Naturalist* **58**, 344–351.

Taylor, R. L., Walker, B. L., Naugle, D. E., and Mills, L. S. (2012). Managing multiple vital rates to maximize greater sage-grouse population growth. *Journal of Wildlife Management* **76**, 336–347. doi:10.1002/jwmg.267

Therneau, T. M. (2015). Coxme: Mixed effects Cox models. R package version 2.5–5. Available at: http://CRAN.R-project.org/package=coxme

Therneau, T. M., and Grambsch, P. M. (2000). 'Modeling Survival Data: Extending the Cox Model.' (Springer: New York.)

Thomas, D. L., and Taylor, E. J. (2006). Study designs and tests for comparing resource use and availability. II. *Journal of Wildlife Management* **70**, 324–336. doi:10.2193/0022-541X(2006)70[324:SDATFC]2.0.CO;2

Thompson, K. M., Holloran, M. J., Slater, S. J., Kuipers, J. L., and Anderson, S. H. (2006). Early brood-rearing habitat use and productivity of

greater sage-grouse in Wyoming. *Western North American Naturalist* **66**, 332–342. doi:10.3398/1527-0904(2006)66[332:EBHUAP]2.0.CO;2

Trivers, R. L. (1974). Parent–offspring conflict. *American Zoologist* **14**, 249–264. doi:10.1093/icb/14.1.249

US Fish and Wildlife Service (2015). Endangered and threatened wildlife and plants: 12 month finding on a petition to list greater sage-grouse (*Centrocercus urophasianus*) as an endangered or threatened species. *Federal Register* **80**, 59858–59942.

Venables, W. N., and Ripley, B. D. (2002). 'Modern Applied Statistics with S.' 4th edn. (Springer: New York.)

Wakkinen, W. L., Reese, K. P., Connelly, J. W., and Fischer, R. A. (1992). An improved spotlighting technique for capturing sage grouse. *Wildlife Society Bulletin* **20**, 425–426.

Walker, B. L. (2008). Greater sage-grouse response to coal-bed natural gas development and West Nile Virus in the Powder River Basin, Montana and Wyoming. Ph.D. Dissertation. Available from ProQuest database.

Wallestad, R. O. (1971). Summer movements and habitat use by sage grouse broods in central Montana. *Journal of Wildlife Management* **35**, 129–136. doi:10.2307/3799881

Wambolt, C. L., Frisina, M. R., Knapp, S. J., and Frisina, R. M. (2006). Effect of method, site, and taxon on line-intercept estimates of sagebrush cover. *Wildlife Society Bulletin* **34**, 440–445. doi:10.2193/0091-7648(2006)34[440:EOMSAT]2.0.CO;2

Werner, E. E., Hall, D. J., Laughlin, D. R., Wagner, D. J., Wilsmann, L. A., and Funk, F. C. (1977). Habitat partitioning in a freshwater fish community. *Journal of the Fisheries Research Board of Canada* **34**, 360–370. doi:10.1139/f77-058

Wilson, A. J., and Nussey, D. H. (2010). What is individual quality? An evolutionary perspective. *Trends in Ecology and Evolution* **25**, 207–214.

Winterstein, S. R., Pollock, K. H., and Bunck, C. M. (2001). Analysis of survival data from radiotelemetry studies. In 'Radio Tracking and Animal Populations'. (Eds J. J. Millspaugh, and J. M. Marzluff.) pp. 352–380. (Academic Press: Cambridge, MA.)

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–168. doi:10.2307/1938423

Wildlife Society Bulletin 37(2):409–415;2013; DOI: 10.1002/wsb.273

*Tools and Technology*

# Mapping Sage-Grouse Fence-Collision Risk: Spatially Explicit Models for Targeting Conservation Implementation

**BRYAN S. STEVENS,**[1,2] *Departments of Fish and Wildlife Sciences and Statistical Sciences, University of Idaho, P.O. Box 441136, Moscow, ID 83844, USA*

**DAVID E. NAUGLE,** *Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA*

**BRIAN DENNIS,** *Departments of Fish and Wildlife Sciences and Statistical Sciences, University of Idaho, P.O. Box 441136, Moscow, ID 83844, USA*

**JOHN W. CONNELLY,** *Idaho Department of Fish and Game, 1345 Barton Road, Pocatello, ID 83204, USA*

**TIM GRIFFITHS,** *United States Department of Agriculture, Natural Resources Conservation Service, 10 E Babcock Street, Bozeman, MT 59718, USA*

**KERRY P. REESE,** *Department of Fish and Wildlife Sciences, University of Idaho, P.O. Box 441136, Moscow, ID 83844, USA*

**ABSTRACT** Recent research suggested greater sage-grouse (*Centrocercus urophasianus;* hereafter, sage-grouse) fence collision may be widespread, and fence-marking methods have been developed for reducing prairie-grouse collision in sagebrush-steppe habitats. However, research also suggested sage-grouse collision was highly variable, and managers implementing mitigation desire targeting tools to prioritize mitigation efforts as a function of risk. We fit collision-risk models using widely available covariates to a sage-grouse fence-collision data set from Idaho, USA, and developed spatially explicit versions of the top model for all known sage-grouse breeding habitats (i.e., within 3 km of leks) in 10 of 11 western states where sage-grouse are found. Our models prioritize breeding habitats for mitigation as a function of terrain ruggedness and distance to nearest lek, and suggest that a relatively small proportion of the total landscape (6–14%) in each state would result in >1 collision over a lekking season. Managers can use resulting models to prioritize fence-marking by focusing efforts on high risk landscapes. Moreover, our models provide a spatially explicit tool to efficiently target conservation investments, and exemplify the way that researchers and managers can work together to turn scientific understanding into effective conservation solutions. © 2013 The Wildlife Society.

**KEY WORDS** avian collision, *Centrocercus urophasianus*, collision mitigation, fence collision, fence markers, infrastructure marking, sage-grouse.

Collision with elevated structures is a common phenomenon for many species of grouse (Catt et al. 1994, Baines and Summers 1997, Wolfe et al. 2007, Stevens et al. 2012*a*). Early research from Europe reported grouse among the most common infrastructure-collision victims, and suggested tetraonid collision susceptibility may be a function of morphology (e.g., heavy body wt, high wing loading; Baines and Summers 1997, Bevanger 1998, Bevanger and Brøseth 2000, Janss 2000). More recently, research in North America suggested prairie-grouse are susceptible to collision with fences (Patten et al. 2005, Wolfe et al. 2007, Stevens et al. 2012*a*). Fence collision was attributed to 39.8% of mortality for lesser prairie chickens (*Tympanuchus pallidicinctus*) in Oklahoma, USA (Wolfe et al. 2007), and uncorrected mean fence-collision rates of 0.38–0.41 strikes/km were reported for greater sage-grouse (*Centrocercus urophasianus;* hereafter, sage-grouse) during the breeding season in Idaho, USA (Stevens 2011). Fences and other anthropogenic structures are ubiquitous across western North America (Braun 1998, Knick et al. 2011); however, population-level impacts of prairie-grouse collision are poorly understood.

Infrastructure marking is a commonly suggested conservation strategy for reducing avian–infrastructure collision (Baines and Andrew 2003, Wolfe et al. 2009, Stevens et al. 2012*b*). Power-line markers appear to reduce collision for a variety of avian species (Morkill and Anderson 1991, Brown and Drewien 1995, Savereno et al. 1996, Barrientos et al. 2011), but assessments of fence-markers are less common. However, orange barrier netting reduced woodland grouse fence-collision in Scotland (Baines and Andrew 2003). Moreover, fence-marking methods have been developed for North American prairie grouse (Wolfe et al. 2009; Fig. 1), and evidence from Idaho suggested marking reduced the count of sage-grouse collisions by 83% during the breeding season (Stevens et al. 2012*b*).

Received: 5 July 2012; Accepted: 10 December 2012
Published: 16 May 2013

[1]*E-mail: stev8930@vandals.uidaho.edu*
[2]*Present address: Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources, East Lansing, MI 48824, USA*



**Figure 1.** Male greater sage-grouse displaying on a lek directly beside a marked fence on an Idaho, USA, study site. Reflective fence markers were shown to reduce sage-grouse collision counts by approximately 83% in high-risk breeding habitats (Stevens et al. 2012*b*).

Managers are forced to make decisions with incomplete information and constrained budgets, and efficient allocation of resources promotes the greatest return on conservation investments (Bottrill et al. 2008). Targeting conservation to ensure that funds are allocated efficiently is often referred to as triage, a process that provides transparency and forces managers to consider opportunity costs of management actions (Bottrill et al. 2008). Sage-grouse collision appears highly variable within and between regions (Stevens et al. 2012*a*, *b*). Variation in collision risk suggests mitigation is unnecessary at many sites and prioritizing mitigation as a function of risk may enable cost-effective implementation of mitigation efforts (Stevens et al. 2012*a*, *b*). Thus, small but targeted investments could potentially alleviate much of the fence-collision risk in breeding habitats, freeing up resources for other conservation efforts.

The science behind conservation planning is often not conducted in partnership with managers, further complicating management decisions and resource allocation. Instead, researchers often conduct studies with little input from end users and hope the conservation community finds it useful (Knight et al. 2008). Steps to alleviate this research-implementation gap include sourcing research questions directly from managers, fostering relationships between researchers and managers, and linking research to implementation of conservation actions. Research showing that fence marking can reduce sage-grouse collisions (Stevens et al. 2012*b*) has spurred fence-marking efforts on public and private lands across 11 western states. However, sage-grouse occupy vast areas of western North America (Schroeder et al. 2004), and wildlife managers desire spatially explicit targeting tools to maximize their return on conservation investments. Therefore, the objective of this study was to bridge the research-implementation gap by developing spatially explicit fence-collision-risk models for sage-grouse in breeding areas across the western United States. Specifically, we developed models by re-analyzing landscape factors influencing collision risk from Stevens et al. (2012*a*), and applied resulting models to spatially predict and map fence-collision risk for all known sage-grouse breeding habitats in 10 of 11 western states.

## STUDY AREA

We developed raster-regression models for areas within 3 km of all known and active sage-grouse leks ($n = 4{,}684$) in 10 of 11 states currently supporting sage-grouse. We used the most recently developed range-wide lek database for this analysis. The database was originally developed by Connelly et al. (2004), but has since been updated to reflect lek locations discovered and leks lost from 2004 to 2007 (Garton et al. 2011, Knick and Hanser 2011). Therefore, our analyses included all known and active sage-grouse leks as of 2007, although two states (ID and NV) provided lek location data updated through 2011.

## METHODS

Stevens (2011) described a cluster sampling design used to survey fences in sage-grouse breeding areas of southern Idaho (2009: $n = 16$ sites; 2010: $n = 14$ sites), where $1 \times 1$-km sampling units were randomly selected and surveyed during the breeding season at each site (Mar–May; 2009: $n = 60$ clusters; 2010: $n = 80$ clusters). The number of sage-grouse collisions per square km was recorded for each sampled cluster, and clusters were sampled on >1 occasion when possible, resulting in 224 collision-count observations (Stevens 2011). Stevens et al. (2012*a*) modeled these collision counts as a function of covariates, including distance from each $1 \times 1$-km cluster's centroid to the nearest active lek, lek size (i.e., max. count) at the nearest lek, and a terrain ruggedness index (TRI; Riley et al. 1999). However, Stevens et al. (2012*a*) did not account for potential bias caused by removal of collision remains by scavengers, and only used a subset of collision-count observations representing the first sampling event at each site ($n = 123$). Therefore, we extended the analyses of Stevens et al. (2012*a*) and 1) used all 224 collision-count observations, 2) incorporated field-experiment data used to measure removal of collision evidence by scavengers, 3) used newly developed statistical models to combine collision-count data with removal-experiment data using joint-likelihood principles to estimate collision and removal process parameters, and 4) developed spatially explicit raster models to extrapolate estimated collision risk to all known sage-grouse breeding areas in 10 of 11 currently occupied states.

We modeled sage-grouse fence-collision counts from Idaho as a function of lek size, distance to lek, and TRI using a stochastic-process model for collision-count data developed by Stevens and Dennis (2013). Stevens et al. (2011) showed that removal of collision evidence prior to fence-collision sampling (i.e., evidence-removal bias) can be large, and removal of collision remains varied across regions of southern Idaho. The model used for our analyses predicts collision-count data with a generalized-regression approach that accounts for removal of collision evidence and accommodates covariates on collision- and removal-process

parameters (Stevens and Dennis 2013). The model treats instantaneous collision counts as a stochastic-linear-immigration-death (SLID) process (Matis and Kiffe 2000), whereby Poisson arrivals represent addition of collisions to the system (immigration) and proportional deaths remove evidence from a site. The SLID model combines collision-count and removal-experiment data sets to estimate collision ($\theta$) and removal ($\psi$) rate parameters using joint likelihood. Stevens and Dennis (2013) showed that regional variation in evidence removal can result in order-of-magnitude differences in expected collision counts between regions with identical collision rates. Thus, the removal rate ($\psi$) is, in effect, a nuisance parameter, and failing to account for evidence removal when modeling avian-collision counts results in parameter estimates that are difficult to interpret (Stevens and Dennis 2013).

We combined data from collision-count surveys (Stevens 2011) with carcass-removal-experiment data (Stevens et al. 2011) to estimate parameters of the SLID model. We fit 14 total models and compared models using Akaike's Information Criterion (hereafter, AIC; Akaike 1973). We fit models using the log link function and seven different covariate combinations, where collision ($\theta$) was modeled as a function of distance to lek, lek size, and TRI, and removal ($\psi$) was modeled as a function of a binary variable indicating study region (i.e., region of ID where removal experiments were conducted; 1 = southeast Idaho, 0 = Magic Valley region). For the region-specific removal, fences west of Craters of the Moon National Monument were considered the Magic Valley, whereas fences east of this location were located in southeast Idaho. We fit each of the seven covariate combinations using the transient and stationary versions of the model, by numerically maximizing the transition (i.e., time dependent) and stationary (i.e., equilibrium and time-independent) distribution joint likelihoods (Stevens and Dennis 2013). We generated profile-likelihood confidence intervals for all model parameters and conducted goodness-of-fit testing for the most supported model (Stevens and Dennis 2013). We used leave-one-out cross-validation and root-mean-squared error to evaluate prediction success, calculating square root of the average squared error between predicted and observed collision counts for each model. We used the R statistical computing language for all model fitting and analyses (R Core Development Team 2006).

We developed spatially explicit models to predict collision as a function of covariates from the top SLID model. Because fence sampling in Idaho focused on areas within approximately 3 km of leks, we buffered all range-wide lek locations by 3 km in a Geographic Information System (GIS; ArcMap 10.0) and focused spatial analyses in these areas. We downloaded U.S. Geological Survey 30-m digital elevation models for each state (www.seamless.usgs.gov; accessed 7–9 Feb 2012), and calculated TRI for each 30-m pixel using ArcInfo. We calculated distance from each 30-m pixel to the nearest sage-grouse lek in GIS using the Euclidean distance function. Lastly, we used the raster calculator in GIS to extrapolate maximum-likelihood estimates of the total number of sage-grouse collisions over a lekking season for each 30-m pixel as a function of distance to lek and TRI, assuming a 78-day lekking season (15 March to 31 May; $\hat{y} = 78 \times \exp(\beta_0 + \beta_1 \times \text{TRI} + \beta_2 \times \text{distance})$). The SLID model explicitly accounts for evidence-removal bias in collision-count data, but does not account for detection error. Thus, our spatially-explicit models portray relative collision risk rather than absolute risk. Moreover, the predicted number of collisions for each 30-m pixel is entirely dependent on fence presence; obviously, not all pixels across the landscape have fences present. Lastly, we used an example collision-risk threshold of >1 collision/lekking season, and calculated the proportion of the 30-m pixels with a collision risk above this value for each state.

## RESULTS

Modeling identified TRI and distance to lek effects on collision rates, and regional differences in removal of collision evidence ($\Delta$AIC = 0; Table 1). The top model suggested collision decreased with increasing TRI ($\beta = -0.25$; 95% CI = $-0.48$ to $-0.10$; Fig. 2) and increasing distance from the nearest sage-grouse lek ($\beta = -0.0006$; 95% CI = $-0.00115$ to $-0.00008$; Fig. 2). Thus, an increase in topographic variation at a site and moving farther from a lek location strongly reduced the number of collisions predicted over a lekking season (Fig. 2), and sites predicted to be high risk were concentrated on flat areas in relatively close proximity to leks (Fig. 3). Goodness-of-fit testing failed to

**Table 1.** Model rankings for the stochastic linear-immigration-death model fit to the greater sage-grouse fence-collision data set from southern Idaho, USA. Covariates were size of nearest lek (lsize), distance to nearest lek (dist), terrain ruggedness index (TRI), and region (SE ID = 1, Magic Valley = 0; Stevens et al. 2011). Models were ranked and compared using Akaike's Information Criterion (AIC; Akaike 1973).

| Model[a,b] | *K*[c] | $\Delta$AIC | AIC |
|---|---|---|---|
| $\theta$(TRI + distance) $\psi$(region) | 5 | 0 | 403.505 |
| $\theta$(TRI + lsize + distance) $\psi$(region) | 6 | 1.582 | 405.086 |
| $\theta$(TRI) $\psi$(region) | 4 | 3.153 | 406.658 |
| $\theta$(TRI + lsize) $\psi$(region) | 5 | 4.581 | 408.086 |
| $\theta$(distance) $\psi$(region) | 4 | 12.210 | 415.715 |

[a] Model form is $\log(\theta) = \beta_0 + \beta_1 Y_1 + \ldots + \beta_k Y_k$ and $\log(\psi) = \gamma_0 + \gamma_1 Y_1 + \ldots + \gamma_k Y_k$, where $\theta$ = daily collision rate and $\psi$ = per capita daily removal rate (Stevens and Dennis 2013).

[b] All top models were fit using the transient joint likelihood for collision-count observations after the first sampling occasion (Stevens and Dennis 2013). No models fit using the stationary joint likelihood for all count observations were supported by the data ($\Delta$AIC > 19).

[c] *K* = no. of model parameters.

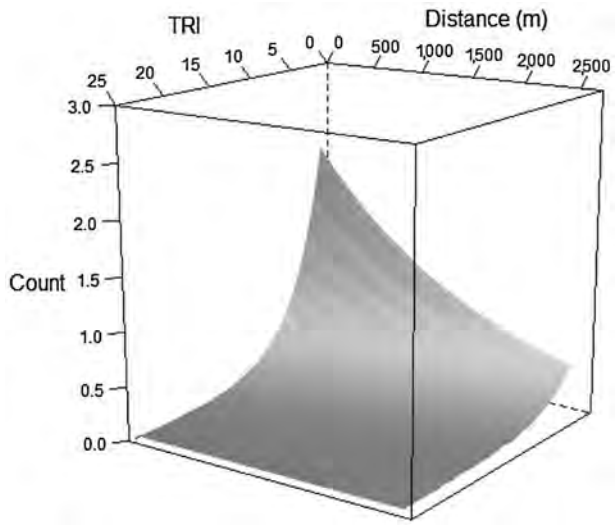



**Figure 2.** Maximum-likelihood estimates of total number of greater sage-grouse fence collisions over the 78-day lekking season from the top stochastic-linear-immigration-death model fit to data from southern Idaho, USA. Collision was a function of terrain ruggedness (TRI) and distance to the nearest lek. Maximum-likelihood estimates of total collisions from the top model = $78 \times \exp\{\beta_0 + \beta_1 \times \text{TRI} + \beta_2 \times \text{distance}\}$.

reject the hypothesis that the top model fit the data ($P = 0.16$, $\chi^2_{249} = 271.22$), and cross-validated prediction error was similar among top three models (range = 0.634–0.648). The raster regression models demonstrated the large variability of predicted collisions per 30-m pixel across the landscape, and suggested that a relatively small proportion of the total landscape (6–14%) in each state would result in >1 collision over a lekking season (Fig. 3; Table 2). Despite spatial variation in collision risk, Idaho, South Dakota, California, Montana, and Oregon all had >10% of their area within 3 km of active leks with >1 predicted collision over a lekking season (Table 2). Montana (465,631 ha), Wyoming (295,770 ha), and Idaho (214,184 ha) had the greatest total area with >1 predicted collision over a lekking season (Table 2). In contrast, Utah (6.3%), North Dakota (7.3%), and Washington (7.5%) had the lowest percentage of pixels within 3 km of leks with >1 predicted collision over a lekking season due to increased terrain ruggedness near lek locations (Table 2).

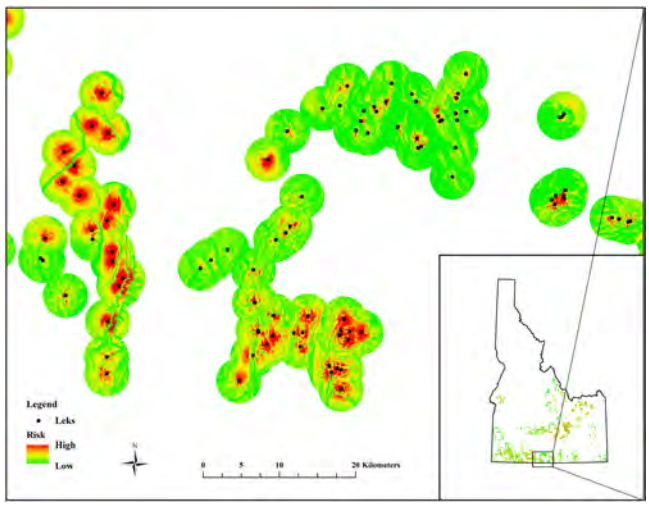



**Figure 3.** Example of spatially explicit fence-collision-risk maps from greater sage-grouse breeding habitats of southern Idaho, USA. Collision risk was a function of terrain ruggedness (TRI) and distance to the nearest lek. Maximum-likelihood estimates of total collisions (i.e., risk) from the top stochastic-linear-immigration-death model = $78 \times \exp\{\beta_0 + \beta_1 \times \text{TRI} + \beta_2 \times \text{distance}\}$.

## DISCUSSION

We created spatially explicit decision-support tools for wildlife and habitat managers who are marking fences to reduce sage-grouse collisions. Many previous avian-collision studies focused on known high-risk sites or used convenience-sampling methods to measure collision frequency, limiting generality of results and inferences. Moreover, rapid removal of collision remains can decrease accuracy of collision counts and bias estimates of collision totals (Smallwood 2007, Huso 2011, Stevens et al. 2011). We attempted to avoid pitfalls in study design by randomly sampling fences from sites spread across southern Idaho ($n$ = 14–16 sites; Stevens et al. 2012*a*), measuring evidence removal with field experimentation (Stevens et al. 2011), and combining these data sets to model collision ($\theta$) and removal ($\psi$) as a function of covariates using joint likelihood and generalized regression (Table 1). The models identified terrain ruggedness and distance from the lek metrics as drivers of fence-collision risk (Fig. 2; Stevens et al. 2012*a*). We hypothesize that collision risk is ultimately influenced by grouse flight behavior in flat terrain, where grouse fly low into leks before dawn and are thus vulnerable to colliding with fences. We found some evidence for the effect of lek size on collision ($\Delta$AIC = 1.5; Table 1). However, our analyses suggested topography and distance were better predictors of collision than counts of displaying males on leks. This does not necessarily mean that local abundance does not influence collision risk, and measurement error in lek count indices may have attenuated the estimated effect on collision. Moreover, other covariates influencing sage-grouse collision were intentionally excluded from our analyses because they were not available at the range-wide extent (e.g., fence density; Stevens et al. 2012*a*). Regardless, terrain ruggedness attenuated other covariate effects and drove collision risk to nearly zero at moderate–high values (Fig. 2).

This study bridges the research-implementation gap by working in partnership with managers implementing mitigation measures to design user-friendly maps that suggest where targeted investments could alleviate much of the breeding season collision risk, freeing up resources for more pressing conservation concerns (Knight et al. 2008, Black and Groombridge 2010). Our models suggest that most of the breeding-area landscape across the West has low collision risk. As such, these models facilitate appropriate regional-scale resource allocation, by suggesting that targeted marking efforts may be beneficial to sage-grouse but that marking efforts are not necessary near all leks. We developed these maps at broad scales using covariate data that are widely available (e.g., terrain ruggedness); additional

**Table 2.** Summary statistics from spatially explicit fence-collision models in sage-grouse breeding habitats across the western United States. Statistics are: mean and standard deviation (SD) of predicted collision count per 30-m pixel, percent of the landscape (i.e., percent of total pixels) with >1 predicted collision over the lekking season (% >1 collision), and the number of hectares within 3 km of known leks (i.e., no. of pixels × 0.09 ha/pixel) with >1 predicted collision over the lekking season for each state. Both the percent of landscape and total area (ha) with >1 predicted collision over the lekking season are predicated on the presence of fence in each 30-m pixel.

| State | $\bar{x}$ | SD | % > 1 collision[a] | Area (ha) > 1 collision |
|---|---|---|---|---|
| ID | 0.509 | 0.472 | 14.413 | 214,184 |
| SD | 0.563 | 0.413 | 13.107 | 6,933 |
| CA | 0.426 | 0.450 | 11.381 | 15,303 |
| MT | 0.477 | 0.415 | 11.157 | 465,631 |
| OR | 0.435 | 0.436 | 10.886 | 91,305 |
| WY | 0.422 | 0.403 | 9.239 | 295,770 |
| NV | 0.393 | 0.399 | 8.544 | 107,758 |
| WA | 0.397 | 0.375 | 7.531 | 4,715 |
| ND | 0.394 | 0.376 | 7.330 | 3,964 |
| UT | 0.319 | 0.369 | 6.264 | 28,380 |

[a] Max. of the predicted no. of collisions per 30-m pixel over a breeding season = 3.027 birds.

information at local scales (e.g., fence locations or densities, local space use) can be used to further inform management actions. Thus, our models can be used for local-scale planning by managers working in conjunction with local working groups and private landowners. Moreover, these models enable the linkage of management action to collision risk, which promotes effective resource use and minimizes the inefficient strategies of mitigating collision risk randomly or everywhere (Black and Groombridge 2010). Lastly, our example threshold of >1 collision/season was somewhat arbitrary, and maps with any desired risk threshold could be constructed in a GIS to delineate areas for fence marking or moving.

Our models provide a useful tool but they should also serve as testable hypotheses, and model validation is a valuable next step because spatial extrapolation and simplifying assumptions can lead to erroneous predictions (Miller et al. 2004). A model predicting blue crane (*Anthropoides paradiseus*) powerline collision in South Africa did not successfully predict high-risk sites (Shaw et al. 2010), but the model was based on expert opinion instead of a designed field study. Our model projected predictions at the 1 × 1-km scale onto 30-m pixels across sage-grouse breeding habitats, and with the exception of distance to lek, we assumed collision risk was independent of each pixel's position on the landscape, both of which could induce error in spatial extrapolation (Miller et al. 2004). Our models also extrapolated collision risk observed in Idaho to other western states, implicitly assuming the relationship observed between collision risk, terrain ruggedness, and lek location remains similar in other regions (Miller et al. 2004). However, prioritizing management actions using the best available science is better than proceeding with mitigation in an unorganized fashion (Miller et al. 2004). Moreover, our results are predicated on the presence of fences at each 30-m pixel. Thus, the true total area (i.e., no. of ha) of high collision risk in sage-grouse breeding areas will likely be considerably less than our models predicted because fences are not present at all sites. Lastly, our spatially-explicit models do account for removal error, but do not account for detection error and thus produce predictions of relative collision frequency over a breeding season. Predictions of relative collision frequency and cross-scale extrapolation of predictions complicate the assessment of demographic effects on grouse populations. Hierarchical statistical models for avian-collision data incorporating both detection and evidence-removal error are a necessary next step that should facilitate predictions of the absolute number of collisions over time as a function of covariates.

We caution readers against making direct inferences to population-level benefits resulting from reduced sage-grouse collision risk. We cannot say, for example, how many sage-grouse would be added to a population by reducing collisions because we lack demographic data to know whether populations can compensate for mortality via increased productivity. Population-level impacts of sage-grouse fence collision also likely depend on proportional mortality of male and female grouse, which is currently unknown (Stevens et al. 2012*a*). Moreover, the ability to compensate for collision mortality probably varies spatially, further complicating our ability to predict the number of birds added to a population as a result of fence-marking efforts. Future work addressing demographic consequences of sage-grouse collision and the conditions under which we would expect additive collision mortality should be a research priority.

## MANAGEMENT IMPLICATIONS

These findings help guide implementation of the Natural Resources Conservation Service's Sage Grouse Initiative and provide decision support to others working in sage-grouse conservation. We attempted to bridge the research-implementation gap by applying our model to 4,684 known lek sites across 10 western states, and provided our GIS-based tool to Natural Resources Conservation Service practitioners and the state wildlife managers responsible for management of sage-grouse populations. Managers can use this tool to identify high-risk fences and to build new fences away from high-risk areas while still accomplishing grazing objectives. To facilitate use we also developed a how-to instructional guide and conducted multiple web-based training sessions. Lastly, we made our decision-support tool

available to the Bureau of Land Management, the federal agency managing >50% of remaining sage-grouse habitats and currently revising their land-use plans for lands that include sage-grouse habitat. We encourage those interested in sage-grouse conservation to contact their state fish and wildlife agency to learn how to obtain a copy of the decision-support tool. Lastly, we remind managers that fence marking in other seasonal habitats, including areas of high sage-grouse concentration during winter, could potentially reduce fence strikes, but resulting benefits have not been measured.

## ACKNOWLEDGMENTS

Funding for this project was provided by the Natural Resources Conservation Service's Sage Grouse Initiative. We thank everyone involved in the various parts of this research: D. Ayers, J. Baumgardt, R. Berkeley, C. Cardinal, L. Cross, C. Earle, C. Hendricks, S. Jackson, A. Locatelli, J. Maestas, P. Makela, A. Moser, N. Muhn, D. Musil, R. Smith, and M. Szczypinski. We thank J. Evans, K. Nicholson, and E. Strand for GIS support and advice during this work. We also thank J. Evans for hosting the site where managers can download GIS shape files, and the 10 state fish and wildlife agencies that provided baseline lek database files for our analyses. Lastly, this manuscript was greatly improved by suggestions from J. Buchanan and 2 anonymous reviewers. Data used for our analyses were contributions from Idaho Federal Aid in Wildlife Restoration Project W-160-R.

## LITERATURE CITED

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Czáki, editors. Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary.

Baines, D., and M. Andrew. 2003. Marking of deer fences to reduce frequency of collisions by woodland grouse. Biological Conservation 110:169–176.

Baines, D., and R. W. Summers. 1997. Assessment of bird collisions with deer fences in Scottish forests. Journal of Applied Ecology 34:941–948.

Barrientos, R., J. C. Alonso, C. Ponce, and C. Palacín. 2011. Meta-analysis of the effectiveness of marked wire in reducing avian collisions with power lines. Conservation Biology 25:893–903.

Bevanger, K. 1998. Biological and conservation aspects of bird mortality caused by electricity power lines: a review. Biological Conservation 86: 67–76.

Bevanger, K., and H. Brøseth. 2000. Reindeer *Rangifer tarandus* fences as a mortality factor for ptarmigan *Lagopus* spp. Wildlife Biology 6:121–127.

Black, S., and J. Groombridge. 2010. Use of a business excellence model to improve conservation programs. Conservation Biology 24:1448–1458.

Bottrill, M. C., L. N. Joseph, J. Carwardine, M. Bode, C. Cook, E. T. Game, H. Grantham, S. Kark, S. Linke, E. McDonald-Madden, R. L. Pressey, S. Walker, K. A. Wilson, and H. P. Possingham. 2008. Is conservation triage just smart decision making? Trends in Ecology and Evolution 23:649–654.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139–156.

Brown, W. M., and R. C. Drewien. 1995. Evaluation of two power line markers to reduce crane and waterfowl collision mortality. Wildlife Society Bulletin 23:217–227.

Catt, D. C., D. Dugan, R. E. Green, R. Moncrieff, R. Moss, N. Picozzi, R. W. Summers, and G. A. Tyler. 1994. Collisions against fences by woodland grouse in Scotland. Forestry 67:105–118.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater-sage grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, unpublished report, Cheyenne, Wyoming, USA.

Garton, E. O., J. W. Connelly, J. S. Horne, C. A. Hagen, A. Moser, and M. A. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Pages 293–381 *in* S. T. Knick, and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series, Vol. 38. University of California Press, Berkeley, USA.

Huso, M. M. 2011. An estimator of wildlife fatality from observed carcasses. Environmetrics 22:318–329.

Janss, G. F. E. 2000. Avian mortality from power lines: a morphologic approach of a species-specific mortality. Biological Conservation 95:353–359.

Knick, S. T., and S. E. Hanser. 2011. Connecting pattern and process in greater sage-grouse populations and sagebrush landscapes. Pages 383–405 *in* S. T. Knick, and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, Vol. 38. University of California Press, Berkeley, USA.

Knick, S. T., S. E. Hanser, R. F. Miller, D. A. Pyke, M. J. Wisdom, S. P. Finn, E. T. Rinkes, and C. J. Henney. 2011. Ecological influence and pathways of land use in sagebrush. Pages 203–251 *in* S. T. Knick, and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, Vol. 38. University of California Press, Berkeley, USA.

Knight, A. T., R. M. Cowling, M. Rouget, A. Balmford, A. T. Lombard, and B. M. Campbell. 2008. Knowing but not doing: selecting priority conservation areas and the research-implementation gap. Conservation Biology 22:610–617.

Matis, J. H., and T. R. Kiffe. 2000. Stochastic population models: a compartmental perspective. Springer lecture notes in statistics. Springer-Verlag, New York, New York, USA.

Miller, J. R., M. G. Turner, E. A. H. Smithwick, C. L. Dent, and E. H. Stanley. 2004. Spatial extrapolation: the science of predicting ecological patterns and processes. BioScience 54:310–320.

Morkill, A. E., and S. H. Anderson. 1991. Effectiveness of marking powerlines to reduce sandhill crane collisions. Wildlife Society Bulletin 19:442–449.

Patten, M. A., D. H. Wolfe, E. Shochat, and S. K. Sherrod. 2005. Habitat fragmentation, rapid evolution and population persistence. Evolutionary Ecology Research 7:235–249.

R Core Development Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:23–27.

Savereno, A. J., L. A. Savereno, R. Boettcher, and S. M. Haig. 1996. Avian behavior and mortality at power lines in coastal South Carolina. Wildlife Society Bulletin 24:636–648.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

Shaw, J. M., A. R. Jenkins, J. J. Smallie, and P. G. Ryan. 2010. Modelling power-line collision risk for the blue crane *Anthropoides paradiseus* in South Africa. Ibis 152:590–599.

Smallwood, K. S. 2007. Estimating wind turbine-caused bird mortality. Journal of Wildlife Management 71:2781–2791.

Stevens, B. S. 2011. Impacts of fences on greater sage-grouse in Idaho: collision, mitigation, and spatial ecology. Thesis, University of Idaho, Moscow, USA.

Stevens, B. S., J. W. Connelly, and K. P. Reese. 2012*a*. Multi-scale assessment of greater sage-grouse fence collision as a function of site and broad scale factors. Journal of Wildlife Management 76:1370–1380.

Stevens, B. S., and B. Dennis. 2013. Wildlife mortality from infrastructure collisions: statistical modeling of count data from carcass surveys. Ecology doi: 10.1890/12-1052.1

Stevens, B. S., K. P. Reese, and J. W. Connelly. 2011. Survival and detectability bias of avian fence collision surveys in sagebrush steppe. Journal of Wildlife Management 75:437–449.

Stevens, B. S., K. P. Reese, J. W. Connelly, and D. D. Musil. 2012*b*. Greater sage-grouse and fences: does marking reduce collisions? Wildlife Society Bulletin 36:297–303.

Wolfe, D. H., M. A. Patten, and S. K. Sherrod. 2009. Reducing grouse collision mortality by marking fences. Ecological Restoration 27: 141–143.

Wolfe, D. H., M. A. Patten, E. Shochat, C. L. Pruett, and S. K. Sherrod. 2007. Causes and patterns of mortality in lesser prairie-chickens *Tympanuchus pallidicinctus* and implications for management. Wildlife Biology 13(Supplement 1):95–104.

*Associate Editor: Buchanan.*

# Viability analyses for conservation of sage-grouse populations:

# Buffalo Field Office, Wyoming

**Final Report**

**27 February 2012**

**Prepared for Bureau of Land Management**

**Buffalo Field Office**

**Buffalo, Wyoming**

**by**

**Rebecca L. Taylor, David E. Naugle and L. Scott Mills**

**Wildlife Biology Program**

**University of Montana**

**BLM Contract 09-3225-0012**

**Number G09AC00013 (8/10/10)**

## EXECUTIVE SUMMARY

Impacts from energy development to sage-grouse (*Centrocercus urophasianus*) present a challenge to public land managers tasked with maintaining large and intact landscapes that support viable populations. We provide decision support to Bureau of Land Management (BLM) managers tasked with maintaining sage-grouse populations in the oil and gas (energy) fields of northeast Wyoming by assessing four aspects of energy development as they relate to sage-grouse. Findings reflect the status of a small remaining sage-grouse population that has already experienced an 82% decline within the expansive energy fields (Walker et al. 2007a), a level of impact that has severely reduced options for delineating core areas that are large enough and in high enough quality habitats to sustain populations.

1) We identified the spatial scale at which energy development most influences sage-grouse populations, as indexed by counts of males at leks. Ignoring state boundaries to include counts from unimpacted leks in Montana was critical to identifying the far reaching impacts of development on grouse in Wyoming. Using a statistical technique (AIC, Burnham and Anderson 1998) that is akin to using a dial to tune a radio to pick up the strongest signal, we detected that development had the greatest influence on male counts within 12.4 mi (20 km) surrounding a lek. The signal is much stronger at the 12.4-mi radius than any of the smaller radii we tested, encompassing a large spatial scale that covers an area of 483 $mi^2$ (1,257 $km^2$).

2) We evaluated the current viability of sage-grouse populations. We linked lek count data to energy development and West Nile virus (WNv) by associating the density of producing wells within the 12.4-mi (20-km) radius to each lek count, and the occurrence of widespread WNv outbreaks in the year preceding the count. Predictions of resulting male lek counts were

consistently within 0 to 1% of the observed counts, underscoring the success of our approach (Table 2).

Declines in number of active leks and number of attending males indicate that both energy development and WNv outbreaks reduce sage-grouse populations. At current well spacing (328 ac spacing, 0.75 wells/km$^2$) and without accounting for WNv outbreaks, our predicted number of males on leks is 3,648 (95% CIs = 3,147, 4,204, Table 3). Absent an outbreak year, the lower 95% confidence limit on the count is 3,147 males, suggesting that immediate extirpation of the northeast Wyoming population is unlikely if all environmental conditions for sage-grouse other than energy development remain favorable.

Wyoming's core area policy will be most effective where implemented in advance of extensive energy development, and in southwest portions of the state where high elevation populations are less susceptible to WNv impacts. But in northeast Wyoming, WNv outbreak years are the wild card in core area management, and predictions made without accounting for WNv are optimistically high. The effect of a WNv outbreak year alone can more than cut a population in half, which is similar to drilling an undeveloped landscape at 4-8 wells/mi$^2$ (1.5-3.1 wells/km$^2$, Table 3). When we include impacts of an outbreak year at all leks, we predict 1,473 males given current well densities (Table 3). With outbreak years as part of the equation, the lower confidence limit on our prediction is 65 males, which, if reached, would indicate functional extinction. Incorporating outbreaks into analyses suggests that even with no additional energy development many local populations may be one bad WNv year away from extirpation.

3) We formulated and simulated potential, realistic future management scenarios for sage-grouse populations, using the models we developed above to evaluate viability. Our results

suggest that if development continues, future viability of the already small sage-grouse populations in northeast Wyoming will be compromised. Small populations are vulnerable to extirpation by chance events (Soule and Mills 1998), and WNv outbreaks are an excellent example of this type of catastrophic event. Despite impacts, the potential may still exist to maintain a population inside core areas, but further drilling in and around cores will compromise their remaining value. Notably, core areas in northeast Wyoming were delineated after widespread development had already occurred, leaving few options for conserving populations. Our findings do not negate the benefits of core areas, in general. However, to achieve maximum effectiveness, core areas must be constructed proactively by conserving high quality habitat, not reactively by drawing borders around planned and existing development.

4) We provide recommendations for evaluating the future viability of sage-grouse populations if restoration efforts begin as the energy play subsides. First and foremost we recommend that BLM commit to monitoring outcomes of restoration as measured by the distribution and number of sage-grouse in northeast Wyoming. Focusing restoration where plugged and abandoned wells are clustered would increase the size of habitats available to birds, thus enhancing the chance of increasing their abundance and distribution. Leaving energy infrastructure such as roads, power lines, and water impoundments on the landscape for other purposes is an unintended impact of development that will compromise restoration success. Appropriate monitoring of leks as wells are removed from production is imperative to allow for a rigorous analysis of restoration success, which cannot be supported by currently available data. Lek counting needs to be conducted at least across the area of northeast Wyoming, and preferably across the entire study region including eastern Montana (Fig 1).

Genetic connectivity is the glue that holds populations together, and remaining core areas, though impacted, may help maintain connectivity among populations further south in Wyoming and those in Montana. Until genetic studies currently underway delineate the degree to which sage-grouse populations are connected, we recommend maintaining the potential areas of connectivity outlined in the Wyoming Governor's Executive Order as undeveloped, contiguous habitat.

## INTRODUCTION

Conservation strategies that target single stressors may be inadequate because they fail to account for the multiple factors at play in ecological systems. Energy development is an ongoing stressor to wildlife populations on public lands throughout the West (McDonald et al. 2009), and in 2002, West Nile virus (WNv) emerged as an additional stressor to these populations (Centers for Disease Control 2010). Given the anticipated magnitude of energy development impacts, identifying and prioritizing lands with low human disturbance is critical for the Bureau of Land Management (BLM) to follow its multiple use mandate (Federal Land Policy and Management Act 1976) by conserving some areas while developing others. The management challenge will be to site future developments in such a way that large, intact landscapes can maintain their biological functions (Kiesecker et al. 2010), even in the presence of multiple stressors such as development and WNv.

The sagebrush (*Artemisia* spp.) ecosystem in the West is representative of the struggle to maintain wildlife populations in a landscape that bears the debt of our ever-increasing demands for natural resources (Knick et al. 2003). The greater sage-grouse (*Centrocercus urophasianus*, hereafter 'sage-grouse') is a landscape species that requires large, intact expanses of sagebrush

habitat during every part of its life cycle to maintain robust populations (Connelly et al. 2011). As a result, the sage-grouse is an umbrella species that represents the conservation needs of many other species that also depend on sagebrush (Hanser and Knick 2011). Loss and degradation of sagebrush habitat has resulted in at least a four decade long sage-grouse population decline (Connelly et al. 2004, Garton et al. 2011) and extirpation of the species from ≥ 46% of its original range (Schroeder et al. 2004).

Wyoming provides habitat for nearly two-thirds of the sage-grouse occupying the eastern portion of their range, and landscapes being developed for energy extraction contain some of the highest sage-grouse abundances in North America (Doherty et al. 2011). The surge in energy development over the past decade (Naugle et al. 2011a) has resulted in rapid, large-scale changes in portions of northeast Wyoming, and a growing recognition of the need to fully understand and monitor potential impacts to wildlife populations.

The potential for management to influence populations is large, and a method currently in place for conserving sage-grouse populations is the core area concept. Core areas have been designated by the state of Wyoming as priority areas for sage-grouse conservation, and by Governor's order, new energy development is limited to one oil or gas well pad per square mile, on average, and a 5% total disturbance cap (EO 201105). Core areas result in a smaller energy footprint than would otherwise occur and provide an avenue for partners to maximize their conservation investments by targeting them within priority landscapes (Copeland et al. 2011, Kiesecker et al. 2011). Conservation planning is most effective when implemented before the number and extent of impacts limit options for maintaining large and intact landscapes that support populations. Large core areas containing a majority of sage-grouse populations in southern and southwest Wyoming were delineated before energy fields became large and

abundant. In contrast, the sizes, shapes and locations of core areas in northeast Wyoming were chosen after substantial energy development had already taken place. From 2001 to 2005, sage-grouse populations declined by 82% within the expansive coal bed natural gas fields (Walker et al. 2007a) in northeast Wyoming, further reducing options for delineating large and intact core areas containing an abundance of high quality sage-grouse habitats. As a result, questions remain regarding the ability of core areas in northeast Wyoming to support viable sage-grouse populations.

For management-oriented science to be of maximum use, it must be conducted at a spatial scale large enough to capture how population status has changed in response to stressors that vary in intensity, both locally and regionally. The goal of management-oriented science is to connect the dynamics of focal species, either likelihood of extirpation or potential for recovery, to actions that managers can implement on the ground to maintain or enhance populations. In practice, however, land management actions are often implemented without a clear connection to how those actions affect the dynamics of the wildlife population of interest. This is particularly true when managers must try to counteract multiple stressor impacts, because the science on which this management is based is often conducted at too small a spatial scale to capture populations responding to multiple stressors that vary in intensity over a large area. Furthermore, the disparity between the scale of individual management actions and the scale at which populations respond is a persistent problem in understanding impacts on population viability (Schultz 2010).

This report links sage-grouse counts and population dynamics with stressors to evaluate the viability of populations under future land use scenarios. Our objectives were to provide decision support to BLM officials at field office, state and national levels by 1) identifying the spatial

scale at which energy development most influences populations, 2) evaluating current viability of sage-grouse populations in northeast Wyoming, 3) formulating and simulating potential, realistic future management scenarios for populations and 4) providing recommendations to evaluate the future viability of sage-grouse populations as the oil and gas play subsides and wells are plugged and abandoned.

## Literature Synthesis

Oil and gas development and WNv are the primary large-scale factors impacting sage-grouse populations in northeast Wyoming. Together, these factors represent large-scale stressors that limit populations and options available to managers to maintain and enhance bird numbers on public lands. Below we synthesize the current scientific literature to provide readers with an understanding of the biological response of sage-grouse populations to these two factors.

### Oil and Gas Development

Oil and gas (energy) development has emerged as a range-wide issue in conservation because areas being developed contain large sage-grouse populations (Connelly et al. 2004) and other sagebrush obligate species (Knick et al. 2003). Breeding sage-grouse populations are severely impacted at oil and gas well densities commonly permitted in Wyoming (Naugle et al. 2011b). Impacts have been indiscernible at < 1 well/mi$^2$ (0.4 wells/km$^2$), but above this threshold, lek losses have been 2-5 times greater inside than outside of development, and abundance at remaining leks declines by 32 to 77% (Doherty et al. 2010). Magnitude of losses vary from one field to another, but impacts are universally negative and typically severe (Harju et al. 2010). High site fidelity, but low survival of adult sage-grouse combined with lek avoidance by younger birds (Holloran et al. 2010) results in time lags of 2-10 years between onset of development activities and local extirpation (Holloran 2005, Walker et al. 2007a, Harju et al. 2010). Energy

development also impacts sage-grouse habitats and vital rates outside the breeding season away from leks. Vital rates are measures such as nest success, hatching and survival which indicate the nature of and possible changes in a population (Taylor et al. 2012). Risk of chick mortality is 1.5 times higher for each additional well site visible within 0.6 mi (1 km) of brood locations compared to random locations (Aldridge and Boyce 2007), and sage-grouse avoid otherwise suitable winter habitat disturbed by energy development (Doherty et al. 2008, Carpenter et al. 2010).

Previous estimates of the spatial extent of oil and gas impacts on sage-grouse have differed depending on whether or not the study region included large, undeveloped areas. Research in already developing locales (Holloran 2005, Walker et al. 2007a, Harju et al. 2010) has detected impacts at smaller spatial extents than have regional studies (Tack 2009, Johnson et al. 2011). Energy impacts in Wyoming's Pinedale anticline were not detectable beyond 4 mi (6 km) from the lek (Holloran 2005); whereas effects across the Great Plains and Wyoming Basin might extend to a distance of 12 mi (20 km, Johnson et al. 2011). Distance from lek to development that explained the most variation in the Powder River Basin (WY and MT) lek counts were 0.5 mi (0.8 km) and 2 mi (3.2 km, Walker et al. 2007a) versus 7.6 mi (12.3 km) across the sage-grouse range of Montana (Tack 2009).

West Nile Virus

West Nile virus emerged as a threat to sage-grouse in 2002 and is now an important new source of mortality in low and mid-elevation populations throughout the West (Walker et al. 2011). West Nile virus simultaneously reduces juvenile, yearling, and adult survival, three vital rates important for sage-grouse population growth. Persistent low-level WNv mortality, combined with severe disease outbreaks, results in local and regional population declines

(Naugle et al. 2004, 2005). Mortality from this disease reduces growth rate of susceptible populations by an average of 6-9% per year (Walker and Naugle 2011), and lab experiments show 100% mortality following infection (Clark et al. 2006). Resistance to WNv in the wild is low (Walker et al. 2007b) and is expected to increase slowly over time (Walker and Naugle 2011). Eliminating mosquito breeding habitat from anthropogenic water sources is crucial for reducing impacts (Zou et al. 2006). Better range-wide data are needed on geographic and temporal variation in infection rates, mortality and seroprevalence.

West Nile virus is a particular problem because it is an exotic disease, and a species is more likely to become extinct in response to a threat that is new, and outside its evolutionary experience (Brook et al. 2008). Small, isolated and peripheral sage-grouse populations are most at risk from WNv, particularly those populations at lower elevations, and those experiencing large-scale increases in distribution of surface water (Walker et al. 2011). Despite the emergence of WNv over a decade ago, and the subsequent occurrence of two outbreak years, to date, lek analyses have averaged over WNv outbreak and non-outbreak years, potentially washing out the effect of a critical new stressor.

## METHODS

### Focal Area and Study Region

The focal area of our analyses, northeast Wyoming, is of particular management interest to the BLM's Buffalo Field Office for multiple reasons, including historically large sage-grouse populations and high realized levels of oil and gas development. Furthermore, sage-grouse have declined concomitant with oil and gas development and northeast Wyoming continues to have high potential for further development.

While our focal area is northeast Wyoming (Figs 1, 2), the study region that provided the strongest foundation for our analyses was the portion of Sage-grouse Management Zone I that lies south of US Hwy 2 (Fig 1). By including leks from areas beyond northeast Wyoming, such as unimpacted leks in eastern Montana, we were able to include a wide range of oil and gas development densities at both local and regional scales, and we maximized our ability to capture the effect of WNv outbreaks (Table 1). West Nile virus has been documented throughout the region in multiple species (Centers for Disease Control 2004), and in sage-grouse specifically in Montana, Wyoming and the Dakotas (Naugle et al. 2004, 2005, Walker et al. 2004, Walker and Naugle 2011). At the same time, our study region is composed of habitat similar to that found in the focal area it encompasses. This habitat is largely dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), with grass cover typical of the eastern portion of the sage-grouse range.

To best estimate the magnitude of development impacts, data must be collected across a range of development levels at both local and regional scales. Estimated development effects may be negatively or positively biased if the study region does not capture the full range of development intensities. Studies contained within already developing areas may incorrectly estimate the spatial extent and magnitude of energy impacts, as any truly landscape scale effects that exist may have already affected all leks in the area. If the spatial extent of impacts to leks is underestimated, the loss of birds may also be underestimated, as loss predictions will not account for impacts of more distant development. Alternatively the same underestimation of scale of impact might also lead to an *overestimate* of loss, as the leks deemed to not be impacted may actually lie on the periphery of development, and peripheral leks may increase in size, at least temporarily, due to the emigration of yearling grouse from highly developed areas to leks on the

edge of development (Holloran et al. 2010). Finally, studies that encompass large undeveloped areas, but only a few point sources of development may fail to capture the full extent of energy development impacts. To resolve these discrepancies of scale, a comprehensive analysis of sage-grouse lek response to energy development needs to be conducted at a scale large enough to encompass regional, as well as local variation in levels of energy development.

To capture the regional variation in lek size and natural landscape attributes, we divided the study region into the focal area (northeast Wyoming) and four supporting areas (Fig 1), based on the Western Association of Fish and Wildlife Agencies (WAFWA) subpopulation designations (Connelly et al. 2004). Our areas (followed by the WAFWA subpopulation name) are as follows: north-central MT (north-central MT), central MT (central MT), eastern MT (eastern interior MT/northeast tip WY), Dakotas (MT/ND/northwest SD) and northeast WY (northeast WY/southeast MT and Fall River SD/eastern edge WY). We combined the latter two because of the small size of the Fall River subpopulation and its proximity to the northeast WY/southeast MT subpopulation.

Notably, each of our areas is large, and the supporting areas contain a range of oil and gas development intensities (Table 1). This is critical for the analysis to correctly distinguish between regional variation in lek size and the variation in lek size due to intensity of oil and gas development. In contrast, each of the core areas in northeast Wyoming is much smaller, and contains little oil and gas development. As a result, we did not assign separate focal area status to each of the cores. Had we done so, we would have confounded area effects with oil and gas effects, negating the purpose of our analyses.

Table 1. Number of lek complex centers used in analysis from focal and supporting areas. Leks are categorized by presence of wells within best fit radius circle (12.4 mi, 20 km radius; Table 1 in Appendix II) and whether or not the most recent count occurred subsequent to a WNv outbreak year [see Results].

| | | Area | | | | | |
|---|---|---|---|---|---|---|---|
| WNv? | Wells? | NE WY | N-cnt MT | Cnt MT | E MT | DK | Category Total |
| No | No | 1 | 88 | 126 | 144 | 15 | 374 |
| No | Yes | 304 | 35 | 84 | 64 | 57 | 544 |
| Yes | No | 0 | 12 | 25 | 54 | 2 | 93 |
| Yes | Yes | 65 | 6 | 27 | 23 | 7 | 128 |
| Area Total | | 370 | 141 | 262 | 285 | 81 | 1,139 |

## Analytical Approaches to Assessing Viability

Count-based methods are used to evaluate size or growth rate of a population via counts of individuals in an area (Fedy and Aldridge 2011) and can be used to assess the effects of management actions or external stressors on viability, thereby connecting management to the dynamics, persistence, and recovery of wildlife populations (Morris and Doak 2002, Mills 2007). Ideally, managers would like extinction probabilities predicted over time based on the effects of different levels of oil and gas development on lek counts. However, data requirements for such an analysis are prohibitive (Fig 3), as they would have to simultaneously account for a stressor that varies markedly over time and space, as well as population indices that vary greatly over time, even in the absence of stressors such as oil and gas development. Just accounting for

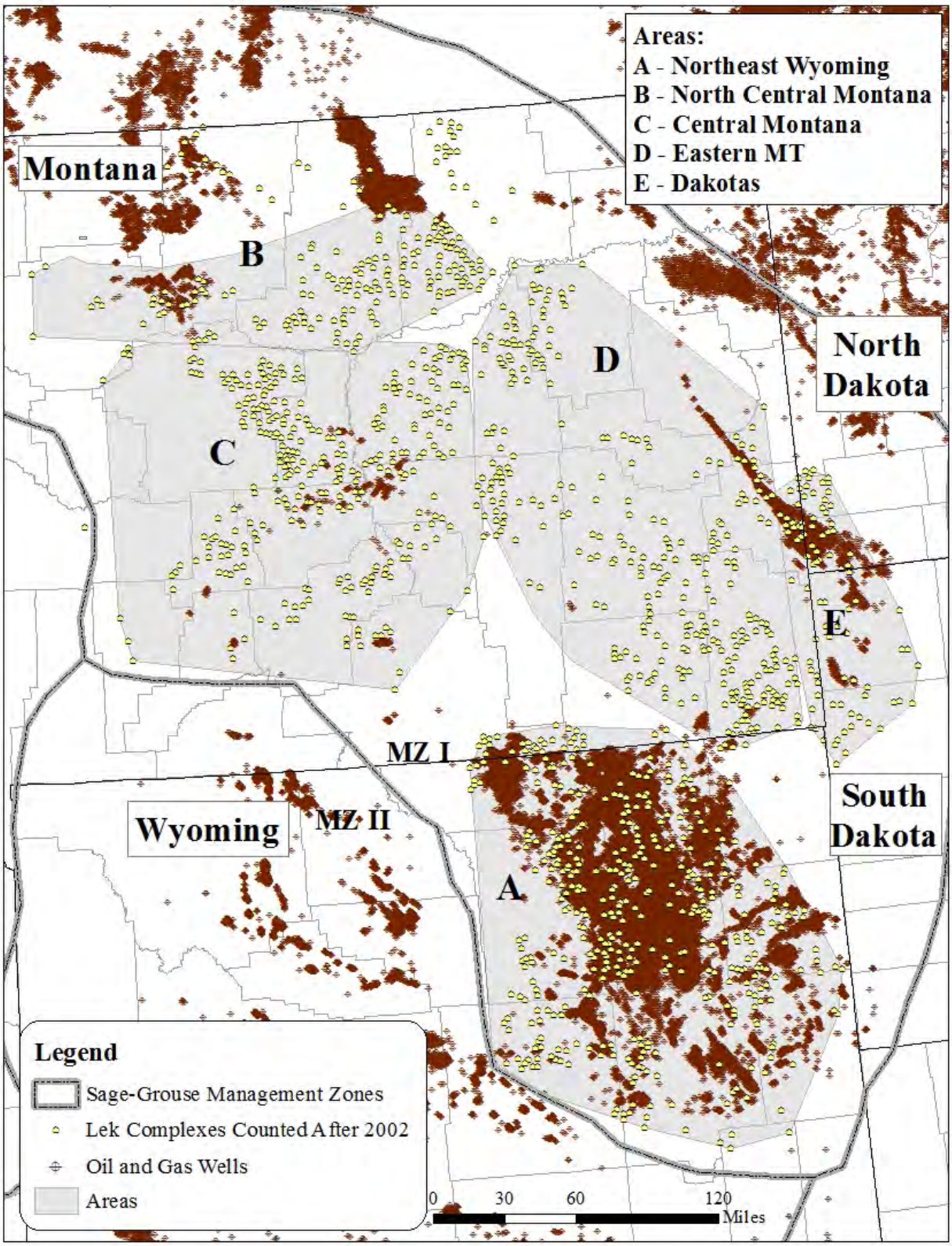



Figure 1. Distribution of oil and gas development and lek complex centers used in analysis with respect to focal and supporting areas.

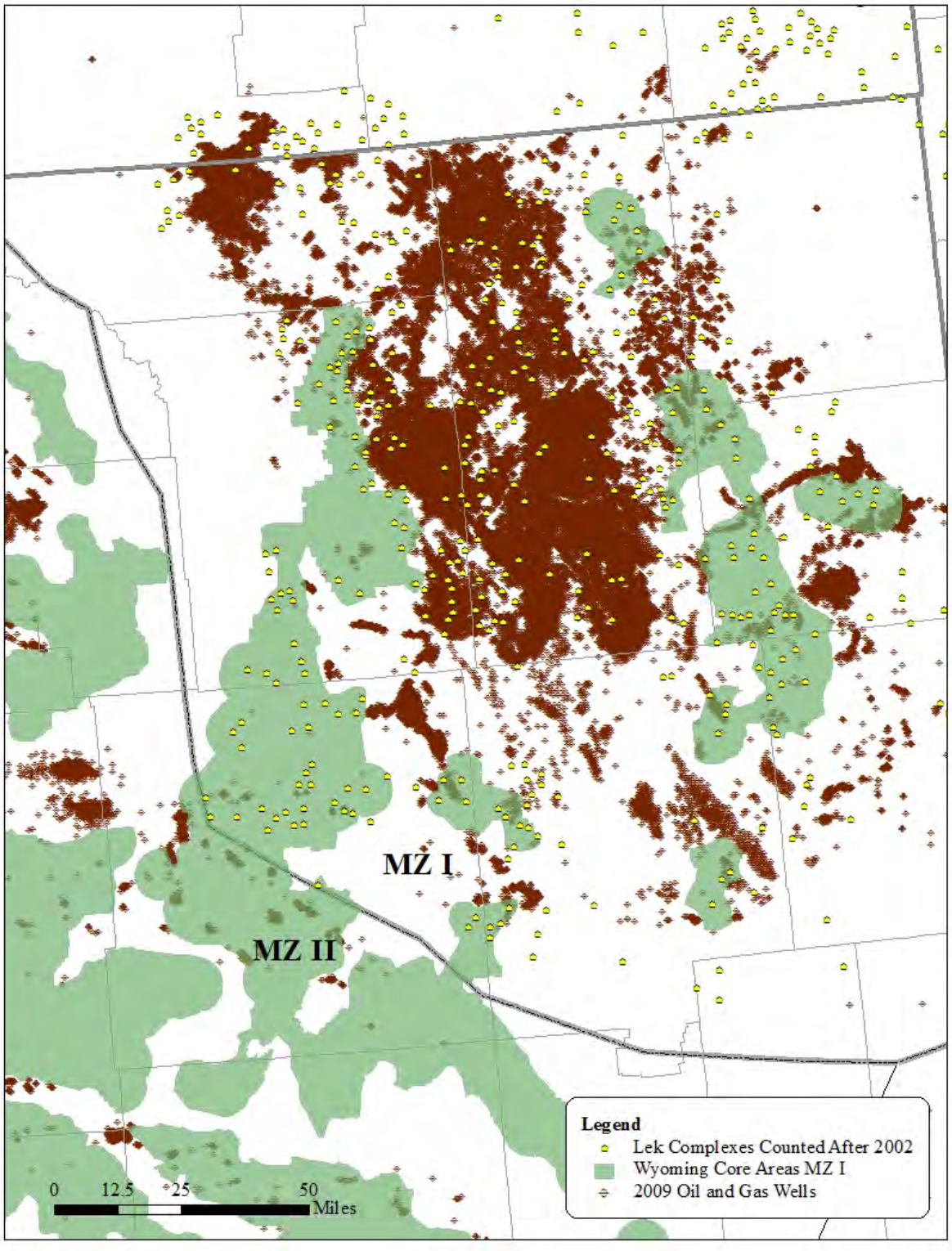



Figure 2. Distribution of oil and gas wells and lek complex centers used in the analysis with respect to northeast Wyoming core areas.

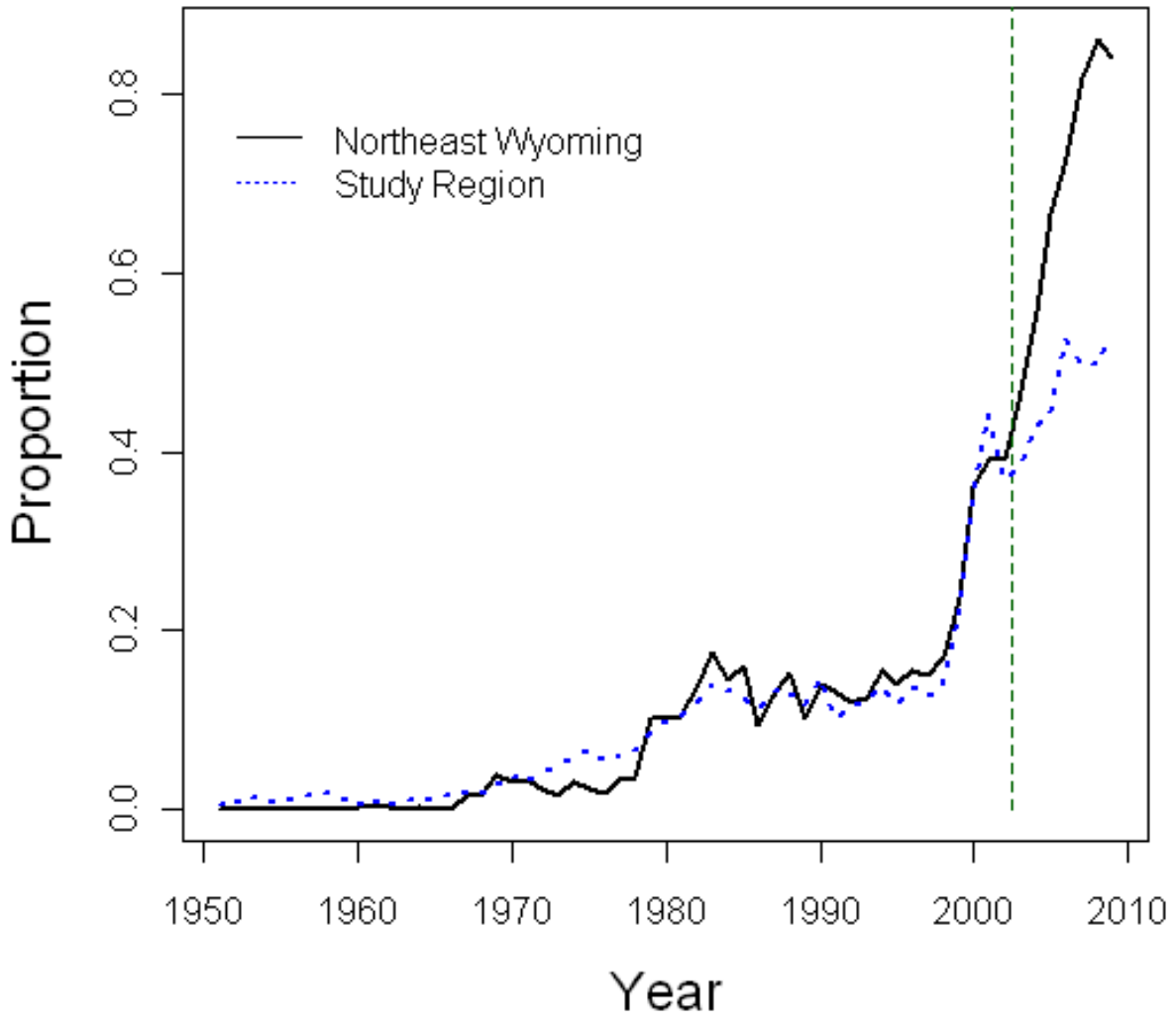



Figure 3. Proportion of lek centers in northeast Wyoming (n=428) and study region (n=1,508) counted during the year. Proportion of northeast Wyoming core area leks counted each year was similar to that in the focal area as a whole (difference < 0.07). Only counts to the right of the dashed line were used for analyses.

fluctuations in time (ignoring site and time specific stressors) requires multiple decades of annual counts (Fedy and Doherty 2010, Garton et al. 2011).

Because of the prohibitive data requirements for an analysis that is both spatially and temporally explicit, two approaches have been taken to evaluate lek counts: a cross-sectional approach that associates a lek count or lek growth rate with the stressors at its locale (Walker et al. 2007a, Harju et al. 2010) and a time series approach that averages counts over large geographic areas to reconstruct the necessary three (Fedy and Doherty 2010) to four (Garton et al. 2011) decade time series. With thirty consecutive years of spatially averaged counts, Fedy and Doherty (2010) used a time series approach to distinguish sage-grouse population cycles from long term population trend across the state of Wyoming. Forty consecutive years of spatially averaged counts allowed the estimation of population growth rate and carrying capacity in thirty populations from across the sage-grouse range (Garton et al. 2011). By adding an assumption that the past trend continues unchanged, these methods can also be used to predict an extinction probability. The time series approach has recently been applied to the Powder River Basin (Garton et al. 2011); however, the spatial averaging used to reconstruct long series of annual counts precluded associating stressors (e.g. oil and gas well density) with counts, and therefore made it impossible for the authors to determine the effect of these stressors on the population.

We took advantage of the large spatial extent of lek counts across our study region (which encompassed a wide range of development intensities) to successfully apply a cross-sectional approach to the data. We linked lek counts to oil and gas development and WNv by associating a well density and the occurrence of a WNv outbreak year with the most recent count at each lek since 2002, the time that WNv was first detected in the study region.

## Data

### Lek Counts

We defined a sage-grouse lek as a site where multiple males have been recorded displaying on multiple visits (Walker et al. 2007a). After obtaining lek count and location data from government agencies responsible for maintaining these databases, we checked the data for errors. We corrected errors, when possible, after consulting with agency personnel. We censored any leks where these errors could not be resolved, as well as any leks that were known to be destroyed by subdivision or mining. If a lek was counted multiple times within a year, we used the maximum count for that year.

Because leks often occur in a complex, that is multiple leks within 1.6 mi (2.5 km) of each other, we defined the largest and most regularly attended lek in the group as the complex center (Connelly et al. 2004). We used the count from each complex center to represent the entire complex, eliminating from the database the counts from the smaller, less regularly attended satellite leks. Hereafter, the term 'lek' refers to the sample unit of our analyses, which included complex centers and single leks that were not part of a complex. We used for each lek the most recent count that was collected from 2003-2009, except for leks known to have become inactive prior to 2003, which we excluded from our analyses. We chose the 2003 cutoff for two reasons. First, in spite of the dramatic increase in lek counting effort this decade, data are still too sparse (especially in the supporting areas) to use counts from only one calendar year. By using the most recent count since 2002, we provided a buffer of at least three relatively high effort years in which observers could ascertain the status of leks that may have become inactive during a time in which they were not regularly monitored.

Furthermore, because WNv is likely to remain a permanent feature of the sagebrush ecosystem, we restricted our study to years when the birds could at least potentially have been exposed to the virus. West Nile virus was first detected in the study region in 2002 (Centers for Disease Control 2010, Fig 4), but leks are counted in early spring, before the majority of WNv transmission occurs in late summer, thus the effects of the disease could not have been apparent in lek counts until spring 2003. By confining our analyses to 2003 and beyond, we ensured that it was at least possible for all birds counted to have been exposed to WNv.

Oil and Gas Development

We quantified energy development for active leks by the density of producing oil and gas wells at 6 scales around the lek as of April 1 in the year of the most recent count, and for leks that became inactive post-2002, as of April 1 in the year of the first zero count. Because of uncertainty about the scale at which sage-grouse show the greatest response to oil and gas development, we calculated the well density within the following radii of leks (in miles): 0.6, 2.0, 3.1, 6.2, 9.3 and 12.4 (in kilometers: 1, 3.2, 5, 10, 15 and 20). The 0.6 mi radius represents processes that impact breeding birds at or near leks (Walker et al. 2007a); the 2 mi radius has previously been used to predict the effects of oil and gas development on

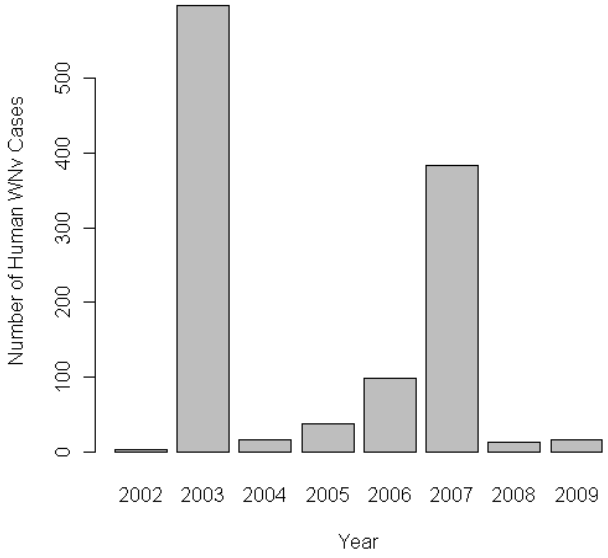



Figure 4. West Nile virus was first detected in the study region in 2002. Outbreaks occurred in 2003 and 2007.

lek counts (Doherty et al. 2010), the 9.3 mi radius should contain > 95% of nests of female grouse associated with the lek (Holloran and Anderson 2005, Tack 2009), and the 12.4 mi radius is the largest scale at which effects may have been detected in our study region (Johnson et al. 2011).

The 6.2 through 12.4 mi radii were also chosen to be larger than the estimated distance for potential edge effects to leks on the periphery of development. While previous studies have consistently demonstrated that leks less than ~ 2 mi (3 km) from oil and gas infrastructure have fewer males than those farther away (Walker et al. 2007, Harju et al. 2010, Holloran et al. 2010), evidence regarding the effect on leks between ~ 2-5 mi (3-8 km) from the nearest well pad is contradictory (Holloran et al. 2010). It is possible that leks on the periphery of development show at least temporary increases from males emigrating away from the center of development, and the upper 95% confidence limit for the mean distance from well pad to lek at which these effects occur is 4.7 mi (7.6 km, Holloran et al. 2010). While assigning outside development status to leks as close as 4.7 mi to a well pad might result in an over-inflated estimate of the count at an 'unimpacted' lek, it is unlikely that the larger scales we tested would be so affected.

West Nile Virus

West Nile virus outbreaks (Fig 4) in sage-grouse were documented in the summer of 2003 (Naugle et al. 2004, 2005, Walker et al. 2004) and the summer of 2007 (Walker and Naugle 2011) in intensively studied populations in Montana, Wyoming, and South Dakota. Because these outbreaks had the potential to affect spring 2004 and 2008 lek counts, respectively, we assigned positive outbreak status to each lek whose count used in the analyses occurred in 2004 or 2008. Although the rest of the document will refer simply to 'WNv outbreak' years, we note that other environmental variables (e.g., drought, low grass height) may have been associated

with those years and may partly explain the population-level effects that occurred during WNv outbreak years.

Statistical Analyses

We analyzed the lek count data in two steps. First, we determined the scale of greatest impact for oil and gas development; and second, we conducted a multiple regression of male counts against the density of oil and gas wells (at its chosen scale) and a factor variable indicating whether or not the count was associated with a WNv outbreak year. Focal and supporting areas were allowed to have their own intercepts. We used a zero-inflated negative binomial error structure (Bolker 2008) and conducted model selection using Akaike's information criterion (AIC, Burnham and Anderson 1998). Detailed methods are provided in Appendix I.

## RESULTS

### Comparison of Actual Counts to Predicted Counts under Current Conditions

Oil and gas development and WNv were related to recent counts of sage-grouse throughout the study region. By building the model with data from the entire study region, and then applying the model to our northeast Wyoming focal area, we developed predictions of present lek count numbers, past numbers that would have been likely before the influence of stressors, and future numbers that would be likely under different

Table 2. Predicted counts for all areas were within 1% of actual counts.

| | Total Male Count | |
|---|---|---|
| Area | Predicted | Actual |
| Northeast Wyoming | 3,315 | 3,316 |
| Central Montana | 3,661 | 3,693 |
| Eastern Montana | 2,789 | 2,770 |
| Dakotas | 661 | 659 |
| North-central Montana | 3,656 | 3,681 |

management scenarios. Underscoring the success of this approach is that the predicted male lek counts, based purely on the model, were consistently within 0 to 1% of the actual lek counts for the focal and supporting areas (Table 2). In particular, our model predicted a total of 3,315 males in northeast Wyoming, and 3,316 males were actually counted at leks. In short, we have high confidence that the use of the data from throughout the study region (Table 1, Fig 1) to link stressors to abundance is useful in making inferences about processes in northeast Wyoming.

## Effects of Stressors

If we dial to zero the amount of energy development present in an area, we are, in practice, asking what the lek counts would have been in that area at a time in the past, before the stressor occurred. For simplicity, we can consider a range of possibilities from 'bad' to 'good' years, with WNv outbreaks being the primary driver of bad years. Thus, under predicted past conditions without energy development, the total expected male count in northeast Wyoming would have been 2,037 birds subsequent to a WNv outbreak year and 4,537 otherwise (Table 3, Fig 5). This 55% reduction in bird numbers resulted from a near doubling of the lek extirpation rate (239/123).

Without energy development, active leks were comprised of roughly 40% small leks (1-10 males), 40% medium-sized leks (11-25 males) and 20% large leks (> 25 males). Absent an outbreak year, development to an average of 80 ac spacing within 12.4 mi (20 km) of leks reduced predicted counts by 61%, from 4,537 to 1,768 males. These reductions resulted from a decrease in average lek size, as shown by a decreasing number of large leks and an increasing number of small leks, beginning with the onset of development. For example, without oil and gas development, the 91 small leks comprised 37% of active leks in the area, and the 60 large leks comprised 24%. At 80 ac spacing, the number of small leks had risen to 232 (83% of the

area's active leks); whereas only 2 large leks remained. Number of medium-sized leks began to decline at 1 well per 160 ac (65 ha), and they declined at a slower rate than did the number of

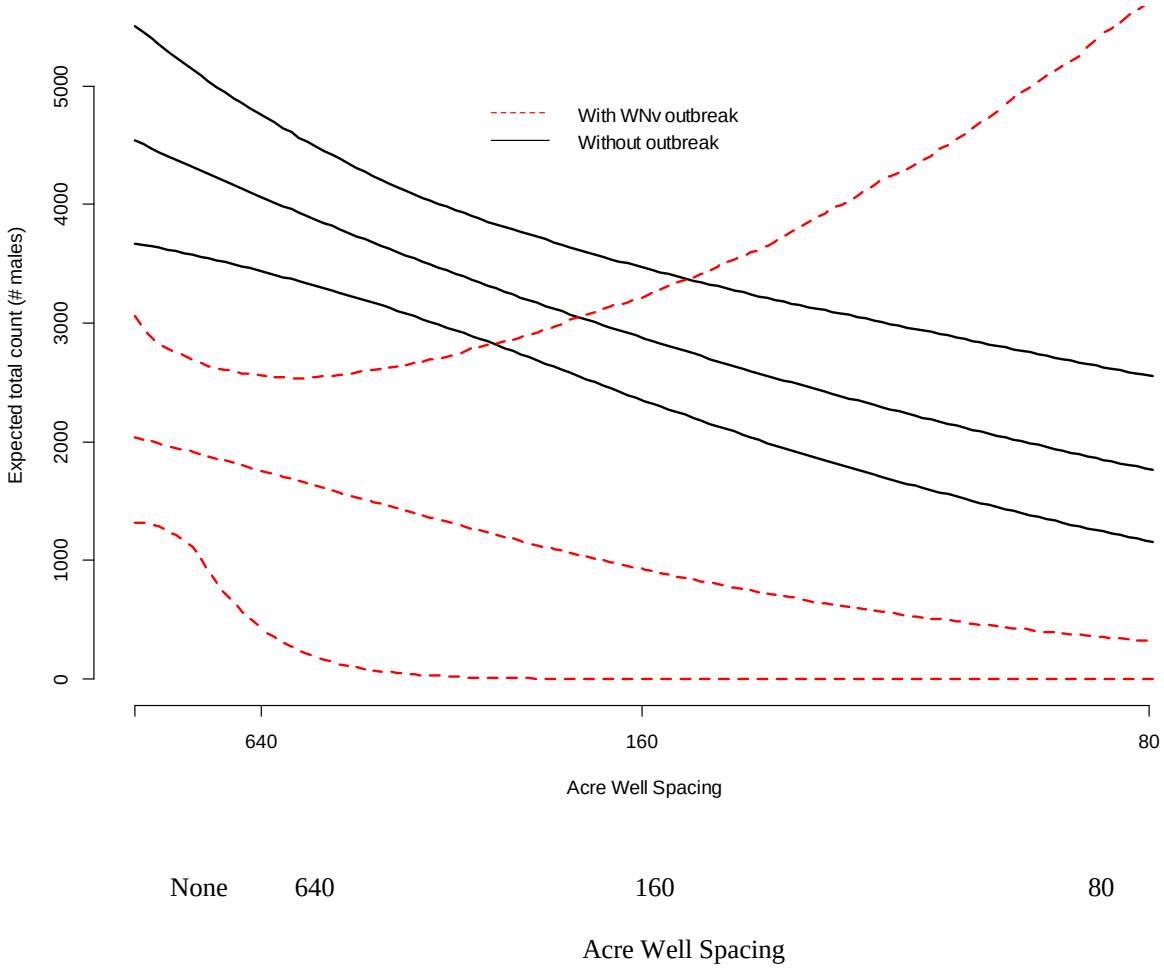



Figure 5. Predicted number of males counted on 370 leks in northeast Wyoming (with 95% confidence bands) versus the average spacing of oil and gas wells within 12.4 mi of each lek.

large leks; comprising only 16% of the active leks at 80 ac spacing. Increasing well density had a negligible effect on lek extirpations, which remained between 25% and 33%, regardless of the intensity of oil and gas development.

In contrast, a WNv outbreak year caused a near doubling of lek extirpations, even in the absence of oil and gas development (239/123, Table 3, Figure 6). Extirpations increased with oil and gas development: when an outbreak year was superimposed on development at 160 ac spacing, the number of extirpated leks more than tripled (337/100, Table 3), and by 80 ac spacing, it quadrupled (364/91, Table 3).

Where sufficient data exist, the relationship between population size and outbreak-year lek extirpations is clear. For example, at the current average well spacing in northeast Wyoming, we predict an outbreak year to reduce the number of males counted on leks by 60% (1-1473/3648). This difference is underscored by non-overlapping confidence intervals on the count predicted with an outbreak year (1473, CI =(65, 2616)) and without (3648, CI= (3147, 4204)). Common sense indicates that the relationship between lek extirpations and the total number of males counted should continue at higher well densities, but data were insufficient to quantify this relationship. In particular, only two active leks at well densities higher than the current average spacing were last counted subsequent to a WNv outbreak year, prohibiting us from estimating the size of active leks under these conditions. This in turn prohibited us from estimating the total expected count in the presence of both an outbreak year and high well densities.

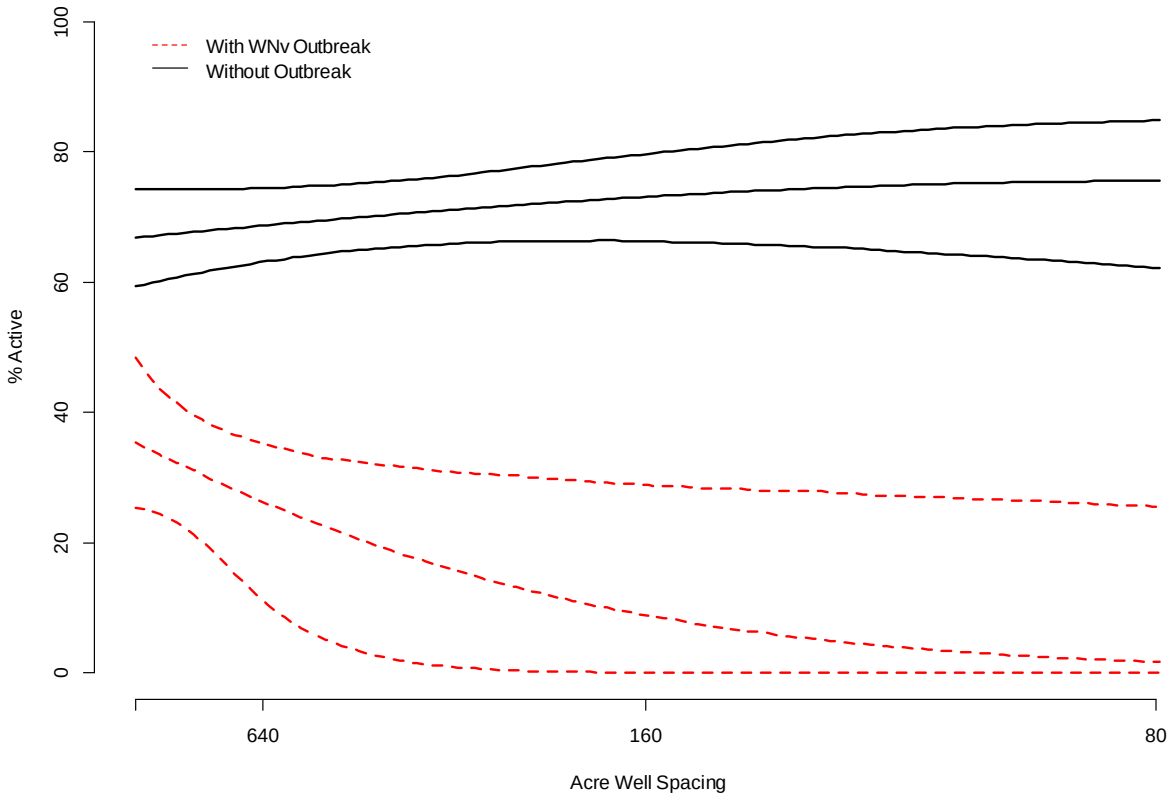



Figure 6. Percent of 370 leks in northeast Wyoming expected to remain active (with 95% confidence bands) versus the average spacing of oil and gas wells within 12.4 mi of each lek.

Table 3. Predicted total lek count and number of leks that are inactive (0 males), small (1-10 males), medium-sized (11-25 males) and large (> 25 males) for northeast Wyoming as a function of oil and gas well density and presence or absence of a West Nile virus outbreak year. As the lower limit of the confidence interval (CI) approaches 0, population extirpation is more likely.

| Without West Nile Virus Outbreak Year | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Acre Spacing[1] | Total Lek Count | | Number of Leks | | | | | | | |
| | | | Inactive | | Small | | Medium-sized | | Large | |
| | Mean | 95% CI | Mean | 95% CI | Mean | 95% CI | Mean | 95% CI | Mean | 95% CI |
| None | 4537 | (3668, 5507) | 123 | (95, 151) | 91 | (73, 111) | 96 | (84, 108) | 60 | (42, 80) |
| 640 | 4062 | (3439, 4753) | 116 | (94, 136) | 108 | (91, 125) | 98 | (89, 108) | 48 | (34, 62) |
| 328 [2] | 3648 | (3147, 4204) | 110 | (91, 129) | 125 | (109, 142) | 99 | (90, 108) | 37 | (26, 49) |
| 160 | 2876 | (2352, 3471) | 100 | (75, 125) | 163 | (138, 190) | 89 | (74, 103) | 18 | (10, 29) |
| 86 [3] | 1895 | (1288, 2670) | 91 | (57, 137) | 224 | (175, 259) | 52 | (25, 84) | 3 | (0, 12) |
| 80 | 1768 | (1162, 2554) | 91 | (56, 140) | 232 | (180, 266) | 46 | (19, 80) | 2 | (0, 10) |

| With West Nile Virus Outbreak Year | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Acre Spacing[1] | Total Lek Count | | Number of Leks | | | | | | | |
| | | | Inactive | | Small | | Medium-sized | | Large | |
| | Mean | 95% CI | Mean | 95% CI | Mean | 95% CI | Mean | 95% CI | Mean | 95% CI |
| None | 2037 | (1318, 3062) | 239 | (191, 277) | 57 | (38, 82) | 51 | (36, 69) | 23 | (11, 41) |
| 640 | 1757 | (430, 2558) | 273 | (240, 329) | 36 | (13, 53) | 38 | (11, 51) | 23 | (2, 37) |
| 328 [2] | 1473 | (65, 2616) | 299 | (252, 361) | 23 | (2, 39) | 27 | (1, 45) | 21 | (0, 39) |
| 160 | 927 | (1, 3212) | 337 | (263, 370) | 7 | (0, 23) | 11 | (0, 35) | 14 | (0, 50) |
| 86 [3] | 373 | (0, 5246) | 362 | (274, 370) | 1 | (0, 11) | 2 | (0, 21) | 5 | (0, 67) |
| 80 | 319 | (0, 5712) | 364 | (275, 370) | 1 | (0, 9) | 1 | (0, 19) | 4 | (0, 68) |

[1] measured within a 12.4-mi (20-km) radius of the lek

[2] average spacing around all leks in the northeast Wyoming area

[3] most dense spacing around any lek in the northeast Wyoming area

# DISCUSSION

## Oil and Gas Development Affects Sage-grouse at a Large Spatial Scale

Our analyses clarify an ongoing debate regarding the spatial scale at which oil and gas development most affects sage-grouse in the eastern portion of their range. Using AIC, as we did, to determine at what spatial scale an effect is best detected is analogous to using a dial to tune an analog radio while driving across a landscape. For oil and gas development, the signal is strongest within a 12.4-mi (20-km) radius of a lek, and it is much stronger at this radius than at any smaller radii. Furthermore, because we conducted analyses across a 30 million ha (74,000,000 ac) area encompassing a wide range of local and regional levels of oil and gas development, our best-fit spatial scale is robust to the conditions in any one locality, and it is generalized to the eastern portion of the sage-grouse range. While previous studies have found the best-fit spatial scale of impact to be anywhere from 2 mi (3.2 km) to over 12 mi (20 km) from the lek (Holloran 2005, Walker et al. 2007a, Tack 2009, Harju et al. 2010, Johnson et al. 2011), the different results are associated with the overall level of oil and gas development in the region analyzed. In particular, effects appear to be more localized if large undeveloped areas are not included in the study region for purposes of comparison. For this reason, sage-grouse in the Powder River Basin may be better served if BLM offices in Wyoming and Montana made their land use management decisions based on population boundaries rather than state boundaries.

The large spatial scale at which oil and gas development affects sage-grouse results from two aspects of the species' biology. First, the sage-grouse is a landscape species that requires large, intact areas of sagebrush in order to flourish (Connelly et al. 2011). Second, female sage-grouse that visit a lek use an approximately 9-mi (15-km) radius surrounding the lek for nesting; a 2-mi (3.2-km) radius encompasses only 35-50% of nests associated with the lek (Holloran and

Anderson 2005, Tack 2009). While a lek provides an important center of breeding activity, and a conspicuous location at which to count birds, its size is merely an index to the population dynamics in the surrounding habitat. Thus attempting to protect a lek, without protecting the surrounding habitat, provides little protection at all.

Past predictions of the number of males at leks impacted by oil and gas development (Doherty et al. 2010) should be updated to account for the large spatial extent of development impacts. Management would benefit from future analyses that include a decay function that quantitatively describes the non-linear relationship between bird numbers and the relative impact of oil and gas wells located at variable distances from the lek (e.g., see Holloran 2005; Fig 5, page 94).

Oil and Gas Development Results in Declining Lek Counts

Oil and gas development alone is a major threat to sage-grouse, and land managers can use Table 3 and Figure 5 to evaluate changes to predicted counts on leks under a myriad of different oil and gas development scenarios. Two scenarios include decisions on whether to develop a landscape from 0 to 4 wells per section (0 to 1.5 wells/$km^2$), and then from 4 to 8 wells per section (1.5 wells/$km^2$ to 3.1 wells/$km^2$). In both cases, the total northeast Wyoming lek count decreased by ~ 37% (1-2,876/4,537 and 1-1,768/2,876, Table 3), leaving only 39% of the original number of males on leks (1,768/4,537, Table 3) when development reached 8 wells per section (80 ac spacing).

A warning signal of declining populations is given by the accompanying decline in large leks, which showed a 70% decrease from no development to 160 ac spacing (1.5 wells/$km^2$, 1-18/60, Table 3). By 80 ac spacing (3.1 wells/$km^2$), only 2 large leks remained on the landscape (Table 3). Because we predicted the immediate effects of oil and gas development on lek size,

we found the decline in the number of large leks to be part of an overall decline in average lek size, but not a decline in lek activity. However, time lags of 2-10 years between onset of development activities and local extirpation (Holloran 2005, Walker et al. 2007a, Harju et al. 2010) are known to result from the high site fidelity, but low survival of adult sage-grouse combined with lek avoidance by younger birds (Holloran et al. 2010).

West Nile Virus Results in Lek Extirpations

Our ability to detect the impact of a WNv outbreak year despite inherent variability in lek monitoring data is evidence of its large effect size. We found a substantial increase in zero counts at leks subsequent to outbreak years, which is consistent with the extreme susceptibility of sage-grouse to WNv and local extirpations observed in the field. Two outbreak years (2003 and 2007) are known since WNv first appeared in the West in 2002 (CDC 2010), and now persistent low-level mortality and periodic, large mortality events are expected (Walker et al. 2011). Our predicted baseline population for northeast Wyoming (3,315 males, Table 2) may be optimistic because < 18% of leks (65/370, Table 1) were last surveyed following an outbreak year. Even if northeast Wyoming were not further developed, a WNv outbreak year would be predicted to reduce the area lek count by 60% compared to a non-outbreak year (1-1,473/3,648, Table 3), as a direct result of a near tripling of lek extirpations (299/110, Table 3).

Findings suggest we may have to live with lower sage-grouse numbers with WNv as part of the system. Decision-makers should incorporate disease impacts into resource management plans to account for potentially frequent outbreaks and the extreme susceptibility of sage-grouse to WNv (Clark et al. 2006). Reducing the threat of WNv by reducing the number of new man-made water sources is a sensible option (Walker et al. 2011). Although we could try to fight WNv with mosquito control, the cost associated with treating tens of thousands of acres may be

prohibitive, and benefits of spraying must be weighed against its likely detrimental effects (Marra et al. 2004).

West Nile Virus and Oil and Gas Development have a Synergistic Effect on Lek Extirpations

Oil and gas development and WNv outbreak years compound each other to increase the rate of lek extirpations. Two possible mechanisms are consistent with a disproportionately high rate of lek extirpation with increasing oil and gas development. First, within coal bed natural gas fields, ponds created from ground water brought to the surface during gas extraction provide additional habitat for mosquitoes that vector WNv (Walker et al. 2004, Zou et al. 2006, Walker et al. 2007b), possibly increasing the prevalence of WNv in these areas (Walker et al 2007, Walker and Naugle 2011). In other types of oil and gas development, the interaction between well density and outbreak year may simply reflect the more likely extirpation of populations that are already small. Regardless of mechanism, the interactive effects of energy development and outbreak years on lek extirpations are severe.

Sage-grouse populations in areas developed for oil and gas are small enough that they are at risk of extirpation due to a stochastic event, such as a WNv outbreak year. While disease is one obvious stressor, small populations are vulnerable to multiple habitat and population stressors. A different stressor, for example an extreme weather event, might also interact with development in a negative, synergistic manner, threatening viability of populations in developed areas.

## MANAGEMENT IMPLICATIONS

### Implications for Further Drilling in the Powder River Basin

Effects of energy development and past WNv outbreaks have depressed sage-grouse numbers in northeast Wyoming (Walker et al. 2007, Walker and Naugle 2011), placing the

remaining small population at risk of extirpation. The species' current lack of adaptation to WNv (Walker et al. 2007b) means that managers will have fewer birds following imminent outbreaks, whether or not drilling continues in northeast Wyoming. At current average well spacing (328 ac spacing, 0.75 wells/km$^2$) 3,316 males remain (Table 2). Even at 80 ac spacing (3.1 wells/km$^2$), northeast Wyoming might have supported a small residual population of 1,768 males (95% CIs = 1162, 2554, Table 3), were it not for the additional impacts of WNv outbreaks. The effect of an outbreak year can more than cut a population in half (1-2037/4537, Table 3), which is similar to drilling an undeveloped landscape at 4-8 wells/mi$^2$ (1.5-3.1 wells/km$^2$, 1-2876/4537 and 1-1768/4537, Table 3).

The severity of WNv impacts has narrowed BLM's decision space if the goal is to maintain a viable sage-grouse population in northeast Wyoming. Decisions to continue drilling heighten the risk to sage-grouse because higher well densities increase the severity of energy impacts and exacerbate lek extirpations resulting from disease. At 80 ac spacing, subsequent to an outbreak year, 98% of northeast Wyoming's leks are predicted to be inactive (364/370, Table 3). Additional monitoring of leks following outbreaks years is crucial if BLM wants to predict the size of the remaining active leks (Fig 5).

## Relevance of Findings to Wyoming's Core Area Policy

Wyoming's state-wide policy will be most effective where core area planning has accounted for the far reaching impacts of oil and gas before widespread development occurs. Such delineation of large and intact core areas in south central and southwest Wyoming will help to conserve sage-grouse populations if the policy continues to be fully implemented. In contrast, core areas in northeast Wyoming were delineated after widespread development had already occurred, leaving few options for conserving populations. In northeast Wyoming, the far

reaching influence of development has already negatively impacted the 103 remaining active leks inside core areas, largely because the large scale of impacts (12.4-mi radius) spans an area 38 times that of a 2-mile radius. Despite impacts, the potential may still exist to maintain a population inside core areas, but further drilling in and around cores will compromise their remaining value. Furthermore, disease outbreaks in northeast Wyoming are the wild card in core area management, and management must be geared to preserving sage-grouse affected by multiple stressors, not just energy development.

Genetic connectivity is the glue that holds populations together, and remaining core areas, though impacted, may help maintain connectivity among populations further south in Wyoming and those in Montana. Sage-grouse follow a pattern of isolation by distance; that is, populations that are closer geographically also tend to be closer genetically (Oyler-McCance et al. 2005). Unfortunately, we lack a detailed understanding of connectivity, and these genetic linkages are being altered as the landscape is altered (Knick and Hanser 2011). Genetic analyses are underway to identify areas important for connectivity, but until these linkage zones are identified, we recommend a cautionary approach to management to at least maintain as undeveloped habitat the connectivity corridors outlined in the Wyoming Governor's Executive Order.

## Future Monitoring to Assess Effectiveness of Restoration

Core areas are small, and the far reaching effects of development extend inside their boundaries, decreasing their intended conservation benefits to populations. Nevertheless, habitat enhancements may bolster sage-grouse populations inside the larger core areas, such as Natrona, and undeveloped areas may provide a source of birds to re-colonize restored habitats after extraction is complete. Maintaining a local population of birds may increase the chance for a

successful restoration because strong site fidelity hinders re-colonization from more distant sites and past precedence shows that translocations, while problematic, are more apt to succeed in areas with resident populations (Reese and Connelly 1997, Baxter et al. 2008).

Carefully planned, landscape scale monitoring of sage-grouse populations will be critical to evaluate the restoration efforts after the oil and gas play has ceased. Data must be collected across a range of development levels at local and regional scales, and failure to do so could result in mis-estimation of the development effects. These problems are compounded when multiple effects (e.g., the effect of development and the effect of abandonment) are considered, because the data must contain a large range of intensities for both land uses, and the different intensities for each land use need to be observed in combination with the different intensities of the other land use. For example, consider conducting a lek count-based analysis when oil and gas wells are just starting to be plugged and abandoned. Plugged and abandoned wells would occur in low to moderate densities in areas where the density of active wells was high. Areas with neither active nor abandoned wells would exist, but there would be no areas in which the density of abandoned wells was high and the density of active wells was low. An analysis based on such data might incorrectly predict that plugging and abandoning wells is detrimental to sage-grouse, simply because the plugged and abandoned wells occurred in areas where the density of active wells was high. While current data will not support an appropriate analysis of the effect of plugging and abandoning wells, such an analysis will be possible once appropriate combinations of active and abandoned well densities exist. We strongly urge that such an analysis be conducted, as it would guide sage-grouse management not only in northeast Wyoming, but also in areas across the West that have been developed for oil and gas.

Lek monitoring to assess restoration outcomes must be large scale, encompassing at least the area of northeast Wyoming that we used, and preferably the entirety of our study region. Furthermore, the statistical methods used herein are repeatable, and they provide a template for a multiple effects analysis. We also note that the metric we used in our analyses, density of active wells, represents intensity of development, and as such it provides a surrogate for the roads, power lines and other infrastructure that accompany wells. Should infrastructure be removed when some wells are abandoned, but not when others are abandoned, these different effects would need to be monitored and included as separate effects in the analysis. For example, water impoundments from coal-bed natural gas development might be retained by private landowners as stock ponds, and might, in fact, provide better breeding habitat for WNv carrying mosquitoes under this new usage. Conversely, we acknowledge and encourage the efforts of some companies to bury power lines and reduce their overall footprint in other ways. The benefits of these actions should be monitored at large scales when they become common enough to assess at biologically relevant scales. We cannot stress enough the importance of monitoring populations at a scale large enough to encompass multiple levels of development, abandonment and lack thereof, and large enough to not be hampered by project or political boundaries unrelated to sage-grouse biology.

The other method likely to provide a fruitful assessment of the impacts of plugging and abandoning wells would be a small scale, but highly intensive, designed before-after-control-impact study. This type of study requires that birds be radio-marked and that data be collected on all vital rates across space and time. Holloran (2005) provides an excellent example of such a design.

LITERATURE CITED

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat based approach for endangered greater sage-grouse. Ecological Applications 17:508-526.

Baxter, R. J., J. T. Flinders, and D. L. Mitchell. 2008. Survival, movements, and reproduction of translocated greater sage-grouse in Strawberry Valley, Utah. Journal of Wildlife Management 72:179-186.

Bolker, B. M. 2008. Ecological models and data in R. Princeton University Press, Princeton, NJ, USA.

Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers under global change. Trends in Ecology and Evolution 23:453-460.

Burnham, K.P., and D.R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.

Carpenter, J., C. Aldridge, and M. S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 74:1806-1814.

Casella, G., and R. L. Berger. 2002. Statistical inference. Duxbury Press, Belmont, CA, USA.

Centers for Disease Control. 2004. URL: http://diseasemaps.usgs.gov/2003/us_human.html Accessed 6 August 2010.

Centers for Disease Control. 2010. URL: substitute last digit of year for ‘X’ in URL below http://www.cdc.gov/ncidod/dvbid/westnile/surv&controlCaseCount0X_detailed.htm Accessed 6 August 2010.

Clark, L., J. Hall, R. Mclean, M. Dunbar, K. Klenk, R. Bowen, and C. A. Smeraski. 2006. Susceptibility of greater sage-grouse to experimental infection with West Nile virus. Journal of Wildlife Diseases 42:14-22.

Connelly, J. W., S. T. Knick, C. E. Braun, W. L. Baker, E. A. Beever, T. J. Christiansen, K. E. Doherty, E. O. Garton, C. A. Hagen, S. E. Hanser, D. H. Johnson, M. Leu, R. F. Miller, D. E. Naugle, S. J. Oyler-McCance, D. A. Pyke, K. P. Reese, M. A. Schroeder, S. J. Stiver, B. L. Walker, and M. J. Wisdom. 2011. Conservation of greater sage-grouse: a synthesis of current trends and future management. Pages 549-564 in Greater sage-grouse: ecology and conservation of a landscape species and its habitats, S. T. Knick, J. W. Connelly, C. E. Braun (editors). Studies in Avian Biology, Number 38, University of California Press, Berkeley, CA, USA.

Connelly, J. W., S. T. Knick, M. A. Schroeder and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Unpublished Report, Western Association of Fish and Wildlife Agencies. Cheyenne, Wyoming.

Copeland, H. E., K. E. Doherty, D. E. Naugle, A. Pocewicz, and J. M. Kiesecker. 2011. Forecasting energy development scenarios to aid in conservation design. Pages 183-193 in D. E. Naugle (editor). Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

Doherty, K. E., D. E. Naugle, H. Copeland, A. Pocewicz, and J. Kiesecker. 2011. Energy development and conservation tradeoffs: systematic planning for sage-grouse in their eastern range. Pages 505-516 in S. T. Knick and J. W. Connelly (editors). Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, Number 38, University of California Press, Berkeley, USA.

Doherty, K. E., D. E. Naugle, and J. S. Evans. 2010. A currency for offsetting energy development impacts: horse-trading sage-grouse on the open market. PLoS One 5:e10339.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187-195.

Dunn, P. K., and G. K. Smyth. 1996. Randomized quantile residuals. Journal of Computational and Graphical Statistics 5:236-244.

Fedy, B. C. and C. L. Aldridge. 2011. The importance of within-year repeated counts and the influence of scale on long-term monitoring of sage-grouse. Journal of Wildlife Management 75:1022-1033.

Fedy, B. C., and K. E. Doherty. 2010. Population cycles are highly correlated over long time series and large spatial scales in two unrelated species: greater sage-grouse and cottontail rabbits. Oecologia 165:915-924.

Garton, E. O., J. W. Connelly, C. A. Hagen, J. S. Horne, A. Moser, and M. A. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Pages 293-381 in Greater sage-grouse: ecology and conservation of a landscape species and its habitats, S. T. Knick, J. W. Connelly, C. E. Braun (editors). Studies in Avian Biology, Number 38, University of California Press, Berkeley, CA, USA.

Hanser, S. E., and S. T. Knick. 2011. Greater sage-grouse as an umbrella species for shrubland passerine birds: a multiscale assessment. Pages 475-503 in Greater sage-grouse: ecology and conservation of a landscape species and its habitats, S. T. Knick, J. W. Connelly, C. E. Braun (editors). Studies in Avian Biology, Number 38, University of California Press, Berkeley, CA, USA.

Harju, S. M., M. R. Dzialaka, R. C. Taylor, L. D. Hayden-Wing, and J. B. Winstead. 2010. Thresholds and time lags in effects of energy development on greater sage-grouse populations. Journal of Wildlife Management 74:437-448.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, WY, USA.

Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742-752.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638-649.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65-72.

Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. L. Amundson and S. T. Knick. 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations, 1997-2007. Pages 407-450 in Greater sage-grouse: ecology and conservation of a landscape species and its habitats, S. T. Knick, J. W. Connelly, C. E. Braun (editors). Studies in Avian Biology, Number 38, University of California Press, Berkeley, CA, USA.

Kiesecker, J. M., H. Copeland, A. Pocewicz, and B. McKenney. 2010. Development by design: blending landscape level planning with the mitigation hierarchy. Frontiers in Ecology and the Environment 8:261-266.

Kiesecker, J. M., H. E. Copeland, B. A. McKenney, A. Pocewicz, and K. E. Doherty. 2011. Energy by design: making mitigation work for conservation and development. Pages 159-181 in D. E. Naugle, (editor). Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634.

Knick, S. T., and S. E. Hanser. 2011. Connecting pattern and process in greater sage-grouse populations and sagebrush landscapes. Pages 383-405 in Greater sage-grouse: ecology and conservation of a landscape species and its habitats, S. T. Knick, J. W. Connelly, C. E. Braun (editors). Studies in Avian Biology, Number 38, University of California Press, Berkeley, CA, USA.

Marra, P. P., S. Griffing, C. Caffrey, A. M. Kilpatrick, R.Mclean, and C. Brand. 2004. West Nile virus and wildlife. BioScience 54:393-402.

McDonald, R. I., J. Fargione, J. Kiesecker, W. M. Miller, and J. Powell. 2009. Energy sprawl or energy efficiency: climate policy impacts on natural habitat for the United States of America. PLoS One 4. e6802.

McSweegan, E. 1996. The infectious diseases impact statement: a mechanism for addressing emerging diseases. Emerging Infectious Diseases 2:103-108.

Naugle, D. E. (editor) 2011. Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: pending crisis for greater sage-grouse. Ecology Letters 7:704-713.

Naugle, D. E., C. L. Aldridge, B. L. Walker, K. E. Doherty, M. R. Matchett, J. Mcintosh, T. E. Cornish, and M. S. Boyce. 2005. West Nile virus and sage-grouse: what more have we learned? Wildlife Society Bulletin 33:1-8.

Naugle D. E., K. E. Doherty, B. L. Walker, M. J. Holloran, and H. E. Copeland. 2011b. Energy development and greater sage-grouse. Pages 489-529 in Greater sage-grouse: ecology and conservation of a landscape species and its habitats, S. T. Knick, J. W. Connelly, C. E. Braun (editors). Studies in Avian Biology, Number 38, University of California Press, Berkeley, CA, USA.

Oyler-McCance, S. J., S. E. Taylor, and T. W. Quinn. 2005. A multilocus population genetic survey of the greater sage-grouse across their range. Molecular Ecology 14:1293-1310.

Reese, K. P., and J. W. Connelly. 1997. Translocations of sage grouse *Centrocercus urophasianus* in North America. Wildlife Biology 3:235-241.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. Mcadam, C. W. Mccarthy, J. J. Mccarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. Condor 106:363-376.

Schultz, C. 2010. Challenges in connecting cumulative effects analysis to effective wildlife conservation planning. Bioscience 60:545-551.

Soule, M. E., and L. S. Mills. 1998. No need to isolate genetics. Science 282**:**1658-1659.

Tack, J. D. 2009. Sage-grouse and the human footprint: implications for conservation of small and declining populations. Thesis, University of Montana, Missoula, MT, USA.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. Scott Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336-347.

Walker, B. L., and D. E. Naugle. 2011. West Nile virus ecology in sagebrush habitats and impacts on greater sage-grouse populations. Pages 127-142 in Greater sage-grouse: ecology and conservation of a landscape species and its habitats, S. T. Knick, J. W. Connelly, C. E. Braun (editors). Studies in Avian Biology, Number 38, University of California Press, Berkeley, CA, USA.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007a. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644-2654.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2007b. West Nile virus and greater sage-grouse: estimating infection rate in a wild bird population. Avian Diseases 51:691-696.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2004. Outbreak of West Nile virus in greater sage-grouse and guidelines for monitoring, handling, and submitting dead birds. Wildlife Society Bulletin 32:1000-1006.

Wyoming Office of the Governor. 2011. State of Wyoming Executive Department Executive Order EO-2011-5 Greater sage-grouse core area protection. http://governor.wy.gov/Documents/Sage-Grouse%20EO.pdf accessed 7 June 2011.

Zou, L., S. N. Miller, and E. T. Schmidtmann. 2006. Mosquito larval habitat mapping using remote sensing and GIS: implications of coalbed methane development and West Nile virus. Journal of Medical Entomology 43:1034-1041.

## APPENDIX 1: STATISTICAL METHODS

We regressed oil and gas well density, a factor for WNv outbreak year and a factor for area on lek counts, using AIC to determine the most parsimonious model. We used our best-fit model to predict the effects of different well densities on lek counts, in the presence of a WNv outbreak year, and in its absence.

### Model Selection

Our model selection proceeded in two steps. First we determined the best fit radius for energy development; second we quantified the effects of energy development and WNv on sage grouse using the best fit radius obtained in the first analysis. We determined which radius best explained the variation in lek counts by repeating, for each radius, a univariate regression of lek count against well density, and comparing the resulting six regressions with AIC (Burnham and Anderson 1998). We then fit a saturated, multivariate model that contained the main effects of well density at its best fit scale, factors for WNv years, well density by WNv interactions, and separate intercepts for each of the five areas. We did not include any interactions with area, as we had no reason to believe that stressors would affect lek counts differently in the different areas; we simply needed to adjust for the different starting sizes of the leks in each area. We reduced the saturated model by testing whether or not removing each interaction would cause AIC to increase by more than two units (Burnham and Anderson 1998). We then reduced main effects in the same fashion, but did not test for removal any of the main effects on which the interactions depended.

### Predictions

We used the best-fit, multivariate model to predict how changing stressors would affect northeast Wyoming's total lek count, which we calculated as the product of the expected size of

a northeast Wyoming lek (including both active and inactive leks) and the number of leks from northeast Wyoming that were used in the analysis. We calculated the number of leks that were extirpated, as well as the number in small (< 11 males), medium (11-25 males) and large (> 25 males) size categories (Tack 2009), by calculating the probability a lek would fall into each of the four size categories and multiplying it by the number of leks from northeast Wyoming that were used in the analysis.

## Error Structure

We used a zero-inflated negative binomial (ZINB) error structure. The ZINB is a mixture of a negative binomial distribution and a point mass at zero, meaning that some zero counts are generated by the negative binomial distribution, and some are generated by the point mass of extra zeros, but all positive counts come from the negative binomial distribution. This structure is ideally suited to overdispersed count data such as ours, where the variance is a strongly increasing function of the mean, and there are an unusually large number of zero counts (Hardin and Hilbe 2007). We parameterized the ZINB so the negative binomial distribution was described by a mean and overdispersion parameter, and the mixing parameter was the probability that a count belonged to the negative binomial distribution. We used a log link for the negative binomial mean and a logit link for the mixing parameter.

## Confidence Intervals and Model Diagnostics

We calculated parameter confidence intervals with profiled likelihoods and used case-based, nonparametric bootstrapping to place 95% confidence bands on the predicted lines. We calculated randomized quantile residuals (Dunn and Smyth 1996) for diagnostic plots because the normal distribution of these residuals make them much more interpretable than other generalized linear model residuals that exhibit only asymptotic normality. Analyses were conducted in the R programming environment, version 2.14.0 (R Development Core Team).

## APPENDIX II: STATISTICAL RESULTS

Table 1. Delta AIC values used to determine the best fit radius surrounding a lek within which to measure the number of oil and gas wells. Univariate models demonstrated that the 12.4 mi radius better explained the variation in the data than did 4 of the 5 other radii (dAIC > 2). While the 12.4 mi radius provided a nominally better fit than did the 3.1 mi radius, it was statistically indistinguishable (dAIC < 2). To confirm whether or not the 12.4 mi radius better explained the variation in the data than did the 3.1 mi radius, we compared AIC values for these two radii using the saturated model. The 3.1 mi radius had a dAIC value > 4 points higher than the 12.4 mi radius, confirming that the best fit was achieved using the 12.4 mi radius.

| | Delta AIC | |
|---|---|---|
| Radius mi (km) | Univariate | Saturated |
| 12.4 (20.0) | 0.00 | 0 |
| 3.1 (5.0) | 1.44 | 4.89 |
| 9.3 (15.0) | 2.09 | NA |
| 0.6 (1.0) | 4.50 | NA |
| 2.0 (3.2) | 4.52 | NA |
| 6.2 (10.0) | 4.78 | NA |

Table 2. Maximum likelihood estimates and profile likelihood confidence intervals for parameters of the reduced model. Parameters belonging to the negative binomial (NB) model component are presented on the log scale. Parameters belonging to the zero-inflation (ZI) model component (mixing parameter) are presented on the logit scale. The mixing parameter was defined as the probability that a count belonged to the negative binomial distribution.

| | Parameter | Model Component | MLE | CI |
|---|---|---|---|---|
| | Overdispersion | NB | 1.539 | (1.354, 1.738) |
| | Intercept | ZI | 2.897 | (2.240, 3.077) |
| | Intercept | NB | 3.352 | (3.211, 3.499) |
| Factor for Area | Central MT | ZI | -1.431 | (-2.329, -0.711) |
| | Central MT | NB | -0.413 | (-0.600, -0.228) |
| | Eastern MT | ZI | -1.047 | (-1.949, -0.305) |
| | Eastern MT | NB | -0.809 | (-0.997, -0.624) |
| | Dakotas | ZI | -0.652 | (-1.778, 0.618) |
| | Dakotas | NB | -1.023 | (-1.277, -0.764) |
| | NE Wyoming | ZI | -2.135 | (-3.044, -1.402) |
| | NE Wyoming | NB | -0.463 | (-0.672, -0.254) |
| | Well Density | ZI | 0.269 | (-0.079, 0.656) |
| | Well Density | NB | -0.369 | (-0.505, -0.230) |
| | Outbreak Year | ZI | -1.328 | (-1.732, -0.930) |
| | Outbreak Year | NB | -0.168 | (-0.351, 0.019) |
| | Well*Outbreak Year Interaction | ZI | -1.406 | (-2.751, -0.380) |
| | Well*Outbreak Year Interaction | NB | 0.765 | (0.199, 1.514) |

ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/318303872

# Evaluating efficacy of fence markers in reducing greater sage-grouse collisions with fencing

**Article** *in* Biological Conservation · September 2017
DOI: 10.1016/j.biocon.2017.06.030

CITATIONS
2

READS
105

**5 authors**, including:



Adam Green
Bird Conservancy of the Rockies
**12** PUBLICATIONS **85** CITATIONS
SEE PROFILE



David C. Pavlacky Jr.
Bird Conservancy of the Rockies
**19** PUBLICATIONS **234** CITATIONS
SEE PROFILE

**Some of the authors of this publication are also working on these related projects:**



Dynamic multiscale occupancy model to account for variation in site selection View project



Avian community ecology in juniper woodlands of southwestern Wyoming: patterns of landscape and habitat utilization View project

All content following this page was uploaded by Adam Green on 09 October 2017.

The user has requested enhancement of the downloaded file.

Biological Conservation 213 (2017) 70–83

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

# Evaluating efficacy of fence markers in reducing greater sage-grouse collisions with fencing

Nicholas J. Van Lanen*, Adam W. Green, Taylor R. Gorman, Laura A. Quattrini, David C. Pavlacky Jr

*Bird Conservancy of the Rockies, 14500 Lark Bunting Lane, Brighton CO 80603, USA*

ARTICLE INFO

*Keywords:*
Greater sage-grouse
Collisions
Mortality
Fence
Sagebrush
*Tetraonid*

ABSTRACT

Anthropogenic infrastructure routinely interferes with wildlife movement, habitat use, and survival. Grouse in the family *Phasianidae* may be particularly susceptible to collisions with fences due to their morphology and life history. Because many *Phasianid* species are of conservation concern, managers often deploy markers on fences to reduce collision-associated mortality. However, scarce information on the effectiveness of different marker styles or the effects of local and landscape features on collision risk exists. Our objectives were to (1) determine the effectiveness of different marker styles in reducing collisions, (2) estimate the effects of local and landscape features on collision risk, and (3) evaluate an existing greater sage-grouse (*Centrocercus urophasianus*) collision risk model. We conducted greater sage-grouse collision surveys within Sublette County, Wyoming, USA in March and April of 2014 and 2015. Data were analyzed in a multi-scale occupancy model accounting for incomplete detection of collisions. We found substantial evidence for the ability of all markers to reduce collisions (~57% reduction), with little difference between the tested marker types. We found strong evidence for lower collision probabilities at fences with wood posts and on fences farther from leks. Our results also indicated a negative relationship between collision probabilities and the difference between fence and vegetation heights. We observed little evidence for differences in collision risk between areas defined as "high" or "moderate" risk in a pre-existing collision risk map. We recommend integrating fence marking into conservation practices requiring fencing, and prioritizing fence marking near leks in areas with greater fence exposure.

## 1. Introduction

Anthropogenic infrastructure such as fences routinely interferes in the movements, habitat use, and survival of a wide variety of wildlife species (Bevanger 1994; Drewitt and Langston 2008; Linnell 2016). Unfortunately, the installation of human infrastructures, including fences, typically witnessed across landscapes of high-income nations is now occurring in low-income countries as well (Bevanger 1994; Drewitt and Langston 2008). The broad-scale erection of fencing has continued due to civil and political unrest throughout the world (Bevanger and Henriksen 1996; Hayward and Kerley 2009; Linnell 2016), the need for maintaining domesticated livestock within an enclosed area (Hayter 1939), the need to exclude undesired animals from certain parcels (Bevanger and Henriksen 1996; Hayter 1939), or to maintain biodiversity (Hayward and Kerley 2009; Linnell et al. 2016).

Wildlife collisions with fencing represent a direct impact on the survival of individuals. Mortality associated with fence collisions has been well documented for numerous avian species, including the *Phasianids* which are thought to be susceptible to collisions with infrastructure due to their high wing loading, lekking behavior, and afoveal retina (Bevanger 1994; Lisney et al. 2012; Sillman 1973). In North America, Wolfe et al. (2007) found that 39.8% of lesser prairie-chicken (*Tympanuchus pallidicinctus*) mortality was caused by collision with fences and, based on a subset of the same data set, Patten et al. (2005) observed elevated mortality rates for female lesser prairie-chickens where habitats were more fragmented by fences, power lines, and roads. Similarly, greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) collisions with fencing have been observed in two studies in western North America (Christiansen, 2009, Stevens et al. 2012a). In Europe, collisions with fences and power lines have been observed for the western capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), red grouse (*Lagopus lagopus scoticus*), and ptarmigan (*Lagopus spp.*) (Baines and Summers 1997; Bevanger 1995; Catt et al. 1994). Although the impact of this collision-associated mortality on populations is not particularly well understood, there is some evidence indicating infrastructure collisions may contribute substantially

* Corresponding author.
*E-mail address:* nick.vanlanen@birdconservancy.org (N.J. Van Lanen).

http://dx.doi.org/10.1016/j.biocon.2017.06.030
Received 20 December 2016; Received in revised form 13 June 2017; Accepted 22 June 2017
0006-3207/ © 2017 Elsevier Ltd. All rights reserved.

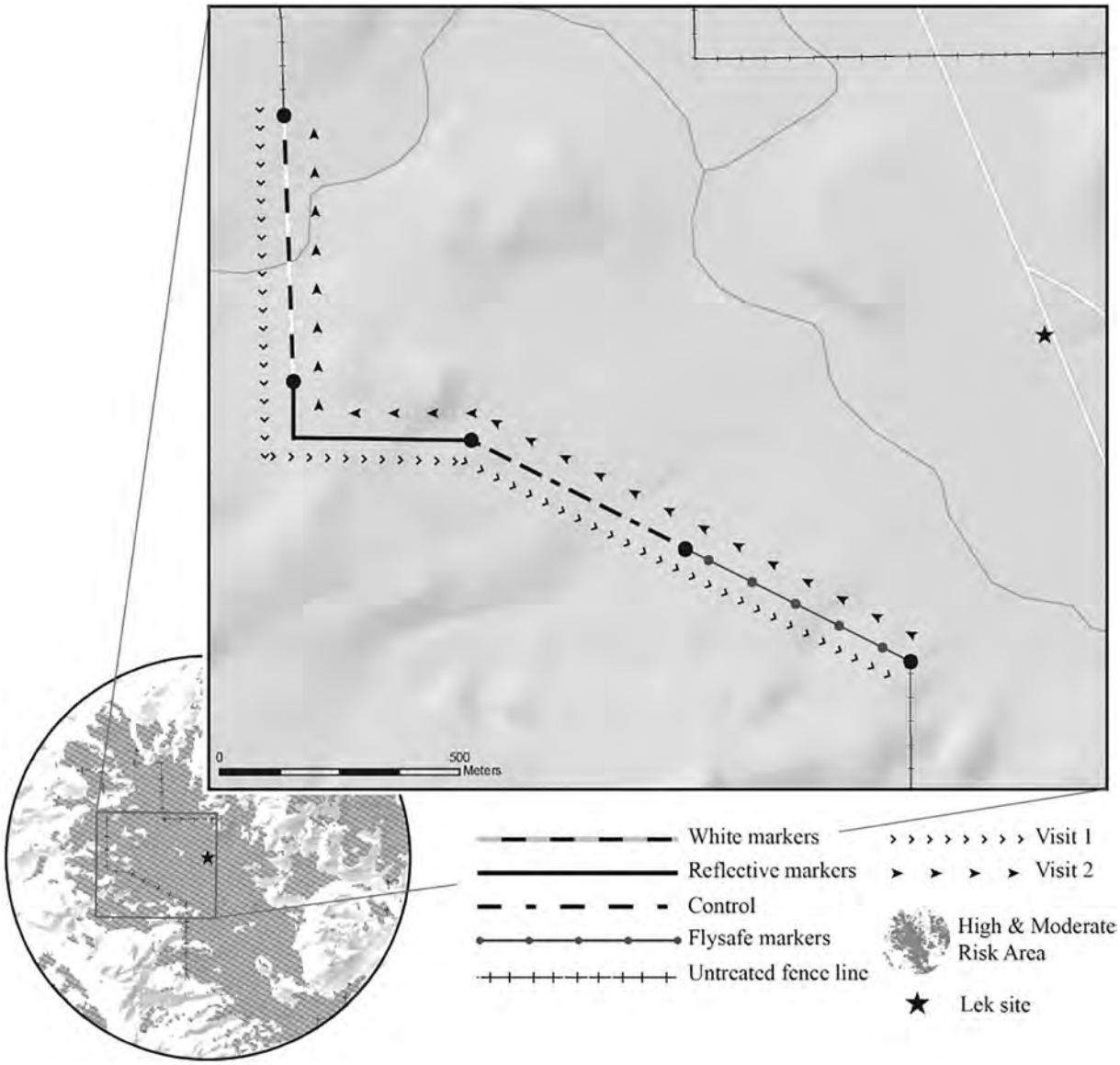



**Fig. 1.** Illustration of four treated segments of fence-line associated with a focal lek.

to population declines in some species (Baines and Andrew 2003; Bevanger 1995; Moss et al. 2000; Smith and Dwyer 2016).

The risk of wildlife collisions with fencing is likely impacted by a variety of site and landscape-scale factors (Stevens et al. 2012a). Site factors may include the density and height of local vegetation, fence height, type of fence, the type of fence posts, the distance between fence posts, the slope or ruggedness of the nearby landscape, and in the case of lekking species, the distance to surrounding leks and the number of individuals attending adjacent leks (Stevens et al. 2012a). Similarly, landscape-scale factors may include surrounding landcover types (Baines and Summers 1997), the density of individuals throughout the landscape (Baines and Andrew 2003), and movement corridors (including prominent ridges or other vegetative or topographic features that funnel animal movement) (Bevanger 1994; von Schweppenburg 1929).

Marking human infrastructure to increase its visibility is a common practice for reducing collisions for a variety of avian species (Luzenski et al. 2016), including *Phasianids* due to their predisposition for colliding with fences and the level of conservation concern regarding several species within this subfamily (Baines and Andrew 2003; Stevens et al. 2012b). The growing application of fence markers to reduce collisions has prompted government agencies and non-profit organizations to provide significant financial and personnel resources to install them at extensive scales (Natural Resources Conservation Service, 2015). This effort spurred one peer-reviewed study to evaluate the effectiveness of this practice. Stevens et al. (2012b) evaluated the effectiveness of fence markers in reducing greater sage-grouse collisions and found marked fences reduced collisions by 83%. Similarly, marking fences reduced black grouse (91%) and capercaillie (64%) collisions (Baines and Andrew 2003). Although these studies have shown that marking deer and stock fencing can reduce *Phasianid* collisions with fences, to date, no study has compared the efficacy of multiple marker types in reducing collisions, while accounting for imperfect detection, and considering site- and landscape-level factors that may influence collision rates. Durability concerns of marker types in Europe underscore the need for evaluating alternative marker styles (Baines and Andrew 2003). Additionally, few studies have empirically tested site- and landscape-scale factors that may influence the risk of grouse collisions with fencing.

Our research objectives were to 1) determine the effectiveness of different fence marker types, 2) estimate the effects of site and landscape features on collision risk and 3) evaluate an existing greater sage-grouse collision risk model. We evaluated the effectiveness of bright yellow FlySafe markers (FlySafe 2016), white markers with reflective



**Fig. 2.** Photographs of fence marker types deployed in our study. From left to right the above images represent the Flysafe, reflective, and white marker treatments.

tape and white markers without reflective tape compared to unmarked fence using a dataset collected in western Wyoming where sage-grouse densities are high and leks are abundant. Additionally, we investigated site and landscape features to identify areas with high collision risk and control for potentially confounding variables related to collision risk at multiple spatial scales. We evaluated an existing collision risk map (Stevens et al. 2013) to determine if observed sage-grouse collisions were correlated with areas predicted to have high or moderate collision risk.

## 2. Methods

### 2.1. Study area

Our study occurred on both private and public lands within Sublette County, Wyoming, USA. Sublette County contains some of the highest sage-grouse population indices within the occupied range (United States Fish and Wildlife Service, USFWS 2010). It lies within Management Zone II as identified by Stiver et al. (2006). The county covers approximately 3.2 million acres, of which, 80% is publicly owned. Elevations within Sublette County range from 6280 ft to 13,400 ft (Wyoming State Historical Society 2016). Lower elevations are largely characterized as sagebrush steppe habitat with riparian corridors along the Green River and its tributaries. Dominant vegetation within the lower elevation sagebrush steppe largely consists of Wyoming big sagebrush (*Artemesia tridentata* ssp. *wyomingensis*) and basin big sagebrush (*Artemesia tridentate* ssp. *tridentata*). Fencing within our study area largely consisted of three to four metal strands with barbs on all wires. A small amount of fencing within our study area consisted of metal woven wire fencing in which the bottom half of the fence consisted of both vertical and horizontal metal strands without barbs and forming rectangles 9 cm by 12 cm. Above the woven wires were typically one or two single horizontal metal wire strands with barbs.

### 2.2. Sampling design

We developed the sampling frame for Sublette County, Wyoming, using the 3 km-radius collision risk polygons (Stevens et al. 2013) for sage-grouse leks represented in the Wyoming Game and Fish Department lek database (Christiansen 2012). We reclassified the high and moderate risk zones into a single collision risk category and omitted the low risk zone for each of the 308 lek polygons in Sublette County (Fig. 1) using a Geographic Information System (GIS; ArcGIS Version 10.0, ESRI 2011). Next, we intersected the combined high and moderate risk zones for the lek polygons with the Bureau of Land Management (BLM) fence database (Bureau of Land Management - Pinedale Field Office, GIS Staff 2013). The sampling frame consisted of 77 lek polygons containing a minimum of 2 km of fence within the combined high and moderate risk zone of the lek polygons. We defined the sampling unit as the lek, which was represented by the 3 km-radius collision risk polygon (Stevens et al. 2013).

We selected a spatially balanced sample of 26 lek polygons (hereafter, we refer to randomly selected leks as “focal leks”) using Generalized Random Tessellation Stratification (GRTS; Stevens and Olsen 2004). We determined land ownership from the Sublette County Assessor's Office and requested permission to access the sampling units in the rank order of the GRTS sample selection. When landowners denied permission, we selected the next highest rank order of the GRTS sample selection. A useful feature of the GRTS design is the spatially balanced property of the sample was maintained when private landowners denied permission to access the sampling units (Stevens and Olsen 2004).

### 2.3. Treatments

Each of the four treatments was randomly applied to 500 m stretches of fencing within the selected sample units. Treatments were defined as control (no marker), white (approximately 7.5 × 5 cm piece of white undersill vinyl siding), reflective (white markers with a 7.5 × 1.8 cm strip of lime-yellow Identi-Tape V97 high intensity reflective tape applied to each side), and Fly Safe markers (approximately 12 × 9 cm yellow plastic markers) (FlySafe 2016) (Fig. 2). We selected the marker treatments because they are representative of the gamut of treatments being implemented within the western U.S. to reduce sage-grouse and lesser prairie-chicken collisions with fencing. For the 500 m stretches receiving the white, reflective, or Fly Safe treatments, markers were spaced approximately 1 m from fence-posts and other markers on the top wire of the fencing to be consistent with fence marking recommendations (United States Department of Agriculture, USDA 2016). The design with all three treatments and the control employed at each sampling unit corresponds to a repeated measures design with random order of the treatments levels (Morrison et al. 2008).

### 2.4. Sampling methods

A total of four observers trained in sage-grouse feather identification and possessing extensive biological survey experience conducted field work throughout the two year study. Observers were intensively trained to ensure they possessed a complete understanding of field protocols, a sufficient ability to identify collision events, and could positively identify sage-grouse remains.

Surveys were conducted approximately biweekly in March and April of 2014 and 2015. A survey of a site entailed either two or four visits. The first visit consisted of an observer walking along the site's fence while scanning for evidence of animal collisions. The observer then crossed the fence and conducted the second visit by doubling back and walking to the starting point of the first visit (Fig. 1). A survey consisted of four visits when a second observer, surveying separately from the first observer, visited the same site on the same day. Observers did not discuss findings during the course of the surveys in order to avoid influencing detection rates.

Observers maintained a distance of 1-2 m from the fence during each visit. While surveying, observers primarily searched the wires of the fence for signs of a collision. Additionally, observers scanned the

**Table 1**
Covariates included in analyses of fence collisions by Greater Sage-Grouse in Wyoming, 2014–2015, and their expected effect on the parameter of interest (positive effect, +; negative effect, −). Parameters include large-scale occupancy (ψ), small-scale occupancy (θ), and detection probability (*p*). Means and ranges are shown for continuous covariates and levels and frequencies for the categorical covariates.

| Covariate | Description | Parameter | Means (ranges) and levels (frequencies) | Expected effect |
|---|---|---|---|---|
| Occ Lek | Number of occupied leks within 3 km of the focal lek | ψ | 1.51 (0–3) | + |
| Lek Ct | Sum of lek counts for leks within 3 km of focal lek | ψ | 72.88 (0–265) | + |
| Year | Year in which survey was conducted | ψ,θ | 2014 (26), 2015 (25) | N/A |
| Trt | Fence marker type | θ | Control (50), FlySafe (51), White (51), Reflective (50) | Risk of control > white > reflective > FlySafe |
| Mark | Fence marked or not | θ | Control (50), Marked (152) | Lower for marked |
| Angle | Angle (°) created by the triangle between the lek and end of fence segment | θ | 16.34° (1°–120°) | + |
| Distance | Distance (km) between the midpoint of the fence segment and the nearest lek | θ | 1.85 km (0.15 km–4.60 km) | − |
| Near Ct | Mean max male lek count for the nearest lek from 2014 to 2015 | θ | 54.63 (1–265) | + |
| Fence Exp | Mean difference (cm) between the top strand of a fence and the top of the surrounding vegetation | θ | 67.69 cm (26.67 cm–96.10 cm) | + |
| Risk | Percentage of the fence segment in high risk areas based on Stevens et al. (2013) | θ | 45.8% (0.0%–100.0%) | + |
| Post | Type of posts used in a fence segment | θ | Wood (138), T-post (4), both (62) | Risk of t-post > both > wood |
| Surv | Biweekly survey (primary) period in which survey was conducted | θ, *p* | 1 (200), 2 (202), 3 (189), 4 (189), 5 (188), 6 (190), 7(186) | None |
| Visit | Visit (secondary period) in which survey took place | *p* | 1 (1019), 2 (1014), 3 (114), 4(112) | None |
| Obs | Observer conducting the survey | *p* | A (432), B (226), C (525), D (1076) | None |
| Trap | "Trap effects" for the 2nd and 4th visits to account for potential lack of independence between visits by the same observer | *p* | 1st/3rd (1133), 2nd/4th (1126) | Higher for 2nd/4th visits |
| Trap2 | "Trap effects" accounting for whether a collision was detected or not on the 1st visit | *p* | Non-detection (1135), detection (1080) | Higher if previously detected |
| Cloud | Cloud cover (%) | *p* | 46.1% (0.0%–100.0%) | − |
| Snow | Snow cover (%) | *p* | 33.8% (0.0%–100.0%) | + |

bushes and ground approximately 10 m out from either side of the fence for feathers or carcasses. Observers recorded ocular estimates of average snow and cloud cover (0–100%) during the course of each survey.

We considered a collision to have occurred when sage-grouse feathers were observed in the wires or barbs of a fence. We believe this represents a more accurate count of collisions as other experts have determined carcass recovery can be low due to scavenging (Stevens et al. 2011) and we believe wounded grouse may travel significant distances after striking fences before they expire. Collisions were recorded on each visit during which they were observed. In the event that feathers were found on the fence at multiple locations between two fence posts (the fencing between two fence-posts hereafter is referred to as a "panel"), the evidence was considered a single collision unless the largest gap between feathers on the wire exceeded the average wingspan of a sage-grouse (Sibley 2000). Analyses did not include any evidence in a fence that may have resulted from perching, prey plucking, or preening events, which were generally characterized by a small amount of feathers loosely affixed to the barbs of the fence and primarily distributed near a wooden post.

Observers thoroughly documented all collisions found via photographs and written notes. Observers recorded collision locations with a hand-held Global Positioning System (GPS) unit. Additionally, observers recorded the following information pertaining to the collision evidence: the distance from the evidence on the fence to the nearest fence-post, the distance from the evidence on the fence to the nearest marker, the distance from the ground (or top of the snow layer, when applicable) to the highest evidence on the fence, and the strand of wire containing the collision evidence. Finally, the observers collected the following data to describe the collision site: the distance between the two fence-posts for the panel containing the evidence, the mean height of the vegetation along the fence panel containing the collision evidence, and the number of strands of wire on the panel of fencing containing the evidence. Photographs of feathers were sent to local experts if the field observers could not be sure of identification. Collision events were only included in analyses when species identification was possible (i.e., diagnostic feathers found).

### 2.5. Covariate data collection

We measured fence exposure by estimating the average height of woody vegetation and the height of the top strand of fencing in centimeters for each panel. We then subtracted the height of the woody vegetation from the height of the top wire of fencing to obtain a value of "fence exposure" in centimeters for the panel. If vegetation was taller than the fence, fence exposure had a negative value. We measured these values for six panels within each 500 m stretch. Values were calculated at the two panels representing the endpoints and systematically at four additional locations at 100 m intervals along each fence segment. The fence exposure values for each of the six panels per stretch were then averaged to derive a single mean fence exposure value for the 500 m stretch. With assistance from BLM personnel, we also noted whether posts within a fence segment were wood posts, metal t-posts, or a combination of the two.

Using ArcGIS 10.0 (ESRI) we calculated several covariates including: 1) the number of occupied sage-grouse leks within 3 km of the focal lek, 2) the sum of mean maximum male lek counts in 2014 and 2015 for all leks within 3 km of the fence segment midpoint, 3) the distance from the midpoint of each fence stretch to the nearest occupied sage-grouse lek and the mean maximum male count for that lek from 2014 to 2015, 4) the proportion of each fence stretch that fell within the high risk category of the collision risk map (Stevens et al. 2013), and 5) the angle of exposure for each stretch of fence (i.e., the angle created by the triangle between the ends of the fence segment and the associated lek).

Lastly, observers estimated cloud cover during each survey and percent of the ground covered by snow to the nearest 10%. In 2014 observers recorded a single value for the average snow cover values surrounding each of the four fence segments during a survey. In 2015 observers recorded a separate value for average percentage of snow

cover along each fence segment. For analyses, we calculated the mean of the 2015 values for each survey to produce a single snow cover value consistent with the 2014 data. Table 1 summarizes all covariates included in our models.

### 2.6. Model justification and hypotheses

We used the method of working hypotheses (Chamberlin 1965) to evaluate alternate a priori hypotheses to understand how different marker types, site- and landscape-features and mapped collision zones affect sage-grouse fence collisions. We used the covariates in Table 1 to represent hypotheses for the objectives and translated the hypotheses into predictive models. We then used the predictive models to evaluate relative strength of evidence for the alternate hypotheses in a model selection framework (Burnham and Anderson 2002). We predicted detection of sage-grouse collisions at the fence segments would be incomplete, potentially biasing the measurement of effect sizes for the fence markers. Therefore, we evaluated several hypotheses for how observers and time occasions may influence the detectability of fence collisions. We predicted the detection of collisions would vary by observer (*Obs*), time of the biweekly surveys (*Surv*), and repeated visits (*Visits*, Table 1). We accounted for potential non-independence of detections when observers visited the fence segment twice on the same day using the *Trap2* covariate (Table 1). In addition, we hypothesized that snow cover (*Snow*) and cloud (*Cloud*) cover may interfere with the ability to detect the signs of collision (Table 1).

When evaluating the effectiveness of fence markers (objective 1), we predicted that collision risk would be lower on fence segments with markers than fence segments without markers (*Mark*, Table 1) since fence marking has been shown to reduce collision risk for grouse species (Stevens et al. 2013). In addition, we hypothesized that collision risk would be lowest on fence segments with yellow Fly Safe markers, intermediate on segments with white markers with reflective tape, and greatest on segments with white markers without reflective tape (*Trt,* Table 1). Because *Phasianid* species are known to see carotenoid-based colors (Mougeot et al. 2007), we predicted the bright yellow Fly Safe markers would be more effective than white markers with reflective tape. We predicted white markers with reflective tape would be more effective than white markers without reflective tape because reflective tape is thought to provide greater visibility for low light and snow background conditions (Stevens et al. 2013). In addition, we hypothesized that fence segments with wood posts would be more effective in reducing collisions than fence segments with iron t-posts and fence segments with both types (*Post*, Table 1) because wooden posts may be more conspicuous than iron t-posts (Stevens et al. 2012a) and sage-grouse are known to avoid areas with vertical woody structure (Stiver et al. 2006).

We evaluated site- and landscape features to identify areas with greater collision risk (objective 2) at multiple scales and to control for potentially confounding variables when evaluating the effectiveness of different marker types (Morrison et al. 2008). At the local scale, we hypothesized that collision risk would be higher on fence segments near active leks (*Distance*) and near leks with greater lek attendance (*Near Ct*, Table 1) as has been shown in previous research (Stevens et al. 2012b). In addition, we predicted that collision risk would be greater on fence segments with greater fence exposure above vegetation and on fence segments (*Fence Exp*) with a larger "exposure angle" in relation to the focal lek (*Angle*, Table 1). Stevens et al. (2012a) considered a variable for the height difference between the fence and the nearest lateral shrub, but did not find strong evidence for this variable. Nevertheless, we felt sage-grouse were more likely to fly above the vegetation than between it and greater fence exposure would therefore lead to greater collision risk. Given the positive association of collisions with lek counts and small lek distances, we hypothesized that birds needing to cross fencing to attend or leave a lek would have a higher risk of collision and used the *Angle* covariate to test this hypothesis. At the landscape scale, we hypothesized that collision risk would be greater in lek polygons with high numbers of occupied leks (*Occ Lek*) and with high lek counts (*Lek Ct*, Table 1). Stevens et al. (2012a, 2012b) measured the distance between fence segments and leks to show that distribution and abundance of leks was related to collision risk at the site-scale. We measured lek density and sage-grouse abundance within the 3-km$^2$ radius lek buffers (28 km$^2$) to evaluate the extent that lek distribution and abundance influenced collision risk of lek polygons at the landscape scale. Because sage-grouse are known to move between leks on the landscape (Emmons and Braun 1984), we predicted that lek polygons containing a greater number of leks and greater numbers of birds would also have greater collision risk. If landscape measures of lek distribution and abundance prove important, these covariates can be used to account for the dependence of the treatments within 3-km$^2$ radius lek polygons using the repeated measures design.

To evaluate an existing collision risk map by Stevens et al. (2013) (objective 3), we predicted that collision risk would be greater along fence segments in areas characterized by high risk than on fence characterized by moderate risk (*Risk*, Table 1). Because the collision risk map was based on terrain ruggedness and distance to nearest lek (Stevens et al. 2013), this hypothesis evaluates collision risk in response to moving farther from a lek with increasing topographic relief.

### 2.7. Statistical analyses

We developed a multi-scale occupancy model (Nichols et al. 2008) to estimate occupancy probabilities of collision evidence, and the factors influencing them at site- and fence-segment levels. The model allowed estimation of three parameters that corresponded to each level in the nested sampling design. We used repeat visits nested within each survey to estimate detection, repeat surveys of fence segments nested within a site (i.e., lek) to estimate small-scale occupancy (the probability of a collision occurring within a 500 m fence segment), and replicate leks nested within the study area to estimate large-scale occupancy (the probability of a collision occurring within any of the four fence segments associated with the focal lek). All analyses were conducted using Program MARK (version 8.0; White and Burnham 1999) via RMARK (version 2.1.14; Laake 2013). We defined our three general parameters as: (1) the probability that evidence of $\geq 1$ new sage-grouse collision was present on $\geq 1$ fence segment at site $i$ during any of the surveys, $\psi_i$, (2) the probability that evidence of $\geq 1$ new collision was present at a fence segment during survey $j$, $\theta_{ij}$, and (3) the probability that a new collision was detected on visit $k$, given the fence segment was occupied during survey $j$ and visit $k$, $p_{ijk}$. The multi-scale occupancy model is well suited for the repeated measures design by allowing the investigation of covariates influencing occupancy at the large-scale (i.e., collisions at any fence segment associated with a focal lek) as well as treatments effects on conditional occupancy at the small-scale (i.e., collisions at individual fence) while accounting for non-independence of fence segments within a lek. This is analogous to how variance is estimated in a mixed model with a random effect on the focal lek (Pavlacky et al. 2012). We assumed fence segments were closed to changes in occupancy within each survey and that new collisions were accurately identified and recorded. The fence segments were allowed to be open between surveys. This model also assumes that detections are independent; however, observers conducted the second visit on the opposite side of the fence immediately after the first visit. We attempted to account for this potential lack of independence by estimating separate detection probabilities for the first and second visits by the same observer during a survey period along with whether a collision was detected during the first visit.

### 2.8. Model set

To investigate our hypotheses regarding the factors influencing large- and small-scale occupancy and detection, the models in our

**Table 2**
Model set for models explaining variation in detection probabilities ($p$) of Greater Sage-Grouse fence collisions in Wyoming, 2014–2015. We fit models using the most general small- (θ) and large-scale (ψ) occupancy probability model structures. Because two covariates on each occupancy probability were different measures of similar hypotheses, we included both model structures on each of those parameters. Covariates included to explain variation in detection probabilities included: fixed visit effects (Visit), fixed survey effects (Surv), fixed observer effects (Obs), "trap effects" for the 2nd and 4th visits (Trap), "trap effects" accounting for whether a collision was detected or not on the 1st visit (Trap.2), cloud cover (Cloud), and snow cover (Snow). Model structure on small-scale occupancy included: fence exposure (Fence Exp), proportion of fence segment in high risk areas (Risk), angle of fence in relation to lek (Angle), Year, biweekly (primary) period (Surv), an interaction between post type and marker type (Post × Trt), and an interaction between distance to nearest lek and the count at that lek (Distance × Near Ct). Model structures on large-scale occupancy included: Year and either the sum of lek counts at nearby leks (Lek Ct) or the number of nearby occupied leks (Occ Lek; indicated in ψ column). The number of parameters (npar), Akaike's Information Criterion adjusted for small sample size ($AIC_c$), difference between a model's $AIC_c$ value and the minimum $AIC_c$ value ($\Delta AIC_c$), and $AIC_c$ weights are also shown for models with $\Delta AIC_c \leq 10$.

| ψ | $p$ | npar | $AIC_c$ | $\Delta AIC_c$ | Weight |
|---|---|---|---|---|---|
| Occ Lek | Null | 25 | 415.082 | 0.000 | 0.582 |
| Lek Ct | Null | 25 | 416.051 | 0.969 | 0.358 |
| Occ Lek | Snow | 26 | 423.116 | 8.034 | 0.010 |
| Occ Lek | Surv | 26 | 423.388 | 8.306 | 0.009 |
| Occ Lek | Cloud | 26 | 423.572 | 8.490 | 0.008 |
| Occ Lek | Trap.2 | 26 | 423.582 | 8.500 | 0.008 |
| Lek Ct | snow | 26 | 424.084 | 9.002 | 0.006 |
| Lek Ct | surv | 26 | 424.358 | 9.275 | 0.006 |
| Lek Ct | cloud | 26 | 424.541 | 9.459 | 0.005 |
| Lek Ct | trap.2 | 26 | 424.551 | 9.469 | 0.005 |

model set consisted of various combinations of covariates on each parameter. We included 3 covariates on large-scale occupancy (ψ), 10 on small-scale occupancy (θ), and 7 on detection ($p$; Table 1). We also included interactions between post type and marker, as well as minimum distance to the nearest lek and maximum male count for that lek on θ. Because the model set was very large when considering all possible combinations of covariates, we used a sequential approach to model selection (Lebreton et al. 1992). We fit models that included all possible additive combinations of covariates on detection, while including additive effects for all covariates for large- (ψ) and small-scale (θ) occupancy. There were two covariates on large-scale occupancy that were different measures of the same hypothesis: (1) the number of occupied leks within 3 km of the focal lek (Occ Lek, Table 1) and (2) the sum of the lek counts for leks within 3 km of the focal lek (Lek Ct). We did not include both covariates in the same model. Therefore, we fit a global model containing all other additive combinations of covariates with Occ Lek and Lek Ct. separately, resulting in two global models. Then, using the most parsimonious detection structure(s), we evaluated hypotheses related to large-scale occupancy. Retaining the best large-scale occupancy model structure(s), we fit models that included all possible combinations of covariates thought to influence small-scale occupancy, including the two interaction terms.

We used an information-theoretic approach for model selection and used Akaike's Information Criterion (AIC) adjusted for sample size ($AIC_c$) for model comparison (Burnham and Anderson 2002). We used Akaike weights, $w_i$, as a measure of the relative amount of evidence for each model. Our model set for small-scale occupancy was not balanced because of the interaction terms and mutually exclusive covariates (i.e., Mark and Trt), so we used a modified version of cumulative weights based on the frequency of the covariate in the model set [$w_+(j)$] (Doherty et al. 2012) to determine the relative importance of our covariates,

$$w_+(j) = \left[\frac{w}{1-w}\right] \Big/ \left[\frac{f}{1-f}\right],$$

where $w$ is the cumulative Akaike weight (sum of Akaike weights for models containing the covariate) and $f$ is the frequency of models containing the covariate in the model set. Weights $\gg 1$ indicate support for the importance of that variable, weights near 1 are inconclusive, and weights $\ll 1$ indicate little support for importance. We used the odds ratio to express the effect sizes (β) in terms of the percentage increase in the odds of collision.

## 3. Results

We found evidence of 64 confirmed fence collisions by sage-grouse during the study, with 15 detected in 2014 and 49 detected in 2015. Additionally, we observed 96 instances of possible or likely collisions which were not included in analyses. Over 60% of sites (16 of 26) and 26% of fence segments (27 of 104) contained evidence of $\geq 1$ confirmed collision. Only two fence segments were constructed using t-posts exclusively, and no collisions were detected at those segments; therefore, we fixed small-scale occupancy (θ) of those segments to zero to assist with numerical convergence.

Our global models used in the sequential model selection, included year and either the number of nearby occupied leks or the sum of the lek counts at those leks effects on large-scale occupancy, ψ (Year + Occ Lek) or ψ (Year + Lek Ct); year, survey, treatment × post type, distance to nearest lek × count for nearest lek, fence angle to lek, proportion in high risk areas, and fence exposure effects on small-scale occupancy, θ (Year + Surv + Distance + Angle + Risk + Fence Exp + Post × Trt + Distance × Near Ct); and observer, cloud cover, snow cover, and visit effects on detection, $p$ (Obs + Cloud + Snow + Visit).

### 3.1. Detection probabilities

Using these two global models, we explored 40 other detection structures, representing simplifications of our general detection structure (Tables 2 and A1). The most parsimonious model included a constant detection probability ($w = 0.59$), as did the 2nd best model, cumulatively accounting for 95.4% of the weight; thus, we retained this detection structure, $p$ (.), in our subsequent models. We estimated the probability of detecting $\geq 1$ collision at 0.935 (SE = 0.026).

### 3.2. Large-scale occupancy

Large-scale occupancy of collisions increased as the sum of nearby lek counts increased and was higher in 2015. However, the 95% confidence intervals for both of these effects included zero. Because of this uncertainty, the most parsimonious model for ψ was the constant model, which accounted for a majority of the $AIC_c$ weight ($w = 0.85$) (Table 3). On average, large-scale occupancy was estimated to be 0.717

**Table 3**
Model set for models explaining variation in large-scale occupancy probabilities (ψ) of Greater Sage-Grouse fence collisions in Wyoming, 2014–2015. We fit models using the most parsimonious model on detection probabilities (i.e., null) and the global model structure on small-scale occupancy probabilities (θ). Model structures on large-scale occupancy included: Year and either the sum of counts at leks with 3 km (Lek Ct) or the number of occupied leks within 3 km (Occ Lek; indicated in ψ column). Model structure on small-scale occupancy included: fence exposure (Fence Exp), proportion of fence segment in high risk areas (Risk), angle of fence in relation to lek (Angle), Year, biweekly (primary) period (Surv), an interaction between post type and marker type (Post × Trt), and an interaction between distance to nearest lek and the count at that lek (Distance × Near Ct). We also include the number of parameters (npar), Akaike's Information Criterion adjusted for small sample size ($AIC_c$), difference between a model's AICc value and the minimum AICc value ($\Delta AIC_c$), and $AIC_c$ weights.

| ψ | npar | $AIC_c$ | $\Delta AIC_c$ | Weight |
|---|---|---|---|---|
| Null | 23 | 402.913 | 0.000 | 0.852 |
| Lek Ct | 24 | 408.447 | 5.534 | 0.054 |
| Year | 24 | 408.498 | 5.585 | 0.052 |
| Occ Lek | 24 | 409.084 | 6.171 | 0.039 |
| Year + Occ Lek | 25 | 415.082 | 12.170 | 0.002 |
| Year + Lek Ct | 25 | 416.051 | 13.139 | 0.001 |

**Table 4**
Cumulative $AIC_c$ model weights for variables thought to influence small-scale occupancy (θ) of greater sage-grouse fence collisions in Wyoming, 2014–2015. Cumulative weights were adjusted based on the frequency of the covariate in the model set (Doherty et al. 2012). Variables included in the model set are: fence exposure (Fence Exp), proportion of fence segment in high risk areas (Risk), angle of fence in relation to lek (Angle), Year, biweekly (primary) period (Surv), wood post or wood and t-post (Post), marker type (Trt), whether a fence was marked or unmarked (regardless of marker type; Mark), the distance to the nearest occupied lek (Distance), the count at the nearest lek (Near Ct), an interaction between post type and marker type (Post × Trt), an interaction between post type and whether a fence was marked (Post × Mark), and an interaction between distance to nearest lek and the count at that lek (Distance × Near Ct). Modified cumulative model weights ≫ 1 suggest strong support for that variable, weights near 1 are ambiguous, and weights ≪ 1 suggest little support for that variable.

| Variable | Cumulative weight |
|---|---|
| Post | 12.797 |
| Mark | 4.188 |
| Distance | 3.349 |
| Fence Exp | 1.699 |
| Year | 1.261 |
| Risk | 1.246 |
| Near Ct | 1.078 |
| Post × Mark | 0.908 |
| Surv | 0.790 |
| Distance × Near Ct | 0.658 |
| Angle | 0.476 |
| Trt | 0.065 |
| Post × Trt | 0.001 |

(SE = 0.127).

### 3.3. Small-scale occupancy

We found strong evidence for effects of post type [$w_+$(Post) = 12.80], whether a fence was marked or not [irrespective or marker type, $w_+$(Mark) = 4.19], and distance to the nearest lek [$w_+$(Distance) = 3.35] on small-scale occupancy (Tables 4, 5, and A2). There was some support for the effects of fence exposure [$w_+$(Fence Exp) = 1.70], year [$w_+$(Year) = 1.26], the amount of fence segment within the high risk areas based on Stevens et al. (2013) [$w_+$(Risk) = 1.25], and the count at the nearest lek [$w_+$(Near Ct) = 1.08; Tables 4 and A2]. Consistent with our hypotheses, wood posts, fence marking, and increasing distance to nearest lek resulted in lower collision occupancy probabilities (Tables 6, A3, and A4 and Fig. 3). The amount of fence exposure and the proportion of fence in high risk areas increased the probability of a collision, as we predicted. Occupancy probabilities were higher in 2015 and as the count at the nearest lek increased, though these coefficients were not significant (Table 6). All marker types performed similarly [β = −0.843,(95% CI = −1.545, −0.141); odds ratio: 0.430, (0.128, 0.732)], with reflective [β = −1.018,(95% CI = −1.967, −0.068); odds ratio: 0.361, (0.018, 0.705)] and white markers [β = −0.808, (−1.703, 0.087); odds ratio: 0.446, (0.047, 0.857)] reducing occupancy probabilities slightly more than Fly Safe markers [β = −0.725, (−1.634, 0.184); odds ratio: 0.484, (0.044, 0.924)] based on the model including treatment and all other covariates with cumulative weights > 1.

## 4. Discussion

We adapted the multi-scale occupancy framework to investigate landscape- and local-scale features influencing the probability of fence collision, and our results support the anecdotal and limited empirical evidence for the threat of fences to sage-grouse (Christiansen 2009; Flake et al. 2010; Scott 1942; Stevens et al. 2012a, 2012b). Our study also provided insight into the factors influencing fence collisions at two spatial scales by using a multi-scale occupancy model. In addition to accounting for imperfect detection of collisions, this approach allowed us to account for the lack of independence between fence segments associated with a particular lek (Nichols et al. 2008; Pavlacky et al. 2012).

Studies regarding potential risk of collision with human-associated infrastructure have noted that risks to lekking species may be higher in close proximity to lek locations (Baines and Summers 1997; Bevanger 1994; Stevens et al. 2012a, 2012b). Therefore, we tested four hypotheses relating to the risk of collision in association to the number of leks, the number of individuals observed at nearby leks, the position of fencing (angle) in relation to a nearby lek, and the distance to the nearest lek. Unlike Stevens et al. (2012a), we found little evidence for an effect of the number of birds using nearby leks on collision probabilities and therefore failed to confirm our hypothesis. Similarly, there

**Table 5**
Model set for models explaining variation in small-scale occupancy probabilities (θ) of Greater Sage-Grouse fence collisions in Wyoming, 2014–2015. We fit models using the most parsimonious model on detection probabilities (i.e., null) and large-scale occupancy probabilities (i.e., null). Model structures on small-scale occupancy included: distance to nearest lek (Distance), the count at the nearest lek (Near Ct), fence exposure (Fence Exp), wood post or t-post (Post), proportion of fence segment in high risk areas (Risk), angle of fence in relation to lek (Angle), marker type (Trt), marked or unmarked fence (regardless of marker type; Mark), Year, biweekly (primary) period (Surv), an interaction between Distance and Near Ct, and an interaction between Post and Mark or Trt. The number of parameters (npar), Akaike's Information Criterion adjusted for small sample size ($AIC_c$), difference between a model's AICc value and the minimum AICc value ($\Delta AIC_c$), and $AIC_c$ weights are also shown for the top 10 models.

| θ | npar | $AIC_c$ | $\Delta AIC_c$ | Weight |
|---|---|---|---|---|
| Fence Exp + Mark + Distance + Post + Risk + Near Ct | 9 | 364.644 | 0.000 | 0.030 |
| Fence Exp + Mark + Distance + Post + Risk + Year | 9 | 364.756 | 0.111 | 0.028 |
| Fence Exp + Mark + Distance + Post + Risk + Year + Near Ct | 10 | 364.903 | 0.259 | 0.026 |
| Fence Exp + Mark + Post + Risk + Distance × Near Ct | 10 | 365.270 | 0.626 | 0.022 |
| Surv + Fence Exp + Mark + Distance + Post + Risk + Year | 15 | 365.647 | 1.003 | 0.018 |
| Fence Exp + Mark + Distance + Post + Near Ct | 8 | 365.762 | 1.118 | 0.017 |
| Fence Exp + Mark + Post + Risk + Year + Distance × Near Ct | 11 | 365.794 | 1.150 | 0.017 |
| Surv + Fence Exp + Mark + Distance + Post + Year | 14 | 365.810 | 1.166 | 0.017 |
| Fence Exp + Mark + Distance + Post + Year + Near Ct | 9 | 365.998 | 1.354 | 0.015 |
| Fence Exp + Mark + Distance + Post + Risk | 8 | 366.015 | 1.371 | 0.015 |

**Table 6**
Coefficient estimates, standard errors (SE), and 95% confidence intervals (CI) for all variables explaining variation in small-scale occupancy (θ) probabilities of Greater Sage-Grouse fence collisioins in Wyoming, 2014–2015. Variables include fence exposure, whether a fence was marked (regardless of marker type; Mark), the distance to nearest lek (Distance), fences with wood and t-posts (wood and t-post), proportion of fence segment in high risk areas (Risk), year (2015), and the count at the nearest lek (Near Ct). The intercept represents an unmarked fence with wood posts in 2014 with all continuous variable values set to 0. Variables included had modified cumulative $AIC_c$ weights > 1. Estimates from the third best model are reported because it is the best model including all variables with cumulative weights > 1. All significant coefficients (i.e., 95% CIs do no overlap 0) are indicated by an asterisk.

| Parameter | Mean | SE | 95% CI |
|---|---|---|---|
| Intercept* | −5.544 | 1.123 | (−7.745, −3.342) |
| Fence Exp* | 0.031 | 0.013 | (0.005, 0.058) |
| Mark* | −0.843 | 0.358 | (−1.545, −0.141) |
| Distance* | −0.586 | 0.192 | (−0.962, −0.210) |
| Wood and T-post* | 1.774 | 0.382 | (1.025, 2.523) |
| Risk* | 1.150 | 0.565 | (0.042, 2.258) |
| 2015 | 0.821 | 0.473 | (−0.105, 1.747) |
| Near Ct | 0.004 | 0.002 | (−0.001, 0.009) |

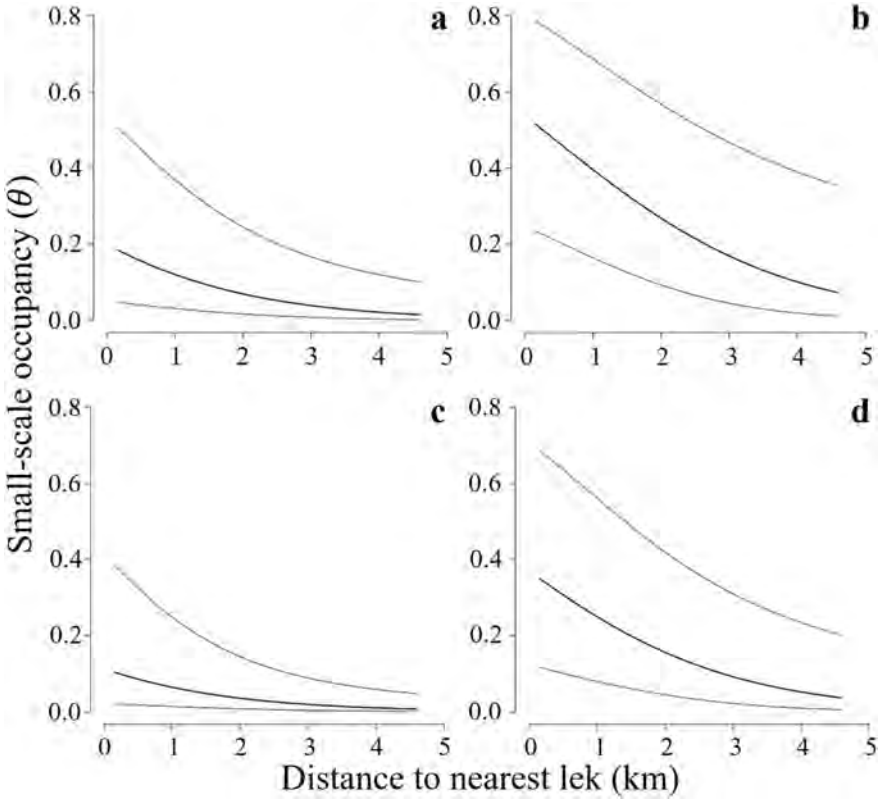



**Fig. 3.** Small-scale occupancy probability (θ, heavy lines) and associated 95% confidence intervals (light lines) as a function of distance to nearest lek for a) unmarked, wood post, b) unmarked, wood and t-post, c) marked, wood post, and d) marked, wood and t-post fence segments.

was no evidence to support an increased risk of collision near fencelines that are near multiple leks. Baines and Andrew (2003) similarly found no effect of lek indices on collision risk indicating that other factors may be more predicitive. Our findings may be partially due to using presence-absence data to detect differences among leks of various sizes, such that the probability of ≥ 1 collision is high for a fence near even a single smaller lek. Addtionally, lek counts have been criticized for their inability to accurately reflect abundance of sage-grouse (Beck and Braun 1980; Johnson and Rowland 2007; Walsh et al. 2004) but have been shown to be a reasonable index of the population of breeding males when standard survey protocols are followed (Jenni and Hartzler 1978; Emmons and Braun 1984; Walsh et al. 2004; Johnson and Rowland 2007). However, lek counts may not accurately represent the number of birds in the area surrounding a lek, and therefore, may be a poor indicator of the likelihood of a collision. We therefore recommend that future efforts to estimate or account for collision risk use estimated densities when possible.

Although there is an abundance of peer-reviewed work indicating that flight paths may greatly increase the risk of bird collisions with human infrastructure (Bevanger 1994; Bevanger 1998; Everaert and Stienen 2007; Henderson et al. 1996; Scott et al. 1972), we found no evidence for increased collision risk with an increased angle of fence exposure in relation to the lek which failed to confirm our hypothesis. It is possible this covariate was confounded with the distance to the nearest lek (closer distances having a larger angle) which we tested and describe in the following text. Nevertheless, we maintain that flight paths may be important in determining collision risk for some systems and species and encourage researchers to consider other potential vegetative, topographical, biological, and environmental factors that may influence or create flight paths in future studies.

We found the proximity of a fence segment to a lek influenced the probability of a collision (Distance); the average occupancy probability decreased by approximately 39% between distances of 153 m (i.e., smallest distance observed) and 1 km. This is consistent with the findings of Stevens et al. (2012a, 2012b) and confirmed our hypothesis. This relationship is likely due to increased encounters between birds and fences when a fence is closer to an area where birds congregate. We therefore recommend that marking efforts preferentially mark fence close to leks in the future. Additionally, we encourage future studies investigating risks of collisions with human-related infrastructure to consider accounting for water and/or food sources, geophagy sites, or other features that may lure large numbers of individuals into a localized area.

As in Stevens et al. (2012a), our results suggest that fence post type has the largest effect on the occupancy probability of sage-grouse collisions, with the lowest occupancy probabilities for fence segments with wooden posts, which confirmed our hypothesis. Only two fence segments in our study had t-posts exclusively and neither of those segments had evidence of a collision on them; therefore, we were unable to estimate occupancy probabilities for segments with only t-posts. Unmarked fence segments with wooden posts had lower occupancy probabilities than segments with both wooden and t-posts and any of the fence markers; yet, collision rates for fence segments with wooden posts were reduced further by the use of fence markers. These results are consistent with those found by Summers and Dugan (2001), in which, they found full length paling (which resemble wooden posts) to be the most visible fence marker. As such, we recommend future marking efforts consider testing the effectiveness of wooden stays woven into the fencing. Additionally, preferentially marking fencing with t-posts or a mixture of wood and t-posts could maximize the reduction in potential *Phasianid* collisions with fencing as our results indicated fences without wooden posts may have high rates of collisions.

We found a small effect of the amount of exposed fencing on collision risk. As vegetation height near a fence decreased, the probability of a collision increased which supported our hypothesis. *Phasianids* are generally classified as “poor flyers” (Bevanger 1994; Rayner 1988) which characteristically engage in short flights (Viscor and Fuster 1987). These morphological constraints likely result in *Phasianids* engaging in proportionately more of their flight at low altitudes, often near the top of exposed vegetation, than many birds with lower wing

loading. As the top of vegetation approaches or exceeds the top of human infrastructure there is thought to be less risk of collisions (Bevanger 1994). Although we observed a weak relationship between the amount of exposed fence and collision risk, we maintain areas with short vegetation may benefit more from the use of markers by making the fence more visible. Similarly, we suggest that taller "elk fences" in the western U.S. and "deer fences" in Europe may increase collision risk beyond that of stock fencing due to the potential for additional fence projection above the vegetation as well as a general increase in total fence area. This idea was not explicitly tested in our study and represents an area for future research.

Our study design was largely based on the collision risk map developed by Stevens et al. (2013) which predicted high risk of collisions in areas close to leks and with little topography. The authors acknowledged their range-wide model was created using data collected within a relatively small geographic area in Idaho. As such, they recommended additional validation efforts be conducted. Our findings suggested a slightly increased collision probability in high risk areas, but this effect was weak. Because we attempted to select fence-line segments within the high and moderate risk areas of this map, much of the fence-line included in our study fell within these areas. Therefore, low risk areas were not well represented in our study, precluding an evaluation of the low risk portions of the risk map. We recommend further investigation of the efficacy of the collision risk map in predicting collision risk, particularly to determine if greater slopes associated with topography do impact collision risk range-wide and to determine if low risk areas on the collision risk map have a lower number of associated fence collisions. Until the collision risk map can be evaluated further, we recommend that managers seeking to reduce sage-grouse collisions focus their fence-marking efforts on fence-lines in both the high and moderate risk zones which are both close to leks and possess local site characteristics which have been shown to increase collision risk in our study and/or in previous studies.

We estimated a detection rate of 0.94, suggesting a false absence rate of 6% in the raw collision data. Our detection rate was similar to the collision detection rate calculated by Baines and Andrew (2003) when they simulated collision events with grouse carcasses. This indicates that detection of collision events is likely quite high when conducting walking surveys, provided that evidence of the collision still persists on the landscape. Stevens et al. (2011) calculated much lower detection rates when conducting walking surveys within 15 m of bird carcasses which were placed in the field; however, their estimates accounted for both detectability and scavenging bias. We suspect the scavenging bias was the driving factor in the reduced detection rates; however, they also placed carcasses beyond the search window of both our study and that of Baines and Andrews (both, of which had an effective search strip width of approximately 5 m). Furthermore, Stevens et al. placed piles of feathers and the carcasses within the habitat whereas in the Baines and Andrews study the carcasses were "vigorously thrown at the fence to simulate flight collisions". Given that we regularly witnessed feathers widely strewn across areas of 30 m or more in our study, we feel the methods used by Stevens et al. (2011) may not have accurately created conditions similar to that of an actual collision event, ultimately underestimating detection probabilities of *Phasianid* collision evidence.

Our results suggest that all three types of fence markers employed in our research were effective at reducing collision probabilities and confirmed our hypothesis, with stretches of marked fence having a 57% (27% - 87%) lower probability of containing $\geq 1$ collision. These results align with previous studies by Stevens et al. (2012b) and Baines and Andrew (2003) which found marking fences reduced *Phasianid* collisions with fencing. Our results provided weak evidence that reflective markers were the most effective marker type in our study, with a 64% (30%–98%) reduction in collision probability. Stevens et al. (2012b) saw an 83% reduction in sage-grouse collisions using reflective markers. The smaller effect observed in our study may be due in part to less resolution to detect covariate effects when using occupancy models compared to abundance measures because counts are summarized to presence or absence. In addition, the smaller effect observed in our study may be partially related to accounting for incomplete detection of sage-grouse collisions, despite detection being quite high. The collision reduction estimated in our study aligns well with the estimated 64% reduction for capercaillie, 91% reduction for black grouse, and 49% reduction for red grouse estimated by Baines and Andrew (2003).

Overall, we found little difference in the effectiveness of the three marker types, as models with a marker effect (for any marker type) had substantially more cumulative $AIC_c$ weight than models with effects for all marker types individually. However, contrary to our hypothesis, Fly Safe markers were slightly less effective than both white and reflective markers. We estimated average per marker costs for white markers at $0.14, reflective markers at $0.71, and Fly Safe markers at $0.40 (USD). Therefore, using the plain white markers without reflective tape, may represent the most cost-effective sage-grouse marking strategy of those we tested. In Europe, the only study to our knowledge, which investigated marker utility in preventing *Phasianid* collisions employed two strips of orange plastic netting on the fence (Baines and Andrew 2003). The authors acknowledged that, although effective in reducing collisions within woodlands, this marker style was not suitable for deployment in areas exposed to weather (i.e., open moorland), where red grouse densities may be high. We witnessed very little damage to the three types of markers we deployed and therefore recommend trials using these marker types in open habitats of Europe.

The effectiveness of the fence markers in reducing *Phasianid* collisions highlights the importance of integrating fence marking into ongoing conservation efforts. Prescribed grazing is often recommended to improve nesting and wintering habitat conditions for lekking-species of conservation concern such as the greater-sage-grouse (Monroe et al. in review) and lesser prairie-chicken (Hagen et al. 2016). Because the implementation of rotational grazing systems involves additional fencing to subdivide an area into several pastures (United States Fish and Wildlife Service, USFWS 2010), we recommend marking exposed fence near leks even in areas thought to have only moderate collision risk due to topography. We suggest fence marking may reduce the potential for ecological traps (Battin 2004) associated with conservation practices that require the creation of additional fencing.

## Acknowledgments

This project was funded entirely through a Conservation Innovation Grant (69-3A75-12-188, 2012) provided through the USDA Natural Resources Conservation Service (NRCS). We thank Tom Christiansen of the Wyoming Game and Fish Department for sharing his expertise on greater sage-grouse feather identification, identifying evidence of collisions on fencing, and survey methodology. Dale Woolwine of the Wyoming Bureau of Land Management provided the fence layer shapefiles used for sample selection, advice regarding survey methods, assistance with covariate data collection used in analysis, and was instrumental in assisting with field logistics and access to survey sites. We thank Tony Mong of Wyoming Game and Fish Department for providing greater sage-grouse lek data used in analyses. We greatly appreciate Bird Conservancy staff, as well as their families and friends, for helping to add the reflective tape to the vinyl markers. We appreciate the efforts of David Kramer, Jenny Berven, Eric DeFonso, as well as Meghann Durbrow and her NRCS staff for their assistance installing fence markers. Additionally, Jenny Berven created maps of the study sites and Brittany Woiderski provided GIS support to measure spatial covariates. We would like to acknowledge Galen Reid who volunteered his time to collect data during the 2014 field season. We also thank field technicians Angela Stemen (2014) and Josh Olsen (2015) for their efforts collecting data in the field.

## Appendix A

Table A1

Model set for models explaining variation in detection probabilities (*p*) of Greater Sage-Grouse fence collisions in Wyoming, 2014–2015. We fit models using the most general small- (θ) and large-scale (ψ) occupancy probability model structures. Because two covariates on each occupancy probability were different measures of similar hypotheses, we included both model structures on each of those parameters. Covariates included to explain variation in detection probabilities included: fixed visit effects (Visit), fixed survey effects (Surv), fixed observer effects (Obs), "trap effects" for the 2nd and 4th visits (Trap), "trap effects" accounting for whether a collision was detected or not on the 1st visit (Trap.2), cloud cover (Cloud), and snow cover (Snow). Model structure on small-scale occupancy included: fence exposure (Fence Exp), proportion of fence segment in high risk areas (Risk), angle of fence in relation to lek (Angle), Year, biweekly (primary) period (Surv), an interaction between post type and marker type (Post × Trt), and an interaction between distance to nearest lek and the count at that lek (Distance × Near Ct). Model structures on large-scale occupancy included: Year and either the sum of lek counts at nearby leks (Lek Ct) or the number of nearby occupied leks (Occ Lek; indicated in ψ column). The number of parameters (npar), Akaike's Information Criterion adjusted for small sample size ($AIC_c$), difference between a model's $AIC_c$ value and the minimum $AIC_c$ value ($\Delta AIC_c$), and $AIC_c$ weights are included.

| ψ | *p* | npar | $AIC_c$ | $\Delta AIC_c$ | Weight |
|---|---|---|---|---|---|
| Occ Lek | Null | 25 | 415.082 | 0.000 | 0.582 |
| Lek Ct | Null | 25 | 416.051 | 0.969 | 0.358 |
| Occ Lek | Snow | 26 | 423.116 | 8.034 | 0.010 |
| Occ Lek | Surv | 26 | 423.388 | 8.306 | 0.009 |
| Occ Lek | Cloud | 26 | 423.572 | 8.490 | 0.008 |
| Occ Lek | Trap2 | 26 | 423.582 | 8.500 | 0.008 |
| Lek Ct | Snow | 26 | 424.084 | 9.002 | 0.006 |
| Lek Ct | Surv | 26 | 424.358 | 9.275 | 0.006 |
| Lek Ct | Cloud | 26 | 424.541 | 9.459 | 0.005 |
| Lek Ct | Trap2 | 26 | 424.551 | 9.469 | 0.005 |
| Occ Lek | Surv + Snow | 27 | 432.197 | 17.115 | < 0.001 |
| Occ Lek | Cloud + Snow | 27 | 432.347 | 17.265 | < 0.001 |
| Occ Lek | Snow + Trap2 | 27 | 432.355 | 17.273 | < 0.001 |
| Occ Lek | Surv + Cloud | 27 | 432.568 | 17.486 | < 0.001 |
| Occ Lek | Surv + Trap2 | 27 | 432.627 | 17.545 | < 0.001 |
| Occ Lek | Trap | 27 | 432.720 | 17.637 | < 0.001 |
| Occ Lek | Cloud + Trap2 | 27 | 432.811 | 17.729 | < 0.001 |
| Lek Ct | Surv + Snow | 27 | 433.166 | 18.084 | < 0.001 |
| Lek Ct | Cloud + Snow | 27 | 433.315 | 18.233 | < 0.001 |
| Lek Ct | Snow + Trap2 | 27 | 433.323 | 18.241 | < 0.001 |
| Lek Ct | Surv + Cloud | 27 | 433.537 | 18.455 | < 0.001 |
| Lek Ct | Surv + Trap2 | 27 | 433.597 | 18.514 | < 0.001 |
| Lek Ct | Trap | 27 | 433.688 | 18.606 | < 0.001 |
| Lek Ct | Cloud + Trap2 | 27 | 433.780 | 18.698 | < 0.001 |
| Occ Lek | Obs | 28 | 439.208 | 24.126 | < 0.001 |
| Lek Ct | Obs | 28 | 440.177 | 25.095 | < 0.001 |
| Occ Lek | Visit | 28 | 440.748 | 25.665 | < 0.001 |
| Lek Ct | Visit | 28 | 441.716 | 26.633 | < 0.001 |
| Occ Lek | Surv + Cloud + Snow | 28 | 442.205 | 27.123 | < 0.001 |
| Occ Lek | Surv + Snow + Trap2 | 28 | 442.276 | 27.194 | < 0.001 |
| Occ Lek | Snow + Trap | 28 | 442.373 | 27.290 | < 0.001 |
| Occ Lek | Cloud + Snow + Trap2 | 28 | 442.426 | 27.344 | < 0.001 |
| Occ Lek | Surv + Trap | 28 | 442.621 | 27.538 | < 0.001 |
| Occ Lek | Surv + Cloud + Trap2 | 28 | 442.647 | 27.565 | < 0.001 |
| Occ Lek | Cloud + Trap | 28 | 442.789 | 27.707 | < 0.001 |
| Lek Ct | Surv + Cloud + Snow | 28 | 443.173 | 28.091 | < 0.001 |
| Lek Ct | Surv + Snow + Trap2 | 28 | 443.245 | 28.163 | < 0.001 |
| Lek Ct | Snow + Trap | 28 | 443.342 | 28.260 | < 0.001 |
| Lek Ct | Cloud + Snow + Trap2 | 28 | 443.394 | 28.312 | < 0.001 |
| Lek Ct | Surv + Trap | 28 | 443.589 | 28.507 | < 0.001 |
| Lek Ct | Surv + Cloud + Trap2 | 28 | 443.616 | 28.534 | < 0.001 |
| Lek Ct | Cloud + Trap | 28 | 443.758 | 28.676 | < 0.001 |
| Occ Lek | Snow + Obs | 29 | 449.910 | 34.828 | < 0.001 |
| Occ Lek | Cloud + Obs | 29 | 450.240 | 35.158 | < 0.001 |
| Occ Lek | Surv + Obs | 29 | 450.246 | 35.164 | < 0.001 |
| Lek Ct | Snow + Obs | 29 | 450.877 | 35.795 | < 0.001 |
| Lek Ct | Cloud + Obs | 29 | 451.208 | 36.126 | < 0.001 |
| Lek Ct | Surv + Obs | 29 | 451.215 | 36.133 | < 0.001 |
| Occ Lek | Visit + Snow | 29 | 451.315 | 36.233 | < 0.001 |
| Occ Lek | Visit + Surv | 29 | 451.656 | 36.573 | < 0.001 |
| Occ Lek | Visit + Cloud | 29 | 451.786 | 36.704 | < 0.001 |
| Occ Lek | Visit + Trap2 | 29 | 451.786 | 36.704 | < 0.001 |
| Lek Ct | Visit + Snow | 29 | 452.283 | 37.200 | < 0.001 |

| | | | | | |
|---|---|---|---|---|---|
| Lek Ct | Visit + Surv | 29 | 452.624 | 37.542 | < 0.001 |
| Lek Ct | Visit + Cloud | 29 | 452.754 | 37.672 | < 0.001 |
| Lek Ct | Visit + Trap2 | 29 | 452.755 | 37.672 | < 0.001 |
| Occ Lek | Surv + Cloud + Snow + Trap2 | 29 | 453.244 | 38.162 | < 0.001 |
| Occ Lek | Surv + Snow + Trap | 29 | 453.256 | 38.173 | < 0.001 |
| Occ Lek | Cloud + Snow + Trap | 29 | 453.403 | 38.320 | < 0.001 |
| Occ Lek | Surv + Cloud + Trap | 29 | 453.607 | 38.525 | < 0.001 |
| Lek Ct | Surv + Cloud + Snow + Trap2 | 29 | 454.212 | 39.130 | < 0.001 |
| Lek Ct | Surv + Snow + Trap | 29 | 454.225 | 39.143 | < 0.001 |
| Lek Ct | Cloud + Snow + Trap | 29 | 454.372 | 39.290 | < 0.001 |
| Lek Ct | Surv + Cloud + Trap | 29 | 454.576 | 39.494 | < 0.001 |
| Occ Lek | Surv + Snow + Obs | 30 | 462.022 | 46.940 | < 0.001 |
| Occ Lek | Cloud + Snow + Obs | 30 | 462.034 | 46.951 | < 0.001 |
| Occ Lek | Surv + Cloud + Obs | 30 | 462.383 | 47.300 | < 0.001 |
| Lek Ct | Surv + Snow + Obs | 30 | 462.989 | 47.907 | < 0.001 |
| Lek Ct | Cloud + Snow + Obs | 30 | 463.000 | 47.917 | < 0.001 |
| Lek Ct | Surv + Cloud + Obs | 30 | 463.351 | 48.269 | < 0.001 |
| Occ Lek | Visit + Surv + Snow | 30 | 463.354 | 48.271 | < 0.001 |
| Occ Lek | Visit + Cloud + Snow | 30 | 463.458 | 48.376 | < 0.001 |
| Occ Lek | Visit + Snow + Trap2 | 30 | 463.458 | 48.376 | < 0.001 |
| Occ Lek | Visit + Trap | 30 | 463.600 | 48.517 | < 0.001 |
| Occ Lek | Visit + Surv + Cloud | 30 | 463.780 | 48.698 | < 0.001 |
| Occ Lek | Visit + Surv + Trap2 | 30 | 463.799 | 48.716 | < 0.001 |
| Occ Lek | Visit + Cloud + Trap2 | 30 | 463.929 | 48.847 | < 0.001 |
| Lek Ct | Visit + Surv + Snow | 30 | 464.321 | 49.239 | < 0.001 |
| Lek Ct | Visit + Cloud + Snow | 30 | 464.425 | 49.343 | < 0.001 |
| Lek Ct | Visit + Snow + Trap2 | 30 | 464.425 | 49.343 | < 0.001 |
| Lek Ct | Visit + Trap | 30 | 464.567 | 49.485 | < 0.001 |
| Lek Ct | Visit + Surv + Cloud | 30 | 464.748 | 49.666 | < 0.001 |
| Lek Ct | Visit + Surv + Trap2 | 30 | 464.767 | 49.685 | < 0.001 |
| Lek Ct | Visit + Cloud + Trap2 | 30 | 464.897 | 49.815 | < 0.001 |
| Occ Lek | Surv + Cloud + Snow + Trap | 30 | 465.335 | 50.252 | < 0.001 |
| Lek Ct | Surv + Cloud + Snow + Trap | 30 | 466.304 | 51.222 | < 0.001 |
| Occ Lek | Visit + Obs | 31 | 474.083 | 59.000 | < 0.001 |
| Lek Ct | Visit + Obs | 31 | 475.051 | 59.969 | < 0.001 |
| Occ Lek | Surv + Cloud + Snow + Obs | 31 | 475.438 | 60.355 | < 0.001 |
| Lek Ct | Surv + Cloud + Snow + Obs | 31 | 476.404 | 61.322 | < 0.001 |
| Occ Lek | Visit + Snow + Trap | 31 | 476.629 | 61.547 | < 0.001 |
| Occ Lek | Visit + Surv + Cloud + Snow | 31 | 476.755 | 61.673 | < 0.001 |
| Occ Lek | Visit + Surv + Snow + Trap2 | 31 | 476.775 | 61.692 | < 0.001 |
| Occ Lek | Visit + Cloud + Snow + Trap2 | 31 | 476.879 | 61.797 | < 0.001 |
| Occ Lek | Visit + Surv + Trap | 31 | 476.984 | 61.902 | < 0.001 |
| Occ Lek | Visit + Cloud + Trap | 31 | 477.020 | 61.938 | < 0.001 |
| Occ Lek | Visit + Surv + Cloud + Trap2 | 31 | 477.201 | 62.119 | < 0.001 |
| Lek Ct | Visit + Snow + Trap | 31 | 477.597 | 62.515 | < 0.001 |
| Lek Ct | Visit + Surv + Cloud + Snow | 31 | 477.723 | 62.641 | < 0.001 |
| Lek Ct | Visit + Surv + Snow + Trap2 | 31 | 477.742 | 62.660 | < 0.001 |
| Lek Ct | Visit + Cloud + Snow + Trap2 | 31 | 477.846 | 62.764 | < 0.001 |
| Lek Ct | Visit + Surv + Trap | 31 | 477.952 | 62.870 | < 0.001 |
| Lek Ct | Visit + Cloud + Trap | 31 | 477.988 | 62.906 | < 0.001 |
| Lek Ct | Visit + Surv + Cloud + Trap2 | 31 | 478.169 | 63.087 | < 0.001 |
| Occ Lek | Visit + Snow + Obs | 32 | 488.636 | 73.554 | < 0.001 |
| Occ Lek | Visit + Cloud + Obs | 32 | 488.987 | 73.905 | < 0.001 |
| Occ Lek | Visit + Surv + Obs | 32 | 488.994 | 73.912 | < 0.001 |
| Lek Ct | Visit + Snow + Obs | 32 | 489.603 | 74.521 | < 0.001 |
| Lek Ct | Visit + Cloud + Obs | 32 | 489.955 | 74.873 | < 0.001 |
| Lek Ct | Visit + Surv + Obs | 32 | 489.962 | 74.880 | < 0.001 |
| Occ Lek | Visit + Surv + Snow + Trap | 32 | 491.496 | 76.413 | < 0.001 |
| Occ Lek | Visit + Cloud + Snow + Trap | 32 | 491.542 | 76.459 | < 0.001 |
| Occ Lek | Visit + Surv + Cloud + Trap | 32 | 491.893 | 76.811 | < 0.001 |
| Lek Ct | Visit + Surv + Snow + Trap | 32 | 492.464 | 77.382 | < 0.001 |
| Lek Ct | Visit + Cloud + Snow + Trap | 32 | 492.510 | 77.427 | < 0.001 |
| Lek Ct | Visit + Surv + Cloud + Trap | 32 | 492.861 | 77.778 | < 0.001 |
| Occ Lek | Visit + Surv + Snow + Obs | 33 | 505.266 | 90.184 | < 0.001 |
| Occ Lek | Visit + Cloud + Snow + Obs | 33 | 505.279 | 90.197 | < 0.001 |
| Occ Lek | Visit + Surv + Cloud + Obs | 33 | 505.653 | 90.571 | < 0.001 |

| | | | | | |
|---|---|---|---|---|---|
| Lek Ct | Visit + Surv + Snow + Obs | 33 | 506.233 | 91.150 | < 0.001 |
| Lek Ct | Visit + Cloud + Snow + Obs | 33 | 506.245 | 91.163 | < 0.001 |
| Lek Ct | Visit + Surv + Cloud + Obs | 33 | 506.621 | 91.539 | < 0.001 |

Table A2
Model set for models explaining variation in small-scale occupancy probabilities (θ) of Greater Sage-Grouse fence collisions in Wyoming, 2014–2015. We fit models using the most parsimonious model on detection probabilities (i.e., null) and large-scale occupancy probabilities (i.e., null). Model structures on small-scale occupancy included: distance to nearest lek (Distance), the count at the nearest lek (Near Ct), fence exposure (Fence Exp), wood post or t-post (Post), proportion of fence segment in high risk areas (Risk), angle of fence in relation to lek (Angle), marker type (Trt), marked or unmarked fence (regardless of marker type; Mark), Year, biweekly (primary) period (Surv), an interaction between Distance and Near Ct, and an interaction between Post and Mark or Trt. The number of parameters (npar), Akaike's Information Criterion adjusted for small sample size ($AIC_c$), difference between a model's AICc value and the minimum AICc value ($\Delta AIC_c$), and $AIC_c$ weights are included for models with $\Delta AIC_c < 4$.

| θ | npar | $AIC_c$ | $\Delta AIC_c$ | weight |
|---|---|---|---|---|
| Fence Exp + Mark + Distance + Post + Risk + Near Ct | 9 | 364.644 | 0.000 | 0.030 |
| Fence Exp + Mark + Distance + Post + Risk + Year | 9 | 364.756 | 0.111 | 0.028 |
| Fence Exp + Mark + Distance + Post + Risk + Year + Near Ct | 10 | 364.903 | 0.259 | 0.026 |
| Fence Exp + Mark + Post + Risk + Distance × Near Ct | 10 | 365.270 | 0.626 | 0.022 |
| Surv + Fence Exp + Mark + Distance + Post + Risk + Year | 15 | 365.647 | 1.003 | 0.018 |
| Fence Exp + Mark + Distance + Post + Near Ct | 8 | 365.762 | 1.118 | 0.017 |
| Fence Exp + Mark + Post + Risk + Year + Distance × Near Ct | 11 | 365.794 | 1.150 | 0.017 |
| Surv + Fence Exp + Mark + Distance + Post + Year | 14 | 365.810 | 1.166 | 0.017 |
| Fence Exp + Mark + Distance + Post + Year + Near Ct | 9 | 365.998 | 1.354 | 0.015 |
| Fence Exp + Mark + Distance + Post + Risk | 8 | 366.015 | 1.371 | 0.015 |
| Fence Exp + Mark + Distance + Post + Year | 8 | 366.230 | 1.586 | 0.014 |
| Surv + Mark + Distance + Post + Year | 13 | 366.584 | 1.940 | 0.011 |
| Surv + Fence Exp + Distance + Post + Risk + Year | 14 | 366.689 | 2.045 | 0.011 |
| Surv + Fence Exp + Mark + Distance + Post + Risk | 14 | 366.791 | 2.147 | 0.010 |
| Surv + Fence Exp + Mark + Distance + Post + Near Ct | 14 | 366.803 | 2.159 | 0.010 |
| Surv + Fence Exp + Mark + Distance + Post + Risk + Near Ct | 15 | 366.871 | 2.227 | 0.010 |
| Surv + Fence Exp + Distance + Post + Year | 13 | 366.883 | 2.239 | 0.010 |
| Surv + Mark + Distance + Post + Risk + Year | 14 | 366.897 | 2.253 | 0.010 |
| Fence Exp + Distance + Post + Risk + Year | 8 | 366.926 | 2.282 | 0.010 |
| Surv + Distance + Post + Risk + Year | 13 | 366.997 | 2.353 | 0.009 |
| Surv + Distance + Post + Year | 12 | 367.005 | 2.361 | 0.009 |
| Angle + Surv + Post + Year | 12 | 367.072 | 2.428 | 0.009 |
| Surv + Fence Exp + Mark + Distance + Post | 13 | 367.177 | 2.533 | 0.008 |
| Fence Exp + Distance + Post + Risk + Year + Near Ct | 9 | 367.183 | 2.538 | 0.008 |
| Angle + Surv + Distance + Post + Year | 13 | 367.336 | 2.692 | 0.008 |
| Surv + Fence Exp + Mark + Distance + Post + Year + Near Ct | 15 | 367.365 | 2.721 | 0.008 |
| Angle + Surv + Mark + Post + Year | 13 | 367.420 | 2.776 | 0.007 |
| Fence Exp + Distance + Risk + Near Ct + Post × Mark | 10 | 367.457 | 2.813 | 0.007 |
| Mark + Distance + Post + Risk + Year + Near Ct | 9 | 367.459 | 2.815 | 0.007 |
| Fence Exp + Distance + Risk + Year + Post × Mark | 10 | 367.587 | 2.942 | 0.007 |
| Fence Exp + Mark + Distance + Post | 7 | 367.590 | 2.946 | 0.007 |
| Surv + Fence Exp + Mark + Distance + Post + Risk + Year + Near Ct | 16 | 367.591 | 2.946 | 0.007 |
| Fence Exp + Distance + Risk + Year + Near Ct + Post × Mark | 11 | 367.717 | 3.073 | 0.006 |
| Angle + Fence Exp + Mark + Distance + Post + Risk + Near Ct | 10 | 367.748 | 3.104 | 0.006 |
| Angle + Fence Exp + Mark + Distance + Post + Risk + Year | 10 | 367.821 | 3.177 | 0.006 |
| Mark + Distance + Post + Risk + Year | 8 | 367.882 | 3.238 | 0.006 |
| Angle + Surv + Mark + Post | 12 | 367.902 | 3.258 | 0.006 |
| Mark + Distance + Post + Risk + Near Ct | 8 | 367.992 | 3.348 | 0.006 |
| Angle + Surv + Mark + Post + Near Ct | 13 | 368.029 | 3.385 | 0.006 |
| Fence Exp + Distance + Post + Risk + Near Ct | 8 | 368.075 | 3.431 | 0.005 |
| Surv + Mark + Distance + Post + Year + Near Ct | 14 | 368.076 | 3.432 | 0.005 |
| Angle + Surv + Post | 11 | 368.076 | 3.432 | 0.005 |
| Fence Exp + Distance + Post + Year + Near Ct | 8 | 368.107 | 3.463 | 0.005 |
| Angle + Fence Exp + Mark + Distance + Post + Risk + Year + Near Ct | 11 | 368.160 | 3.516 | 0.005 |
| Fence Exp + Distance + Post + Year | 7 | 368.210 | 3.566 | 0.005 |
| Mark + Distance + Post + Year + Near Ct | 8 | 368.239 | 3.595 | 0.005 |
| Angle + Surv + Mark + Distance + Post + Year | 14 | 368.255 | 3.611 | 0.005 |
| Surv + Distance + Post + Year + Near Ct | 13 | 368.264 | 3.620 | 0.005 |
| Fence Exp + Mark + Post + Distance × Near Ct | 9 | 368.276 | 3.632 | 0.005 |
| Fence Exp + Risk + Post × Mark + Distance × Near Ct | 11 | 368.284 | 3.640 | 0.005 |
| Surv + Mark + Distance + Post + Near Ct | 13 | 368.308 | 3.664 | 0.005 |
| Surv + Distance + Post + Risk + Year + Near Ct | 14 | 368.328 | 3.684 | 0.005 |
| Angle + Fence Exp + Mark + Post + Risk + Distance × Near Ct | 11 | 368.379 | 3.735 | 0.005 |
| Angle + Surv + Post + Near Ct | 12 | 368.397 | 3.753 | 0.005 |

| | | | | |
|---|---|---|---|---|
| Surv + Mark + Distance + Post + Risk + Year + Near Ct | 15 | 368.414 | 3.770 | 0.005 |
| Surv + Fence Exp + Distance + Post + Year + Near Ct | 14 | 368.431 | 3.787 | 0.005 |
| Distance + Post + Risk + Year + Near Ct | 8 | 368.445 | 3.801 | 0.004 |
| Angle + Fence Exp + Mark + Distance + Post + Near Ct | 9 | 368.449 | 3.805 | 0.004 |
| Angle + Fence Exp + Mark + Distance + Post + Year | 9 | 368.468 | 3.824 | 0.004 |
| Fence Exp + Post + Risk + Year + Distance × Near Ct | 10 | 368.499 | 3.855 | 0.004 |
| Fence Exp + Distance + Near Ct + Post × Mark | 9 | 368.531 | 3.886 | 0.004 |
| Mark + Distance + Post + Year | 7 | 368.550 | 3.906 | 0.004 |
| Surv + Fence Exp + Distance + Post + Risk + Year + Near Ct | 15 | 368.591 | 3.947 | 0.004 |
| Mark + Distance + Post + Near Ct | 7 | 368.623 | 3.979 | 0.004 |

Table A3
Coefficient estimates, standard errors (SE), and 95% confidence intervals (CI) for all variables from the best model explaining variation in small-scale occupancy (θ) probabilities of Greater Sage-Grouse fence collisions in Wyoming, 2014–2015. Variables include fence exposure (Fence Exp), whether a fence was marked (regardless of marker type; Mark), the distance to nearest lek (Distance), fences with wood and t-posts (wood and t-post), proportion of fence segment in high risk areas (Risk), and the count at the nearest lek (Near Ct). The intercept represents an unmarked fence with wood posts with all continuous variable values set to 0. All significant coefficients (i.e., 95% CIs do no overlap 0) are indicated by an asterisk.

| Parameter | Mean | SE | 95% CI |
|---|---|---|---|
| Intercept* | − 5.104 | 1.068 | (− 7.197, − 3.012) |
| Fence Exp* | 0.033 | 0.013 | (0.007, 0.059) |
| Mark* | − 0.922 | 0.359 | (− 1.623, − 0.217) |
| Distance* | − 0.500 | 0.197 | (− 0.886, − 0.113) |
| Wood and T-post* | 1.783 | 0.387 | (1.025, 2.541) |
| Risk* | 1.128 | 0.565 | (0.020, 2.235) |
| Near Ct | 0.005 | 0.002 | (0.000, 0.010) |

Table A4
Coefficient estimates, standard errors (SE), and 95% confidence intervals (CI) for all variables from the second best model explaining variation in small-scale occupancy (θ) probabilities of Greater Sage-Grouse fence collisioins in Wyoming, 2014–2015. Variables include fence exposure (Fence Exp), whether a fence was marked (regardless of marker type; Mark), the distance to nearest lek (Distance), fences with wood and t-posts (wood and t-post), proportion of fence segment in high risk areas (Risk), and the count at the nearest lek (Near Ct). The intercept represents an unmarked fence with wood posts with all continuous variable values set to 0. All significant coefficients (i.e., 95% CIs do no overlap 0) are indicated by an asterisk.

| Parameter | Mean | SE | 95% CI |
|---|---|---|---|
| Intercept* | − 5.181 | 1.090 | (− 7.317, − 3.046) |
| Fence Exp* | 0.032 | 0.013 | (0.006, 0.058) |
| Mark* | − 0.818 | 0.356 | (− 1.515, − 0.121) |
| Distance* | − 0.650 | 0.186 | (− 1.015, − 0.285) |
| Wood and T-post* | 1.685 | 0.374 | (0.952, 2.418) |
| Risk* | 1.161 | 0.557 | (0.069, 2.253) |
| 2015* | 0.875 | 0.431 | (0.030, 1.720) |

## References


Baines, D., Andrew, M., 2003. Marking of deer fences to reduce frequency of collisions by woodland grouse. Biol. Conserv. 110 (2), 169–176.

Baines, D., Summers, R.W., 1997. Assessment of bird collisions with deer fences in Scottish forests. J. Appl. Ecol. 941–948.

Battin, J., 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conserv. Biol. 18, 1482–1491.

Beck, T.D.I., Braun, C.E., 1980. The strutting ground count: variation, traditionalism, management needs. In: Proceedings of the Western Association of Fish and Wildlife Agencies. 60. pp. 558–566.

Bevanger, K., 1994. Bird interactions with utility structures: collision and electrocution, causes and mitigating measures. Ibis 136 (4), 412–425.

Bevanger, K., 1995. Estimates and population consequences of tetraonid mortality caused by collisions with high tension power lines in Norway. J. Appl. Ecol. 32, 745–753.

Bevanger, K., 1998. Biological and conservation aspects of bird mortality caused by electricity power lines: a review. Biol. Conserv. 86, 67–76.

Bevanger, K., Henriksen, G., 1996. Faunistiske effekterav gjerder og andre menneskeskapte barrierer. (In Norwegian with English Summary: Faunistic Consequences of Fences and Other Man-Made Barriers.) Norwegian Institute for Nature Research, Oppdragsmelding. 393. pp. 1–26.

Bureau of Land Management - Pinedale Field Office, GIS Staff. 2013. Unpublished Material. vector digital data.\\ilmwypd6na1\gis\gisdata\Range\fences.shp. Location of Fences within the Bureau of Land Management Pinedale Field Office in Southwest Wyoming, 1:100,000. University of Wyoming Spatial Data and Visualization Center, Laramie, Wyoming.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer-Verlag, New York, New York, USA.

Catt, D.C., Dugan, D., Green, R.E., Moncrieff, R., Moss, R., Picozzi, N., Summers, R.W., Tyler, G.A., 1994. Collisions against fences by woodland grouse in Scotland. Forestry 67, 105–118.

Chamberlin, T.C., 1965. The method of multiple working hypotheses. Science 148, 754–759.

Christiansen, T., 2009. Fence marking to reduce greater sage-grouse (*Centrocercus urophasianus*) collisions and mortality near Farson. In: Wyoming – Summary of Interim Results. Wyoming Game and Fish Department.

Christiansen, T., 2012. Chapter 12: sage grouse (*Centrocercus urophasianus*). In: Tessmann, S.A., Bohne, J.R. (Eds.), Handbook of Biological Techniques, Third edition. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA, pp. 1–55.

Doherty, P.F., White, G.C., Burnham, K.P., 2012. Comparison of model building and selection strategies. J. Ornithol. 152, 317–323.

Drewitt, A.L., Langston, R.H., 2008. Collision effects of wind-power generators and other obstacles on birds. Ann. N. Y. Acad. Sci. 1134 (1), 233–266.

Emmons, S.R., Braun, C.E., 1984. Lek attendance of male sage grouse. J. Wildl. Manag. 48 (3), 1023–1028.

ESRI, 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.

Everaert, J., Stienen, E.W.M., 2007. Impact of wind turbines on birds in Zeebrugge (Belgium): significant effect on breeding tern colony due to collisions. Biodivers. Conserv. 16 (12), 3345–3359.

Flake, L.D., Connelly, J.W., Kirschenmann, T.R., Lindbloom, A.J., 2010. Grouse of Plains and Mountains: The South Dakota Story. South Dakota Department of Game, Fish, and Parks, Pierre, South Dakota, USA.

FlySafe, 2016. Fly Safe, LLC. http://www.flysafellc.com (accessed 12.16).

Hagen, C.A., Pavlacky Jr., D.C., Adachi, K., Hornsby, F.E., Rintz, T.J., McDonald, L.L., 2016. Multiscale occupancy modeling provides insights into range-wide conservation needs of lesser prairie-chicken (*Tympanuchus pallidicinctus*). Condor 118, 597–612.

Hayter, Earl W., 1939. Barbed wire fencing: a prairie invention: its rise and influence in the Western States. Agric. Hist. 13 (4), 189–207.

Hayward, M.W., Kerley, I.H., 2009. Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes? Biol. Conserv. 142, 1–13.

Henderson, I.G., Langston, R.H.W., Clark, N.A., 1996. The response of common terns

*Sterna hirundo* to power lines: an assessment of risk in relation to breeding commitment, age and wind speed. Biol. Conserv. 77, 185–192.
Jenni, D.A., Hartzler, J.E., 1978. Attendance at a sage grouse lek: implications for spring censuses. J. Wildl. Manag. 46–52.
Johnson, D.H., Rowland, M.M., 2007. The Utility of Lek Counts for Monitoring Greater Sage-grouse. Monitoring Populations of Sage-grouse. 88. College of Natural Resources Experiment Station Bulletinpp. 15–23.
Laake, J., 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, Washington, USA.
Lebreton, J.D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case-studies. Ecol. Monogr. 62, 67–118.
Linnell, J.D., 2016. Border controls: refugee fences fragment wildlife. Nature 529 (7585), 156.
Linnell, J.D., Trouwborst, A., Boitani, L., Kaczensky, P., Huber, D., Reljic, S., Kusak, J., Majic, A., Skrbinsek, T., Potocnik, H., Hayward, M.W., Milner-Gulland, E.J., Buuveibaatar, B., Olson, K.A., Badamjav, L., Bischof, R., Zuther, S., Breitenmoser, U., 2016. Border security fencing and wildlife: the end of the transboundary paradigm in Eurasia? Plos Boil 14 (6), e1002483.
Lisney, T.J., Iwaniuk, A.N., Kolominsky, J., Bandet, M.V., Corfield, J., 2012. Interspecific variation in eye shape and retinal topography in seven species of galliform bird (*Aves*: *Galliformes*:*Phasianidae*). J. Comp. Physiol. A. 198, 717–731.
Luzenski, J., Rocca, C.E., Harness, R.E., Cummings, J.L., Austin, D.D., Landon, M.A., Dwyer, J.F., 2016. Collision avoidance by migrating raptors encountering a new electric power transmission line. Condor 118, 402–410.
Monroe, A.P., C.L. Aldridge, T.J. Assal, K.E. Veblen, D.A. Pyke, and M.L. Casazza. In review. Patterns in greater sage-grouse population dynamics correspond with public grazing records at broad scales. Ecol. Appl.
Morrison, M.L., Block, W.M., Strickland, M.D., Collier, B.A., Peterson, M.J., 2008. Wildlife Study Design. Springer, New York, New York, USA.
Moss, R., Picozzi, N., Summers, R.W., Baines, D., 2000. Capercaillie *Tetrao urogallus* in Scotland-demography of a declining population. Ibis 142 (2), 259–267.
Mougeot, F., Martinez-Padilla, J., Perez-Rodriguez, L., Bortolotti, G.R., 2007. Carotenoid-based colouration and ultraviolet reflectance of the sexual ornaments of grouse. Behav. Ecol. Sociobiol. 61, 741–751.
Natural Resources Conservation Service, 2015. Sage Grouse Initiative 2014 Progress Report. http://www.nrcs.usda.gov/wps/portal/nrcs/detailfull/national/programs/initiatives/?cid=steldevb1027671 (accessed 02.16).
Nichols, J.D., Bailey, L.L., O'Connell Jr., A.F., Talancy, N.W., Grant, E.H.C., Gilbert, A.T., Annand, E.M., Husband, T.P., Hines, J.E., 2008. Multi-scale occupancy estimation and modelling using multiple detection methods. J. Appl. Ecol. 45, 1321–1329.
Patten, M.A., Wolfe, D.H., Shochat, E., Sherrod, S.K., 2005. Effects of microhabitat and microclimate selection on adult survivorship of the lesser prairie-chicken. J. Wildl. Manag. 69 (3), 1270–1278.
Pavlacky Jr., D.C., Blakesley, J.A., White, G.C., Hanni, D.J., Lukacs, P.M., 2012. Hierarchical multi-scale occupancy estimation for monitoring wildlife populations. J. Wildl. Manag. 76, 154–162.
Rayner, J.M.V., 1988. Form and function in avian flight. In: Johnston, R.F. (Ed.), Current Ornithology. vol. 5. Plenum, New York, pp. 1–66.
von Schweppenburg, H.F., 1929. "Zugstraßen" – Leitlinien. J. Ornithol. 77 (4), 17–32.
Scott, J.W., 1942. Mating behavior of the sage-grouse. Auk 59, 477–498.
Scott, R.E., Roberts, L.J., Cadbury, C.J., 1972. Bird deaths from power lines at Dungeness. British Birds 65, 273–286.
Sibley, D.A., 2000. In: Alfred, A. (Ed.), The Sibley Guide to Birds. Knopf, New York, NY.
Sillman, A.J., 1973. Avian vision. In: Farner, D.S., King, J.R. (Eds.), Avian Biology. vol. III. Academic Press, London, pp. 349–387.
Smith, J.A., Dwyer, J.F., 2016. Avian interactions with renewable energy infrastructure: an update. Condor 118, 411–423.
Stevens Jr., D.L., Olsen, A.R., 2004. Spatially balanced sampling of natural resources. J. Am. Stat. Assoc. 99, 262–278.
Stevens, B.S., Reese, K.P., Connelly, J.W., 2011. Survival and detectability bias of avain fence collision surveys in sagebrush steppe. J. Wildl. Manag. 75 (2), 437–449.
Stevens, B.S., Connelly, J.W., Reese, K.P., 2012a. Multi-scale assessment of greater sage-grouse fence collision as a function of site and broad scale factors. J. Wildl. Manag. 76 (7), 1370–1380.
Stevens, B.S., Reese, K.P., Connelly, J.W., Musil, D.D., 2012b. Greater sage-grouse and fences: does marking reduce collisions? Wildl. Soc. Bull. 36 (2), 297–303.
Stevens, B.S., Naugle, D.E., Connelly, J.W., Griffiths, T., Reese, K.P., 2013. Mapping sage-grouse fence-collision risk: spatially explicit models for targeting conservation implementation. Wildl. Soc. Bull. 37 (2), 409–415.
Stiver, S.J., Apa, A.D., Bohne, J.R., Bunnell, S.D., Deibert, P.A., Gardner, S.C., Hilliard, M.A., McCarthy, C.W., Schroeder, M.A., 2006. Greater Sage-grouse Comprehensive Conservation Strategy. Western Association of Fish and Wildlife Agencies. (Unpublished Report. Cheyenne, Wyoming).
Summers, R.W., Dugan, D., 2001. An assessment of methods used to mark fences to reduce bird collisions in pinewoods. Scott. For. 55 (1), 23–29.
United States Department of Agriculture (USDA), 2016. How To Make and Install Fence Markers For Sage-grouse. http://www.sagegrouseinitiative.com/wp-content/uploads/2013/07/NRCD-SGI_FenceMarker_Instructions.pdf accessed 06.16).
United States Fish and Wildlife Service (USFWS), 2010. Endangered and Threatened Wildlife and Plants; 12-month Findings for Petitions to List the Greater Sage-grouse (*Centrocercus urophasianus*) as Threatened or Endangered. 50 CFR Part 17.
Viscor, G., Fuster, J.F., 1987. Relationships between morphological parameters in birds with different flying habits. Comp. Biochem. Physiol. A Physiol. 87 (2), 231–249.
Walsh, D.P., White, G.C., Remington, T.E., Bowden, D.C., 2004. Evaluation of the lek-count index for greater sage-grouse. Wildl. Soc. Bull. 32 (1), 56–68.
White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Suppl. 1), S120–S139.
Wolfe, D.H., Patten, M.A., Shochat, E., Pruett, C.L., Sherrod, S.K., 2007. Causes and patterns of mortality in lesser prairie-chickens *Tympanuchus pallidicinctus* and implications for management. Wildl. Biol. 13 (1), 95–104.
Wyoming State Historical Society 2016. Accessed 3/8/2016. http://www.wyohistory.org/encyclopedia/sublette-county-wyoming.



View publication stats

This manuscript contains unpublished, peer-reviewed, scientific information. It has been accepted for future publication in a special volume of the Cooper Ornithological Society scientific series "Studies in Avian Biology." No waiver of proprietary rights to the information is granted by this release on the part of the Cooper Ornithological Society and its publisher, the USGS, or the author(s) of the manuscript.

## Document cover Sheet—Studies in Avian Biology

Title: WEST NILE VIRUS ECOLOGY IN SAGEBRUSH HABITAT AND IMPACTS ON GREATER SAGE-GROUSE POPULATIONS

File name: walker and naugle.doc

RH: Sage-grouse and West Nile virus—*Walker and Naugle*

Number of figures: 5

Number of tables: 2

Number of appendices: 1

Author to receive correspondence:

Brett L. Walker
Colorado Division of Wildlife
711 Independent Ave.
Grand Junction, CO 81505
970-255-6125
970-255-4111 FAX
brett.walker@state.co.us

Carl D. Marti, Editor
Studies in Avian Biology
1310 E Jefferson St.
Boise, ID 83712 USA
Tel: 208-426-8996
Email: sab@boisestate.edu

# WEST NILE VIRUS ECOLOGY IN SAGEBRUSH HABITAT AND IMPACTS ON GREATER SAGE-GROUSE POPULATIONS

BRETT L. WALKER AND DAVID E. NAUGLE

*Abstract.* Emerging infectious diseases can act as important new sources of mortality for wildlife. West Nile virus (Flaviviridae, *Flavivirus*) has emerged as a potential threat to Greater Sage-Grouse (*Centrocercus urophasianus*) populations since 2002. We review the ecology of West Nile virus in sagebrush (*Artemisia* spp.) ecosystems of western North America, summarize the influence of the virus on Greater Sage-Grouse mortality and survival, use demographic models to explore potential impacts on population growth, and recommend strategies for managing and monitoring such impacts. The virus was an important new source of mortality in low and mid-elevation Greater Sage-Grouse populations range-wide from 2003–2007. West Nile virus can simultaneously reduce juvenile, yearling, and adult survival—three vital rates important for population growth in this species, and persistent low-level West Nile virus mortality and severe outbreaks may lead to local and regional population declines. West Nile virus mortality in simulations was projected to reduce population growth (i.e., finite rate of increase, $\lambda$) of susceptible populations by an average of 0.06–0.09/yr. However, marked spatial and annual fluctuations in nest success, chick survival, and other sources of adult mortality are likely to mask population-level impacts in most years. Impacts of severe outbreaks may be detectable from lek-count data, but documenting effects of low to moderate mortality will require intensive monitoring of radio-marked birds. Resistance to West Nile virus-related disease appears to be low and is expected to increase slowly over time. Eliminating mosquito breeding habitat from anthropogenic water sources is crucial for reducing impacts. Better data are needed

on geographic and temporal variation in infection rates, mortality, and seroprevalence range-wide. Small, isolated, and peripheral populations, particularly those at lower elevations, and those experiencing large-scale increases in distribution of surface water may be at higher risk.
*Key words*: *Centrocercus urophasianus*, *Culex tarsalis*, emerging infectious disease, flavivirus, Greater Sage-Grouse, resistance, sagebrush, survival, West Nile virus.

ECOLOGÍA DEL VIRUS DE WEST NILE EN HABITAT DE SAGEBRUSH E IMPACTOS EN MAYORES POBLACIONES DE GREATER SAGE-GROUSE

*Resumen*. Las enfermedades infecciosas emergentes pueden actuar como nuevas fuentes importantes de mortalidad para la vida silvestre. El virus del Oeste del Nilo (Flaviviridae, *Flavivirus*) ha emergido como una amenaza potencial para poblaciones del Greater Sage-Grouse (*Centrocercus urophasianus*) desde 2002. Nosotros Revisamos la ecología del virus del Oeste del Nilo en ecosistemas de Artemisa (*Artemisia* spp.) en el oeste de Norte America, resumimos la influencia del virus sobre la mortalidad y la supervivencia del Greater Sage-Grouse, usamos modelos demográficos para explorar impactos potenciales sobre el crecimiento de la población, y recomendamos estrategias para monitorear y manejar tales impactos. El virus fue una importante fuente nueva de mortalidad en poblaciones de Greater Sage-Grouse en altitudes medias y bajas en el lapso de 2003–2007. El virus del Oeste del Nilo puede reducir simultáneamente la supervivencia del Greater Sage-Gruose juvenil, de añeros, y de adultos, tres componentes vitales importantes para el crecimiento de la población en éstas especies, y una mortalidad baja persistente, por West Nile virus, y unos brotes severos pueden llevar a una disminución de la población local y regional. En simulaciones se proyectó que la mortalidad por West Nile virus reduce el crecimiento de la pobalción (es decir, la tasa finita de incremento, $\lambda$), de poblaciones

susceptibles, en un promedio de 0.06–0.09 por año. Sin embargo, fluctuaciones marcadas, de tipo anual y de espacio, en éxito de nidación, supervivencia de polluelos, y otras fuentes de mortalidad de adultos es probable que enmascaren los impactos, a nivel poblacional, la mayoría de los años. Los impactos de brotes severos se pueden detectar en los datos de los lek-count, pero documentar los efectos de la mortalidades baja a moderada requerirá de un intenso monitoreo de pájaros radio-marcados. La resistencia a enfermedades relacionadas con West Nile parece ser baja y se espera que se incremente lentamente en el tiempo. El eliminar los hábitats de reproducción de mosquito, de fuentes antropogénicas de agua es crucial para reducir impactos. Se necesitan mejores datos acerca de la variación geográfica y temporal en las tasas de infección, mortalidad, y de seroprevalencia gama-ancho. Las poblaciones pequeñas, aisladas, y perisféricas, especialmente aquellas en altitudes bajas, y aquellas que están experimentando incrementos a gran escala en la distribución de superficies de agua pueden estar en mayor riesgo.

Infectious diseases are now widely recognized as important sources of mortality in wild bird populations and have emerged as a major issue in avian conservation, particularly for sensitive, threatened, and declining species (Daszak et al. 2000, Dobson and Foufopoulos 2001, Friend et al. 2001, Chomel et al. 2007). Timely and appropriate management and mitigation of disease impacts requires detailed information on ecological interactions between the pathogen and its hosts, vectors, and environment. Assessing the importance of disease for prioritizing conservation efforts requires data on disease spread, distribution, and impacts on population demographics and growth.

A major new concern for conservation of wild bird populations in North America is the

recent arrival and rapid spread of West Nile virus (WNV; Flaviviridae, *Flavivirus*). West Nile virus is a mosquito-borne flavivirus that can cause debilitating or fatal neuroinvasive disease in wild birds (Marra et al. 2004, Hayes et al. 2005b, McLean 2006). The virus persists largely within a mosquito-bird-mosquito infection cycle (Campbell et al. 2002). West Nile virus has expanded across the continent at an unprecedented rate since 1999 (Marra et al. 2004, McLean 2006, Kilpatrick et al. 2007) and is now considered the predominant arthropod-borne disease in the US (Kilpatrick et al. 2006b, Kramer et al. 2008). The virus is known from at least 317 wild, captive, and domestic bird species in North America, of which 254 are native (Centers for Disease Control and Prevention 2008). Over 48,000 infected dead birds had been reported as of 2005 (McLean 2006), but because most WNV mortality in wild populations goes unnoticed or unreported (Ward et al. 2006), the virus is thought to have caused the deaths of millions of wild birds since 1999 (McLean 2006, Gubler 2007). Although confirmed as a new source of mortality, population-level effects of the virus on wild bird populations remain largely unknown (Marra et al. 2004, McLean 2006). Only recently have studies documented local and regional population declines in common and widespread birds following the arrival of WNV, e.g., American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), Yellow-Billed Magpie (*Pica nuttalli*), Western Scrub-Jay (*Aphelocoma californica*), Steller's Jay (*Cyanocitta stelleri*), American Robin (*Turdus migratorius*), Eastern Bluebird (*Sialia sialis*), Black-Capped Chickadee (*Poecile atricapillus*), Carolina Chickadee (*Poecile carolinensis*), Tufted Titmouse (*Baeolophus bicolor*), and House Wren (*Troglodytes aedon*) (Koenig et al. 2007, LaDeau et al. 2007). WNV-related mortality rates in the American Crow can reach 40–68% (Caffrey et al. 2003, 2005; Yaremych et al. 2004, Koenig et al. 2007, LaDeau et al. 2007). West Nile virus

reduced Yellow-Billed Magpie populations in California by as much as 49% from 2003–2006 (Crosbie et al. 2008). WNV-related mortality resulted in a 10-fold reduction in survival, from 0.44 to 0.04, in American White Pelican (*Pelecanus erythrorhynchos*) chicks (Sovada et al. 2008).

West Nile virus has also recently emerged as a potential threat to sage-grouse (*Centrocercus* spp.) populations (Naugle et al. 2004). Greater Sage-Grouse and Gunnison Sage-Grouse (*C. minimus*) are gallinaceous birds native to western sagebrush (*Artemisia* spp.) habitats (Schroeder et al. 1999). Previously widespread, both species have been extirpated from much of their original range (Schroeder et al. 2004) and experienced long-term population declines due to loss, fragmentation, and degradation of sagebrush habitat (Connelly et al. 2004). This has precipitated repeated attempts to list the species under the Endangered Species Act and range-wide efforts to assess risks to populations (Connelly et al. 2004, Stiver et al. 2006, Aldridge et al. 2008).

A series of studies on Greater Sage-Grouse have documented reductions in survival due to WNV since 2003 (Naugle et al. 2004, 2005; Walker et al. 2004, 2007a; Aldridge 2005, Kaczor 2008, Walker 2008), near-extirpation of a local population following a WNV outbreak (Walker et al. 2004), high mortality following infection (Clark et al. 2006), WNV-related mortality events in unmarked birds (US Geological Survey 2006), and links between West Nile virus mortality, mosquito abundance, and changes in land use (Zou et al. 2006b, Doherty 2007, Walker 2008). Historical population declines and range contraction and continued loss and degradation of sagebrush habitat have led to concern over the conservation status of sage-grouse (Schroeder et al. 1999, Connelly et al. 2004, Schroeder et al. 2004, Stiver et al. 2006) and repeated attempts to

list both species under the Endangered Species Act of 1973. Understanding the impact of WNV on Greater Sage-Grouse populations is important for assessing this species' conservation status, but requires an updated synthesis of recent scientific data. The objectives of this paper are to: (1) review the ecology of WNV in sagebrush ecosystems of western North America, (2) summarize recent data on distribution of WNV mortality events, impacts on mortality and survival rates, and resistance to WNV disease, (3) use demographic models to explore potential impacts of WNV-related mortality on population growth, and (4) recommend strategies for monitoring and mitigating impacts of the virus on sage-grouse populations.

## ECOLOGY OF WEST NILE VIRUS IN SAGEBRUSH HABITAT

The transmission cycle of WNV in sagebrush habitats involves complex interactions among vectors, reservoirs, amplifying hosts, and environmental factors, including temperature and the distribution of surface water. The main vectors for WNV worldwide are mosquitos, particularly those in the genus *Culex* (Goddard et al. 2002; Turell et al. 2001, 2005). Other ectoparasites, including ticks (Hutcheson et al. 2005, Dawson et al. 2008), hippoboscid flies (Farajollahi et al. 2005), and biting midges (Naugle et al. 2004) may also be involved in WNV transmission, but few data are available on their role as WNV reservoirs or vectors (van der Meulen et al. 2005). WNV infection has been documented in several genera of mosquitoes (*Culex*, *Aedes*, *Ochlerotatus*, *Culiseta*; Goddard et al. 2002, Doherty 2007) and at least one other arthropod family, biting midges (Naugle et al. 2004), in sagebrush habitats of western North America. The dominant vector of WNV in sagebrush habitats is the mosquito *Culex tarsalis* Coquillett (Goddard et al. 2002, Naugle et al. 2004, Turell et al. 2005, Doherty 2007). *Culex tarsalis* is a highly competent vector (Goddard et al. 2002, Turell et al. 2005), in part because it

can inoculate hosts with high doses of virus ($10^{4.3}$–$10^{5.0}$ plaque-forming units [PFU]) directly into the bloodstream while feeding (Reisen et al. 2007; Styer et al. 2007a,b). The species is abundant and widely distributed in arid sagebrush habitats (DiMenna et al. 2006, Doherty 2007), and individuals may disperse as much as 18 km to colonize newly-available surface water (Bailey et al. 1965, Beehler and Mulla 1995, Reisen et al. 2003). The species prefers sites with submerged vegetation on which to oviposit and warm, standing water that promotes rapid larval development, including ephemeral puddles, vegetated pond edges, and hoof prints (Milby and Meyer 1986, Buth et al. 1990, Doherty 2007). *Culex tarsalis* feeds primarily on birds in spring and early summer, then shifts its feeding patterns to also include mammals in late summer (Lee et al. 2002). The important role of *Culex* mosquitoes in WNV epidemics may be due to their broad range of hosts and seasonal shifts in host preferences (Kilpatrick et al. 2006a). *Aedes vexans*, a floodwater mosquito common in western sagebrush habitats, primarily feeds on mammals has recently been demonstrated capable of transmitting WNV from infected chickens (*Gallus gallus domesticus*; Tiawsirisup et al. 2008).

Much is known about WNV vectors in sagebrush habitat, but reservoirs for WNV are poorly understood. Reservoirs are those species that harbor the virus and serve as sources for naïve host-feeding mosquitoes that initiate the WNV transmission cycle each year. Both resident and migratory birds can be competent hosts and may act as a source of virus in spring or early summer due to reactivation of a chronic infection (McLean 2006). Infected birds are known to exhibit migratory behavior and may be able to carry the virus long distances (Owen et al. 2006). Migratory birds are widely thought to be responsible for spread of WNV across North America, but direct evidence is lacking (Reed et al. 2003, Rappole and Hubálek 2003, Peterson et al.

2003). Most migratory breeding passerines in sagebrush habitats, e.g., Brewer's Sparrow (*Spizella breweri*), Vesper Sparrow (*Pooecetes gramineus*), Sage Sparrow (*Amphispiza belli*), Horned Lark (*Eremophilus alpestris*), Western Meadowlark (*Sturnella neglecta*), arrive in early spring prior to the emergence of host-feeding mosquitoes, so it is unclear whether they are involved in initiating WNV transmission in sagebrush habitat. Migratory birds passing through in late spring or early summer or those returning south in mid- to late summer that congregate on or near water sources in sagebrush habitat—songbirds, waterfowl, shorebirds—may also be a source of the virus. Exotic species commercially raised and released into sage-grouse habitat that carry the virus but are largely resistant to WNV disease, e.g., Ring-Necked Pheasant (*Phasianus colchicus*), Chukar (*Alectoris chukar*), Gray Partridge (*Perdix perdix*), may also serve as WNV reservoirs (Meece et al. 2006, Wünschmann and Ziegler 2006). WNV in some regions is known to overwinter in infected diapausing mosquitos, including *Culex tarsalis* (Nasci et al. 2001, Goddard et al. 2003, Reisen et al. 2006b), and it is possible that infected mosquitoes emerge in spring to begin WNV transmission anew. Offspring of *C. tarsalis* infected via vertical transmission from mother to offspring via eggs may also overwinter as eggs or larvae and emerge as infected adults the following spring (Goddard et al. 2003).

Wild birds are clearly the most important amplifying hosts for WNV (Marra 2004, McLean 2006, Kramer et al. 2008), but identifying and targeting specific species for management is extremely difficult (Lord and Day 2001, Kilpatrick et al. 2006b). Sagebrush habitats typically support lower avian diversity than other western ecosystems, e.g., riparian areas, but numerous avian hosts, mammals, reptiles, and amphibians could be involved in either maintaining or attenuating transmission (Marra et al. 2004, van der Meulen et al. 2005, Lord et

al. 2006, McLean 2006), including sparrows, ducks, Wilson's Snipe (*Gallinago delicata*), Sora (*Porzana carolina*), Short-Eared Owl (*Asio flammeus*), Red-Tailed Hawk (*Buteo jamaicensis*), Ring-Necked Pheasant, Greater Sage-Grouse, House Wren, American Robin, Common Yellowthroat (*Geothlypis trichas*), Western Meadowlark, and Bullock's Oriole (*Icterus bullockii*) (Kato et al., in press). Potential mammalian hosts were also detected—cows (*Bos taurus*), sheep (*Ovis aries*), horses (*Equus caballus*), deer (*Odocoileus* spp.), pronghorn (*Antilocapra americana*), moose (*Alces alces*), rabbits, felines, and skunks (Kato et al., in press). Viremia in mammals less commonly reaches levels required to infect host-feeding mosquitos (Turell et al. 2000, Sardelis et al. 2001, van der Meulen et al. 2005), but recent studies have documented several potential mammalian hosts for WNV (Tiawsirisup et al. 2005; Platt et al. 2007, 2008), and mammals may be involved in nonviremic transmission (Higgs et al. 2005, Reisen et al. 2007).

Numerous studies purport to have identified key amplifying hosts or species- and habitat-specific exposure or infection rates of WNV based on seroprevalence—the proportion of live individuals with neutralizing antibodies to WNV (Komar et al. 2005, Beveroth et al. 2006). However, species with low seroprevalence do not necessarily experience low infection rates nor does are they precluded from transmitting WNV (Walker et al. 2007a). Species that are immune to the virus and highly susceptible species that die quickly prior to infecting additional vectors may serve as dead-end hosts that attenuate transmission (Lord and Day 2001, Reisen et al. 2006a). The relative abundance of different reservoir and amplifying host species can vary by season, among years, and among locations. Levels of viremia in infected Greater Sage-Grouse exceed the host-to-vector transmission threshold of $10^{5.0}$ PFU/ml and the birds live sufficiently

long to infect new mosquitoes; thus, despite their susceptibility, sage-grouse are considered competent amplifying hosts (Clark et al. 2006, but see Van der Meulen et al. 2005). In mid-summer, sage-grouse often congregate in flocks near both natural and man-made water sources (Schroeder et al. 1999, Connelly et al. 2000, Walker et al. 2004). These habitats often support populations of breeding mosquitoes (Doherty 2007) and, because sage-grouse are competent hosts, congregations of sage-grouse around water sources may lead to rapid spread of the virus within sage-grouse flocks and lead to severe local mortality events (Walker et al. 2004, 2007a). Host competency of other avian species using sagebrush habitats in late summer has not been studied. The difficulty of identifying both reservoir and amplifying hosts severely limits management options for WNV with most strategies focusing on water management and vector control.

West Nile virus transmission is also regulated by environmental factors, including temperature, precipitation, and distribution of anthropogenic water sources that support breeding mosquito vectors (Brust 1991, Dohm et al. 2002, Reisen et al. 2006a, Zou et al. 2006a,b). Sagebrush habitats are characterized by cold winters, cool, wet springs, and hot, dry summers. Extremely cold temperatures largely preclude mosquito activity and virus amplification in sagebrush habitats in winter, and it is unlikely that enzootic transmission occurs outside the known summer transmission period. Spring temperatures may allow WNV transmission as early as mid-May (Zou et al. 2006*a*) and in fall, as late as mid-September. All documented WNV-related mortality in sage-grouse has occurred from mid-May through mid-September with a peak in July and August (Walker et al. 2007a; Walker 2008; D. E. Naugle, unpub. data).

Temperature and precipitation both directly influence potential for WNV transmission.

The specific annual or seasonal temperature and precipitation profiles that promote outbreaks in sagebrush habitats have not been identified, but some general patterns are evident. Reduced and delayed WNV transmission has been documented in years with lower summer temperatures in sage-grouse (Naugle et al. 2005, Walker et al. 2007b) and migratory passerines (Bell et al. 2006). It has been suggested in other ecosystems that high temperatures associated with drought conditions increases West Nile virus transmission (Epstein and Defilippo 2001, Shaman et al. 2005). Higher temperatures facilitate greater nocturnal host-seeking activity by mosquitoes, more rapid larval development, and shorter extrinsic incubation periods for the virus—the time it takes for the virus to replicate inside the mosquito and invade its salivary glands (Reisen et al. 2006a). Summer drought is an annual occurrence in sage-grouse habitats range-wide. Temperature can also influence exposure of Greater Sage-Grouse to WNV by influencing habitat use. Greater Sage-Grouse throughout their range congregate in mesic habitats in mid- to late summer (Connelly et al. 2000) and often use ponds, springs, and other standing water sources during hot weather (Dalke et al. 1963, Connelly and Doughty 1989). *Culex tarsalis* exploits such habitats for breeding (Goddard et al. 2002, Doherty 2007), and risk of exposure to WNV for Greater Sage-Grouse may be elevated if WNV outbreaks coincide with drought conditions that aggregate birds in mesic areas or near remaining water sources (Naugle et al. 2004). Temperature, mosquito activity, and *Culex tarsalis* abundance decrease with elevation, and Greater Sage-Grouse inhabiting high-elevation sites in summer are generally thought to be less vulnerable than low-elevation populations (Naugle et al. 2004, Kaczor 2008). Similarly, populations farther north may be relatively less susceptible than those at similar elevations farther south because summer temperatures are generally lower at higher latitudes (Naugle et al. 2005). The highest confirmed

elevation at which Greater Sage-Grouse have been infected with WNV is ~2,300 m in the Lyon-Mono population of eastern California (Naugle et al. 2005). Increasing temperatures associated with changing climate may exacerbate WNV risk for sage-grouse (Epstein 2001), but risk also depends on complex interactions with other environmental factors including precipitation and distribution of water.

Man-made water sources may also facilitate the spread of WNV within sage-grouse habitats (Zou et al. 2006b, Doherty 2007, Walker et al. 2007b). For example, construction of ponds for water produced during coal-bed natural gas extraction increased larval mosquito habitat around pond edges by 75%, from 619 to 1,085 ha, during a 5-yr period of development (1999–2004) across a 21,000-$km^2$ area of northeastern Wyoming (Zou et al. 2006b). These ponds support abundant *Culex tarsalis*, and they support them longer than natural, ephemeral water sources (Doherty 2007). West Nile virus mortality associated with coal-bed natural gas ponds is thought to have contributed to extirpation of at least one local sage-grouse population in northeastern Wyoming (Walker et al. 2004, 2008). Projects that create mesic zones around stock tanks or ponds as habitat improvements for sage-grouse may inadvertently contribute to the WNV problem, because *Culex tarsalis* readily take advantage of water-filled hoof prints around tanks and ponds for breeding (Doherty 2007). Sage-grouse may use standing water in summer and fall when it is available, but do not require standing water (Dalke et al. 1963, Schroeder et al. 1999, Connelly et al. 2004). Estimated WNV infection rates were relatively low from 2003–2005 in undeveloped sagebrush habitats of the Powder River Basin (Walker et al. 2007b, Walker 2008), due, in part, to lack of available surface water in late summer, but were higher in areas with surface water provided by coal-bed natural gas ponds (Walker 2008).

The major ecological factors that regulate WNV transmission are known, but local outbreaks remain difficult to predict. Specific environmental conditions , e.g., temperature-precipitation profiles and water sources, must coincide with biotic factors, including infected reservoirs, competent host-feeding vectors, suitable amplifying hosts, and susceptible naïve individuals, for an outbreak to occur. Recent attempts to model WNV transmission events based on degree-day models appear promising (Zou et al. 2006a), but need to incorporate changes in the distribution of larval breeding sites over time (Zou et al. 2006b) and spatial variation in temperature-precipitation profiles to improve predictive ability (Walker 2008).

Several recent discoveries further complicate our understanding of WNV transmission and may have important implications for how WNV might affect sage-grouse populations, including: (1) acquired temporary immunity in juveniles, (2) vertical (mother-to-offspring) or horizontal (bird-to-bird) virus transmission, (3) changes in virulence, (4) impacts of the virus on mosquito demographics and behavior, and (5) non-viremic or non-propagative virus transmission among co-feeding mosquitoes. First, in raptors, owls, and domestic chickens, young can acquire temporary immunity for up to 33 d via maternal transmission of antibodies (Gibbs et al. 2005, Hahn et al. 2006, Nemeth and Bowen 2007). Chicks of infected females may be temporarily buffered from impacts of the virus if this phenomenon occurs in sage-grouse. Second, vertical transmission of WNV from mother to offspring has not been documented and is considered unlikely, but horizontal transmission between adult sage-grouse has been demonstrated in captivity (Clark et al. 2006). Whether horizontal transmission occurs in free-ranging populations remains unknown. Third, birds can contract arthropod-borne viruses by consuming infected vectors (Gilbert et al. 2004), such as in Red Grouse (*Lagopus lagopus*), but sage-grouse have not

been reported to actively feed on adult or larval mosquitos or ticks (Schroeder et al. 1999). Fourth, infection with WNV increases blood-feeding rates in female *Culex tarsalis* but may also decrease fecundity (Styer et al. 2007b), so it is unclear whether these effects together result in acceleration or attenuation of WNV transmission. Fifth, studies have documented multiple strains of WNV and competitive displacement of the NY99 strain by the WN02 strain since 1999 (Davis et al. 2005); implications of these discoveries are unclear. One study documented a virus strain with a shorter extrinsic incubation period that could lead to shorter intervals between transmission events (Moudy et al. 2007), while other studies have reported decreased replication rates and reduced neuroinvasiveness (Davis et al. 2004). Most disturbing however, are reports of transmission of WNV between infected and uninfected *Culex* mosquitoes co-feeding on uninfected vertebrate hosts in a laboratory setting (Higgs et al. 2005, Reisen et al. 2007). Amplifying hosts may not be required for transmission if nonviremic transmission occurs in the wild, and transmission among vectors could occur much more rapidly.

## SAGE-GROUSE AND WEST NILE VIRUS

Demographic impacts of WNV on Greater Sage-Grouse are relatively well-known compared with other North American species. Recent studies of radio-marked sage-grouse have allowed testing for neutralizing antibodies to WNV at capture and for WNV infection following mortality (Naugle et al. 2004, 2005; Walker et al. 2004, 2007a; Aldridge 2005, Kaczor 2008). The most reliable data on WNV mortality and infection rates come from research studies using marked individuals. However, WNV mortality rates using data from radio-marked birds may be underestimated because many carcasses cannot be recovered and tested (Walker et al. 2004).

### *Distribution and spread*.

West Nile virus was first detected within Greater Sage-Grouse range in 2002 (Kilpatrick et al. 2007), and a WNV-positive Greater Sage-Grouse mortality was first documented in Wyoming that same year (Naugle et al. 2004). WNV infections in humans, horses, and sentinel species (mosquitoes, chickens) had been documented in all 11 US states and two Canadian provinces within current sage-grouse range as of December 2007 (Kilpatrick et al. 2007), and WNV-positive mortalities in Greater Sage-Grouse had been confirmed in 10 states and one province (Table 1, Fig. 1). No WNV-positive Greater Sage-Grouse have been reported from Washington or Saskatchewan (Fig. 1). However, the combination of WNV-positive mortalities in extreme northeastern Montana in 2007, regular cross-border and long-distance movements between Montana and Saskatchewan (J. D. Tack, pers. comm.), and previously documented mortalities in southeastern Alberta in 2003–2005 (Naugle et al. 2004, 2005; Walker 2006) suggest that Saskatchewan populations have also been affected.

*WNV mortality and survival.*

Impacts of WNV have been reported in the literature in different ways: the number of confirmed WNV-positive mortalities (US Geological Survey 2006), minimum and maximum possible WNV-related mortality rates (Walker 2007a, Kaczor 2008), and differences in survival between areas with and without WNV mortality (Naugle et al. 2004, 2005). Most published data is from the eastern half of the species' range.

WNV-related mortality reduced late-summer survival of adult females across much of the eastern edge of the species' range in 2003, a year with persistent high summer temperatures and extreme drought (Naugle et al. 2004). Late-summer survival (15 Jul–31 Aug) at four study locations with confirmed WNV mortality in Wyoming, Montana, and Alberta declined an

average of 0.25 between pre-WNV years (1998–2002; 0.89 ± 0.01) and the first year that WNV was detected (2003; 0.64 ± 0.07), whereas survival remained high (0.90 pre-WNV vs. 0.85 in 2003) at a study site in western Wyoming where WNV was not detected. Late-summer survival across the four study areas with WNV mortality averaged 0.26 lower (0.64) than at the one study area where WNV was not detected (0.90). Individuals in populations exposed to the virus during July–August 2003 were 3.3 times more likely to die than birds in uninfected populations (Naugle et al. 2004). Female survival in the Powder River Basin of northeastern Wyoming and southeastern Montana during the July–September WNV transmission season was 0.20 (95% CI 0.01-0.44; N = 10) in areas with confirmed WNV mortality and 0.76 (95% CI 0.63-0.91; N = 34) in areas without WNV mortality (Walker et al. 2004). The 2003 outbreak near Spotted Horse, Wyoming was associated with extirpation of the local breeding population. The five leks in that region showed 76%, 95%, and 91% declines in maximum, median, and mean male counts respectively, from spring 2003 to spring 2004 (Walker et al. 2004). Mean males per count declined from 5.1 ± 0.5 SE in 2003 to 0.5 ± 0.2 SE in 2004, whereas counts at nearby unaffected leks did not change (10.2 ± 1.5 SE in 2003 vs. 10.4 ± 1.4 SE in 2004). Females also largely disappeared. At the five affected leks, 36 females were counted on 19 lek visits in spring 2003 whereas only one female was counted on 21 visits in spring 2004 (Walker et al. 2004). All five affected leks were inactive by 2005 and remained inactive through 2007 (Wyoming Game and Fish Department, unpubl. data).

Later timing of mortalities and dramatically fewer case rates of WNV in humans, horses, and other wild birds in 2004 in the eastern portion of the species' range suggested that below-average spring precipitation and summer temperatures limited mosquito production and reduced

WNV transmission compared with 2003 (Naugle et al. 2005, Bell et al. 2006, McLean 2006). July-September survival in 2004 was consistently lower ($\tilde{}$= 0.86, range 0.83–0.92) at four sites across the species' range with confirmed WNV-positive mortalities than at eight sites without ($\tilde{}$ = 0.96, range 0.92–0.100) (Naugle et al. 2005). WNV-related mortality among radio-marked females from 1 July–15 September in the Powder River Basin was between 3.7–9.4% (n = 118) (Walker et al. 2007b, 2008).

Moderate summer temperatures may have again attenuated mosquito production, virus amplification, or transmission in the eastern half of the species' range in 2005 (Walker 2006). WNV-related mortality rates in northeastern Wyoming and southeastern Montana from 1 July–15 September 2005 were between 2.4–8.2% (N = 123) (Walker et al. 2007b, 2008). California, Nevada, Utah, and Alberta reported WNV-positive mortalities in 2005, but did not report mortality or survival rates.

The first confirmed WNV-positive mortality in 2006 was documented on 14 June in Bighorn Co. in southeastern Montana, almost a month earlier than in previous years (Walker 2008). Elevated late-summer mortality was also reported on the Charles M. Russell National Wildlife Refuge in Montana (M. R. Matchett, USDI Fish and Wildlife Service, pers. comm.). WNV-related mortality from 15 June–15 September 2006 in southeastern Montana and northeastern Wyoming was between 5–15% of radio-marked females (N = 123) (D. E. Naugle, unpub. data). Kaczor (2008), working in northwestern South Dakota, reported minimum and maximum possible WNV-related mortality rates among radio-marked juvenile sage-grouse as 6.5–71.0% (N = 31) from 12 July–31 September 2006.

A confirmed outbreak of WNV in South Dakota in 2007 contributed to a 44% mortality rate (N = 80) among radio-marked females from mid-July to mid-September (K. C. Jensen, pers. comm.). Kaczor (2008) reported minimum and maximum possible WNV-related mortality rates among juveniles as 20.8–62.5% (N = 24) from 12 July–31 September 2007 in northwestern South Dakota. In northeastern Montana (Valley Co.), 26% of radio-marked females (N = 30) died during a 2-wk period in early August immediately following the first detection of WNV in mosquito pools with confirmation of two WNV-positive mortalities (J. D. Tack, pers. comm.). WNV-related mortality among radio-marked females from 15 June–6 September in the Powder River Basin was between 8 and 21% (N = 85) (D. E. Naugle, unpub. data), with one WNV-positive mortality collected May 17.

Reports of WNV-related mortality events among unmarked birds provide additional evidence that sage-grouse populations are impacted by WNV. For example, mortalities reported by landowners near the town of Burns, Oregon in August 2006 resulted in recovery of several freshly dead sage-grouse that tested positive for WNV and discovery of >60 other decomposed sage-grouse carcasses and a sick WNV-positive Northern Harrier (*Circus cyaneus*) (US Geological Survey 2006). Summer mortality events also occurred in several areas of Idaho and along the Idaho-Nevada border in 2006; at least 55 carcasses were discovered, and although not all were testable, 11 tested positive for WNV infection (US Geological Survey 2006). Unusually large mortality events reported by hunters and landowners in Owyhee County, Idaho led to closure of the hunting season in that area in 2006 (US Geological Survey 2006). Another large, but unexplained sage-grouse mortality event was reported near Jordan Valley, Oregon, in 2006, but remains were either not available or not testable (US Geological Survey 2006). Severe

declines in North Dakota populations between 2007 and 2008 were associated with high WNV mortality in summer 2007 (A. Robinson, pers. comm.).

*Resistance to WNV.*

The prevalence, geographic distribution, and spread of resistance to WNV disease among sage-grouse populations will have important implications for both short- and long-term effects of the virus. Here we define resistance as the ability to survive WNV exposure, WNV infection, or both, and we assume the individuals with neutralizing antibodies to WNV were at minimum, exposed to the virus. Under this definition, resistant individuals may still experience sublethal or residual effects of WNV infection.

The extent and distribution of resistance to WNV in wild populations remains unknown, but high mortality rates during severe WNV outbreaks and following experimental infection suggest that resistance is extremely low (Naugle et al. 2004, Clark et al. 2006, Walker et al. 2007b). Serum and tissues from 363 live and hunter-killed birds were tested for WNV in late 2003 and early 2004 following the 2003 outbreak, but no evidence of resistance to WNV was found—no birds tested seropositive for neutralizing antibodies to WNV (Naugle et al. 2004, 2005). The susceptibility of Greater Sage-Grouse to WNV was confirmed in 2004 when, in separate laboratory trials, all unvaccinated birds (N = 44) experimentally infected with WNV died within 6–8 da, regardless of dosage (Clark et al. 2006; T. E. Cornish, pers. comm.). Infected birds exhibited copious oral and nasal discharge, loss of mobility, shivering and piloerection of feathers, weakness, drooped wings, tilted heads, ataxia, labored breathing, and shedding of the virus from the cloaca (Clark et al. 2006). The first report of Greater Sage-Grouse surviving exposure to WNV was in the Powder River Basin of northeastern Wyoming and southeastern

Montana in 2005, when 10.3% of 58 individuals captured in spring tested seropositive. However, in spring 2006, only 1.8% of 109 birds tested seropositive (Walker et al. 2007b). Seropositive live birds have not yet been reported from other parts of the species' range, but because sage-grouse are capable of dispersing long distances and demonstrate a genetic pattern of isolation by distance (Oyler-McCance et al. 2005), other populations may also contain resistant individuals. The duration of immunity among birds that survive WNV infection is unknown (Marra et al. 2004). As in other flaviviruses, immunity is suspected to confer life-long resistance to WNV, but it may or may not cross-protect seropositive individuals from other flaviviruses (Fang and Reisen 2006).

*Carryover effects of WNV infection*

It remains unclear whether sage-grouse experience sublethal or residual effects of WNV infection on productivity or overwinter survival, in part because high mortality during outbreaks has left few infected survivors for observation (Walker et al. 2004, 2007a). However, as in other birds (e.g., raptors and owls; Nemeth et al. 2006a,b; Saito et al. 2007), sage-grouse infected with WNV may suffer persistent symptoms that reduce subsequent survival, reproduction, or both. Non-lethal cases of WNV infection often result in chronic symptoms and lengthy recovery periods in other species (Marra et al. 2004; Hayes et al. 2005a; Nemeth et al. 2006a,b). The nature and severity of carryover effects of WNV on Greater Sage-Grouse deserve further study.

## IMPACTS OF WNV ON POPULATION GROWTH

Matrix population models are valuable for understanding how impacts of potential stressors on vital rates translate into consequences for population growth. Life-stage simulation analyses (LSA) in particular, allow consideration of changes in both the mean and variance of

specific vital rates on changes in population growth (Wisdom et al. 2000, Reed et al. 2002). However, assumptions associated with matrix models suggest these models are best used to identify changes in population growth rate under different scenarios, rather than absolute estimates of growth rate (Reed et al. 2002). To better understand population-level impacts of WNV on sage-grouse, we estimated differences in population growth under different scenarios of WNV impacts using a life-stage simulation analysis model (Wisdom et al. 2000). We parameterized the model with vital rate means and variances from across the species' range to adequately capture the full background range of spatial and temporal variation in demographics.

ANALYSES

We conducted life-stage simulation analysis in MATLAB version R2007a (Mathworks, Inc., 2007) to test the importance of mean vital rate values and their variability in predicting population growth (finite rate of increase, $\lambda$) for each of four WNV impact scenarios. We then generated and compared means for $\lambda$ for each scenario based on 1,000 LSA simulations. Variance of demographic rates can strongly influence model results and interpretation (Wisdom et al. 2000). We used the variance discounting method of White (2000) to remove sampling variance from total variance estimates, and obtain an estimate of actual spatial and temporal variance for each vital rate. We used a two-stage, female-based, life-cycle model to summarize stage-specific rates of fertility and survival. We then used vital rates for each stage and associated estimates of process variance based on range-wide data (Appendix 1) to parameterize a corresponding 2 x 2 stage-specific population projection model based on a pre-breeding, birth-pulse census and a 1-yr projection interval with birds censused on ~1 April just prior to the initiation of nesting. The two stages were yearling and adult. Chick (<35 d of age) and juvenile

(>35 d of age) survival were not considered separate stages but were incorporated into fertility rates. Vital rates for each simulation were randomly selected from either a beta or stretched beta distribution (Morris and Doak 2002). We conducted analyses both with and without correlations among vital rates to see how correlation structure influenced estimates of λ (Morris and Doak 2002). Complete details regarding model structure, vital rate estimation, variance discounting, and correlations among vital rates are summarized in Walker (2008).

### WNV Impact Scenarios

Scenarios included models: (1) without WNV-related mortality, i.e., based on vital rate data prior to 2003, or data excluding WNV-related mortalities; (2) with WNV-related mortality based on observed infection and mortality rate data reported from 2003–2007 (Walker et al. 2007b); and (3) with WNV-related mortality, but with increasing resistance to WNV over time. Scenarios for WNV impacts that model the effects of increasing temperature due to climate change and of increasing anthropogenic water sources due to energy development would also be valuable, but were beyond the scope of the current analysis. We estimated means and variances of survival for juveniles >35 d of age, yearlings, and adults from range-wide data collected prior to 2003 or from data that excluded WNV-related mortalities (Walker 2008). We randomly selected infection rates for each simulation replicate in scenarios 2 and 3 from a stretched beta distribution with mean = 0.07, SD = 0.05, minimum = 0.005, maximum = 1.0 (Morris and Doak 2002, Box 8.3). This resulted in a distribution of infection rates (0–50%) and mortality rates (0-38%) consistent with published estimates (Walker et al. 2007b), allowed most simulated years to have low rates of WNV infection (median = 0.055) and mortality (median = 0.053), and produced some years with extreme values for infection rate (~50%) (Walker 2008). We

calculated mortality due to WNV (M) for each simulation replicate using infection rate (I) and resistance to WNV-related disease (R) as: M = I - (I x R) (i.e., proportion infected minus proportion infected but resistant to disease following exposure or infection). We used mortality rates to appropriately reduce juvenile, yearling, and adult survival by increasing mortality during the 2.5-mo WNV period (1 July–15 September) for each replicate. We assumed that resistance was constant in scenario 2 and used a value of 0.04, the mean spring seroprevalence value reported by Walker et al. (2007a). We assessed in scenario 3 how an increase in resistance to WNV might change population growth rate by calculating changes in the proportion of resistant individuals in the population under simulated rates of WNV infection and WNV mortality using 0.04 as the starting value for resistance. We assumed in this scenario that all resistance to WNV infection and disease was heritable and that all female offspring of a resistant female inherited traits that conferred resistance (heritability of resistance = 1). We conducted each simulation with 20 replicates to simulate responses within a 20-yr management time frame, and conducted the entire simulation 1,000 times to generate means and standard deviations for $\lambda$ for each year during the 20-yr period.

## FINDINGS

The addition of WNV mortality resulted in a projected average estimated reduction in $\lambda$ of -0.059 to -0.086, depending on the scenario and whether vital rates were correlated or uncorrelated (Table 2). However, substantial annual variation in vital rates that influence $\lambda$ resulted in wide variation in simulated values for $\lambda$ in all scenarios (Fig. 2). Results of LSA indicated that several different groups of vital rates were important for population growth; vital rates most highly correlated with population growth in LSA included nest success, chick

survival, juvenile survival, and adult and yearling survival (Fig. 3). The proportion of resistant individuals in the population was projected to increase only marginally over a 20-yr time period, from 0.04–0.15 using current estimates of infection rates (Fig. 4). The increase in resistance was projected to shift the distribution of WNV-related mortality rates lower over time (Fig. 5).

## DISCUSSION

West Nile virus is a new source of mortality that complicates efforts to conserve Greater Sage-Grouse. Growth is expected to decline in susceptible populations, birds appear to show little resistance to WNV, and management options for controlling the spread of WNV in sage-grouse habitat are limited. Prior to emergence of WNV, little evidence implicated disease, exotic or otherwise, as a major threat to Greater Sage-Grouse (Schroeder et al. 1999; Connelly et al. 2000, 2004). Several lines of evidence suggest that WNV represents a new risk to sage-grouse populations, including: (1) documented presence of the virus throughout the species' range, (2) persistent, and sometimes substantial, declines in late-summer survival due to WNV mortality, (3) large mortality events attributed to WNV in both marked and unmarked populations, (4) local extirpation of a breeding population following a severe WNV outbreak, (5) projected declines in simulated population growth in susceptible populations based on empirical infection and mortality rate data, (6) documented low levels of resistance to WNV disease in captive populations, (7) low potential for increasing resistance over time, and (8) potential for large-scale increases in mosquito breeding habitat, and consequently WNV risk, due to increases in surface water associated with energy development.

These conclusions may be conservative regarding the impact of WNV. First, limited evidence suggests that in some years, early-season WNV mortality may also reduce survival of

chicks <35 d of age either directly or indirectly by affecting survival of hens with dependent broods (Aldridge 2005, Walker 2008). Second, the distribution of mortality rates used in simulations may underestimate mortality in wild populations. Third, the presence of neutralizing antibodies in seropositive, live birds does not always reliably indicate resistance. Fourth, as in other species, it is entirely plausible that birds that survive WNV infection may later experience reduced survival or reproduction. Finally, WNV mortality typically comes at a time of year (July–September) when survival is typically high (Schroeder et al. 1999), suggesting it is additive to other sources of mortality.

The long-term response of different sage-grouse populations to WNV is expected to vary markedly depending on factors that influence susceptibility including: (1) annual and seasonal temperature-precipitation profiles, (2) land uses that influence the distribution of surface water, (3) population size, (4) genetic diversity, and (5) connectivity with other populations. Small, isolated, or genetically depauperate populations and those on the fringe of the species' range as in eastern California, Washington, North and South Dakota, Alberta, and Saskatchewan, are likely at higher risk. WNV outbreaks in small populations are more likely to reduce population size below a threshold from which recovery is unlikely and the likelihood of demographic or genetic rescue by adjacent populations is low (Morris and Doak 2002). Large, intact, low- to mid-elevation populations affected annually by WNV in northern Nevada, southeastern Idaho, central Montana, may absorb impacts of WNV if the quality and extent of available habitat still supports positive population growth. Impacts from WNV in some populations such as northeastern Wyoming, may act synergistically with other stressors like energy development, and tillage agriculture to substantially reduce population size, distribution, or persistence

(Walker et al. 2007a). Conservation of large, high-elevation populations, such as those in northwestern Colorado and western Wyoming, where WNV risk is relatively lower, will be important for offsetting impacts of WNV at a range-wide scale. Changes in virulence or epizootiology as the virus adapts to new environments and new hosts and vectors in North America will also influence long-term impacts of WNV on sage-grouse populations, but whether such changes will ameliorate or exacerbate current impacts is unknown.

Understanding long-term impacts of WNV will require intensive monitoring of radio-marked populations. Population models suggest that, except during severe outbreaks (Walker et al. 2004), natural geographic and temporal fluctuation in vital rates that drive population growth can mask impacts of WNV in any given year. Impacts of WNV mortality, and even severe WNV outbreaks, may go undetected without radio-marked individuals (Walker et al. 2004, US Geological Survey 2006) and lead to the misperception among managers and policy-makers that WNV is no longer an issue for Greater Sage-Grouse. Moreover, in the absence of radio-marked birds, population declines due to severe or persistent WNV mortality may be incorrectly attributed to other potential stressors and lead to inappropriate policy decisions and management or mitigation actions. Radio-marking is known to reduce reproductive effort and survival in other species (Withey et al. 2001), but mass mortality events of unmarked individuals and high late-summer survival among unaffected, radio-marked birds range-wide (Naugle et al. 2005) suggest that radio marking itself does not predispose individuals to greater risk of mortality following WNV infection. We strongly recommend continued range-wide monitoring and testing of radio-marked populations to estimate WNV-related mortality and testing of serum samples from live birds to document the extent and distribution of resistance to WNV. Failure to do so will hinder

our understanding of how this emerging disease influences sage-grouse populations and may diminish our ability to maintain the species' distribution and abundance (Friend et al. 2001).

Vaccines have been used to guard against catastrophic mortality in captive populations but are unlikely to be available or effective for protecting wild sage-grouse populations from impacts of WNV (Clark et al. 2006, Kilpatrick et al. 2007). Equine and fowl WNV vaccines administered via intramuscular injection have reduced mortality in captive birds (Bertelsen et al. 2004, McLean 2006, Bunning et al. 2007). However, fowl vaccine used on captive sage-grouse was only marginally effective; the vaccine reduced mortality rates from 100% to 80% (N = 5), increased average time to mortality from 3.7 to 6.7 d, and reduced average peak viremia from $10^{6.4}$ PFU to $10^{2.4}$ PFU (Clark et al. 2006). The lack of market incentives to produce a vaccine specifically for sage-grouse and lack of an effective delivery mechanism to large numbers of wild birds are major barriers to implementation (Clark et al. 2006, McLean 2006). Moreover, vaccinations only benefit treated individuals rather than conferring long-term immunity to offspring, so any vaccination program would require annual treatments (Kilpatrick et al. 2007).

Managing production of mosquito vectors from man-made water sources, reducing the distribution of man-made mosquito breeding habitats in sage-grouse habitat, or both, are potential options for reducing impacts of WNV. Previous studies, published prior to the arrival of WNV, have recommended use of water developments in arid sagebrush landscapes to benefit sage-grouse, but cautioned this should be done only if such actions clearly benefit the birds (Paige and Ritter 1999, Connelly et al. 2000). Sage-grouse use standing water when it is available (Dalke et al. 1963), but they do not require it (Connelly and Doughty 1989, Schroeder et al. 1999, Connelly et al. 2004). Addition of man-made water sources that increase the

distribution or abundance of *Culex tarsalis* in sage-grouse habitat may be particularly detrimental. Man-made water sources known to support breeding *Culex tarsalis* in sage-grouse habitat include overflowing stock tanks, stock ponds, seep and overflow areas below earthen dams, irrigated agricultural fields, and ponds constructed for coal-bed natural gas development (Zou et al. 2006b, Doherty 2007). Several strategies are recommended to reduce mosquito production from man-made water sources without eliminating the water source. First, ponds and tanks can be constructed,modified, or managed in ways that discourage breeding mosquitoes (Doherty 2007). It may also be possible to control mosquitoes with mosquitofish (*Gambusia* sp.) or native fish species that eat mosquito larvae, biological or chemical larvicides (BTI, *Bacillus thuringiensis v. israelensis*), or spraying for adults (Doherty 2007). Mosquito control programs appear effective for reducing WNV risk but only if applied appropriately and consistently by qualified mosquito control personnel (Gubler et al. 2000, Reisen and Brault 2007). The costs and benefits of control need to be weighed against potential detrimental or cascading ecological effects of widespread spraying (Marra et al. 2004). Requiring infectious disease impact statements as part of planned, large-scale changes in land use for energy development (McSweegan 1996) may also improve coordinated management of WNV risk in sage-grouse habitat.

ACKNOWLEDGMENTS

We thank J. C. Owen, V. O. Ezenwa, and M. W. Miller for discussion and comments on earlier drafts of this manuscript, L. S. Mills and C. Hartway for assistance with population modeling in MATLAB, and researchers and wildlife managers throughout the west for sharing unpublished data on WNV mortality. Comments by C. E. Braun and S. T. Knick improved the

manuscript.

LITERATURE CITED

ALDRIDGE, C. L. 2005. Identifying habitats for persistence of Greater Sage-Grouse (*Centrocercus urophasianus*) in Alberta, Canada. Ph.D. dissertation, University of Alberta, Edmonton, AB.

ALDRIDGE, C. L., S. E. NIELSEN, H. L. BEYER, M. S. BOYCE, J. W. CONNELLY, S. T. KNICK, AND M. A. SCHROEDER. 2008. Range-wide patterns of Greater Sage-Grouse persistence. Diversity and Distributions. In press.

BAILEY, S. F., D. A. ELIASON AND B. L. HOFFMAN. 1965. Flight and dispersal patterns of the mosquito *Culex tarsalis* Coquillett in the Sacramento Valley of California. Hilgardia 37:73–113.

BEEHLER, J. W., AND M. S. MULLA. 1995. Effects of organic enrichment on temporal distribution and abundance of culicine egg rafts. Journal of the American Mosquito Control Association 11:167–171.

BELL, J. A., C. M. BREWER, N. J. MICKELSON, G. W. GARMAN, AND J. A. VAUGHAN. 2006. West Nile virus epizootiology, central Red River valley, North Dakota and Minnesota, 2002–2005. Emerging Infectious Diseases 12:1245–1247.

BERTELSEN, M. F., R.-A. ØLBERG, G. J. CRAWSHAW, A. DIBERNARDO, L. R. LINDSAY, M. DREBOT, AND I. K. BARKER. 2004. West Nile virus infection in the eastern loggerhead shrike (*Lanius ludovicianus migrans*): pathology, epidemiology, and immunization. Journal of Wildlife Diseases 40:538–542.

BEVEROTH, T. A., M. P. WARD, R. L. LAMPMAN, A. M. RINGIA, AND R. J. NOVAK. 2006. Changes in seroprevalence of West Nile virus across Illinois in free-ranging birds from 2001 through 2004. American Journal of Tropical Medicine and Hygiene 74:174n179.

BRUST, R. A. 1991. Environmental regulation of autogeny in *Culex tarsalis* (Diptera Culicidae) from Manitoba, Canada. Journal of Medical Entomology 28:847–853.

BUNNING, M. L., P. E. FOX, R. A. BOWEN, N. KOMAR, G.-J. J. CHANG, T. J. SPEAKER, M. R. STEPHENS, N. M. NEMETH, N. A. PANELLA, S. A. LANGEVIN, P. GORDY, M. TEEHEE, P. R. BRIGHT, AND M. J. TURELL. 2007. DNA vaccination of the American Crow (*Corvus brachyrhynchos*) provides partial protection against lethal challenge with West Nile virus. Avian Diseases 51:573–577.

BUTH, J. L., R. A. BRUST, AND R. A. ELLIS. 1990. Development time, oviposition activity and onset of diapause in *Culex tarsalis*, *Culex restuans* and *Culiseta inornata* in southern Manitoba. Journal of the American Mosquito Control Association 6:55–63.

CAFFREY, C., S. C. R. SMITH, AND T. J. WESTON. 2005. West Nile virus devastates an American Crow population. Condor 107:128–132.

CAFFREY, C., T. J. WESTON, AND S. C. R. SMITH. 2003. High mortality among marked crows subsequent to the arrival of West Nile virus. Wildlife Society Bulletin 31:870-872.

CAMPBELL, G. L., A. A. MARFIN, R. S. LANCIOTTI, AND D. J. GUBLER. 2002. West Nile virus. Lancet: Infectious Diseases 2:519–529.

CENTERS FOR DISEASE CONTROL AND PREVENTION. 2008. <http://www.cdc.gov/ncidod/dvbid/westnile/> (15 October 2008).

CHOMEL, B. B., A. BELOTTO, AND F. X. MESLIN. 2007. Wildlife, exotic pets, and emerging zoonoses. Emerging Infectious Diseases 13:6–11.

CLARK, L., J. HALL, R. MCLEAN, M. DUNBAR, K. KLENK, R. BOWEN, AND C. A. SMERASKI. 2006. Susceptibility of Greater Sage-Grouse to experimental infection with West Nile virus. Journal of Wildlife Diseases 42:14–22.

CONNELLY, J. W., AND L. A. DOUGHTY. 1989. Sage grouse use of wildlife water developments in southeastern Idaho. Pp. 167–172 *in* G. K. Tsukamoto, and S. J. Stiver (editors). Wildlife water development: a proceedings of the wildlife water development symposium. Nevada Department of Fish and Game, Reno, NV.

CONNELLY, J. W., M. A. SCHROEDER, A. R. SANDS, AND C. E. BRAUN. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

CONNELLY, J. W., S. T. KNICK, M. A. SCHROEDER, AND S. J. STIVER. 2004. Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, WY.

CROSBIE, S. P., W. D. KOENIG, W. K. REISEN, V. L. KRAMER, L. MARCUS, R. CARNEY, E. PANDOLFINO, G. M. BOLEN, L. R. CROSBIE, D. A. BELL, AND H. B. ERNEST. 2008. Early impact of West Nile virus on the Yellow-Billed Magpie (*Pica nuttalli*). Auk 125:542–550.

DALKE, P. D., D. B. PYRAH, D. C. STANTON, J. E. CRAWFORD, AND E. F. SCHLATTERER. 1963. Ecology, productivity, and management of sage grouse in Idaho. Journal of Wildlife Management 27:811–841.

DASZAK, P., A. A. CUNNINGHAM, AND A. D. HYATT. 2000. Emerging infectious diseases of wildlife—threats to biodiversity and human health. Science 287:443–449.

DAVIS, C. T., D. W. C. BEASLEY, H. GUZMAN, M. SIIRIN, R. E. PARSONS, R. B. TESH, AND A. D. T. BARRETT. 2004. Emergence of attenuated West Nile virus variants in Texas, 2003. Virology 330:342–350.

DAVIS, C. T., G. D. EBEL, R. S. LANCIOTTI, A. C. BRAULT, H. GUZMAN, M. SIIRIN, A. LAMBERT, R. E. PARSONS, D. W. C. BEASLEY, R. J. NOVAK, D. ELIZONDO-QUIROGAG, E. N. GREEN, D. S. YOUNG, L. M. STARK, M. A. DREBOT, H. ARTSOB, R. B. TESH, L. D. KRAMER, AND A. D. T. BARRETT. 2005. Phylogenetic analysis of North American West Nile virus isolates, 2001-2004: evidence for the emergence of a dominant genotype. Virology 342:252–265.

DAWSON, J. R., W. B. STONE, G. D. EBEL, D. S. YOUNG, D. S. GALINSKI, J. P. PENSABENE, M. A. FRANKE, M. EIDSON, AND L. D. KRAMER. 2008. Crow deaths caused by West Nile virus during winter. Emerging Infectious Diseases 13:1912–1914.

DIMENNA, M. A., R. BUENO JR., R. R. PARMENTER, D. E. NORRIS, J. M. SHEYKA, J. L. MOLINA, E. M. LABEAU, E. S. HATTON, AND G. E. GLASS. 2006. Emergence of West Nile virus in mosquito (Diptera: Culicidae) communities of the New Mexico Rio Grande valley. Journal of Medical Entomology 43:594–599.

DOBSON, A., AND J. FOUFOPOULOS. 2001. Emerging infectious pathogens of wildlife. Philosophical Transactions of the Royal Society of London Series B Biological Science 356:1001–1012.

DOHERTY, M. K. 2007. Mosquito populations in the Powder River Basin, Wyoming: a comparison of natural, agricultural and effluent coal-bed natural gas aquatic habitats. M.S. thesis, Montana State University, Bozeman, MT.

DOHM, D. J., M. L. O'GUINN, AND M. J. TURELL. 2002. Effect of environmental temperature on the ability of *Culex pipiens* (Diptera: Culicidae) to transmit West Nile virus. Journal of Medical Entomology 39:221–225.

EPSTEIN, P. R. 2001. West Nile virus and the climate. Journal of Urban Health: Bulletin of the New York Academy of Medicine 78:367–371.

EPSTEIN, P. R., AND C. DEFILIPPO. 2001. West Nile virus and drought. Global Change and Human Health 2:105–107.

FANG, Y., AND W. K. REISEN. 2006. Previous infection with West Nile or St. Louis encephalitis viruses provides cross protection during reinfection in House Finches. American Journal of Tropical Medicine and Hygiene 75:480–485.

FARAJOLLAHI, A., W. J. CRANS, D. NICKERSON, P. BRYANT, B. WOLF, A. GLASER, AND T. G. ANDREADIS. 2005. Detection of West Nile virus RNA from the louse fly *Icosta americana* (Diptera: Hippoboscidae). Journal of the American Mosquito Control Association 21:474–476.

FRIEND, M., R. G. MCLEAN, AND F. J. DEIN. 2001. Disease emergence in birds: challenges for the twenty-first century. Auk 118:290–303.

GIBBS, S. E. J., D. M. HOFFMAN, L. M. STARK, N. L. MARLENEE, B. J. BLITVICH, B. J. BEATY, AND D. E. STALLKNECHT. 2005. Persistence of antibodies to West Nile virus in naturally

infected Rock Pigeons (*Columba livia*). Clinical and Diagnostic Laboratory Immunology 12:665–667.

GILBERT, L., L. D. JONES, M. K. LAURENSON, E. A. GOULD, H. W. REED, AND P. J. HUDSON. 2004. Ticks need not bite their Red Grouse hosts to infect them with louping ill virus. Proceedings of the Royal Society of London, Series B (Supplement) 271:S202–S205.

GODDARD, L. B., A. E. ROTH, W. K. REISEN, AND T. W. SCOTT. 2002. Vector competence of California mosquitos for West Nile virus. Emerging Infectious Disease 8:1385–1391.

GODDARD, L. B., A. B. ROTH, W. K. REISEN, T. W. SCOTT. 2003. Vertical transmission of West Nile virus by three California *Culex* (Diptera: Culicidae) species. Journal of Medical Entomology 40:743–747.

GUBLER, D. J. 2007. The continuing spread of West Nile virus in the western hemisphere. Emerging Infections 45:1039–1046.

GUBLER, D.J., G. L. CAMPBELL, R. NASCI, N. KOMAR, L. PETERSEN, AND J. T. ROEHRIG. 2000. West Nile virus in the United States: guidelines for detection, prevention, and control. Viral Immunology 13:469–475.

HAHN, D. C., N. M. NEMETH, E. EDWARDS, P. R. BRIGHT, AND N. KOMAR. 2006. Passive West Nile virus antibody transfer from maternal Eastern Screech-Owls (*Megascops asio*) to progeny. Avian Diseases 50:454–455.

HAYES. E. B., N. KOMAR, R. S. NASCI, S. P. MONTGOMERY, D. R. O'LEARY, AND G. L. CAMPBELL. 2005*a*. Epidemiology and dynamics of transmission of West Nile virus disease. Emerging Infectious Disease 11:1167–1173.

HAYES. E. B., J. J. SEJVAR. S. R. ZAKI, R. S. LANCIOTTI, A. V. BODE, AND G. L. CAMPBELL. 2005b. Virology, pathology, and clinical manifestations of West Nile virus disease. Emerging Infectious Disease 11:1174–1179.

HIGGS, S., B. S. SCHNEIDER, D. L. VANLANDINGHAM, K. A. KLINGLER, AND E. A. GOULD. 2005. Nonviremic transmission of West Nile virus. Proceedings of the National Academy of Sciences 102:8871–8874.

HUTCHESON, H. J., C. H. GORHAM, C. MACHAIN-WILLIAMS, M. A. LORONO-PINO, A. M. JAMES, N. L. MARLENEE, B. WINN, B. J. BEATY, AND C. D. BLAIR. 2005. Experimental transmission of West Nile virus (Flaviviridae: *Flavivirus*) by *Carios capensis* ticks from North America. Vector Borne Zoonotic Diseases 5:293–295.

KACZOR, N. W. 2008. Nesting and brood-rearing success and resource selection of Greater Sage-Grouse in northwestern South Dakota. M.S. thesis, South Dakota State University, Brookings, SD.

KATO, C. Y., A. W. FABIAN, E. T. SCHMIDTMANN, G. D. JOHNSON, D. E. NAUGLE, AND R. T. MAYER. 2008. Cytochrome *b* analyses of mosquito blood meals: identifying wildlife reservoirs of West Nile virus in sagebrush habitats of western North America. Journal of Wildlife Diseases. In press.

KILPATRICK, A. M., P. DASZAK, M. J. JONES, P. P. MARRA, AND L. D. KRAMER. 2006*a*. Host heterogeneity dominates West Nile virus transmission. Proceedings of the Royal Society of London, Series B 273:2327–2333.

KILPATRICK, A. M., L. D. KRAMER, M. J. JONES, P. P. MARRA, AND P. DASZEK. 2006b. West Nile virus epidemics in North America are driven by shifts in mosquito feeding behavior. Public Library of Science—Biology 4:1–5.

KILPATRICK, A. M., S. L. LADEAU, AND P. P. MARRA. 2007. Ecology of West Nile virus transmission and its impact on birds in the western hemisphere. Auk 124:1121–1136.

KOENIG, W. D., L. MARCUS, T. W. SCOTT, AND J. L. DICKINSON. 2007. West Nile virus and California breeding bird declines. EcoHealth 4:18–24.

KOMAR, N., N. PANELLA, S. LANGEVIN, A. BRAULT, M. AMADOR, E. EDWARDS, AND J. OWEN. 2005. Avian hosts for West Nile virus in St. Tammany Parish, Louisiana. American Journal of Tropical Medicine and Hygiene 73:1031–1037.

KRAMER, L. D., L. M. STYER, AND G. D. EBEL. 2008. A global perspective on the epidemiology of West Nile virus. Annual Review of Entomology 53:4.1–4.21.

LADEAU, S. L., A. M. KILPATRICK, AND P. P. MARRA. 2007. West Nile virus emergence and large-scale declines of North American bird populations. <http://nationalzoo.si.edu/Publications/ScientificPublications/pdfs/nature05829.pdf> (15 October 2008).

LEE, J. H., H. HASSAN, G. HILL, E. W. CUPP, T. B. HIGAZI, C. J. MITCHELL, M. S. GODSEY JR., AND T. R. UNNASCH. 2002. Identification of mosquito avian-derived blood meals by polymerase chain reaction-heteroduplex analysis. American Journal of Tropical and Medicine and Hygiene 66:599–604.

LORD, C. C., AND J. F. DAY. 2001. Simulation studies of St. Louis encephalitis and West Nile viruses: the impact of bird mortality. Vector Borne and Zoonotic Diseases 1:317–329.

LORD, C. C., R. RUTLEDGE, AND W. J. TABACHNICK. 2006. Relationships between host viremia and vector susceptibility for arboviruses. Journal of Medical Entomology 43:623–630.

MARRA, P. P., S. GRIFFING, C. CAFFREY, A. M. KILPATRICK, R. MCLEAN, AND C. BRAND. 2004. West Nile virus and wildlife. BioScience 54:393–402.

MCLEAN, R. G. 2006. West Nile virus in North American birds. Ornithological Monographs 60:44–64.

MCSWEEGAN, E. 1996. The infectious diseases impact statement: a mechanism for addressing emerging diseases. Emerging Infectious Diseases 2:103–108.

MEECE, J. K., T. A. KRONENWETTER-KOEPEL, M. F. VANDERMAUSE, AND K. D. REED. 2006. West Nile virus infection in commercial waterfowl operation, Wisconsin. Emerging Infectious Diseases 12:1451–1453.

MILBY, M. M., AND R. P. MEYER. 1986. The influence of constant versus fluctuating water temperatures on the preimaginal development of *Culex tarsalis*. Journal of the American Mosquito Control Association 2:7–10.

MORRIS, W. F. AND D. DOAK. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Inc., Sunderland, MA.

MOUDY, R. M., M. A. MEOLA, L. L. MORIN, G. D. EBEL, AND L. D. KRAMER. 2007. A newly emergent genotype of West Nile virus is transmitted earlier and more efficiently by *Culex* mosquitos. American Journal of Tropical Medicine and Hygiene 77:365–370.

NASCI, R. S., H. M. SAVAGE, D. J. WHITE, J. R. MILLER, B. C. CROPP, M. S. GODSEY, A. J. KERST, P. BENNETT, K. GOTTTFREID, AND R. S. LANCIOTTI. 2001. West Nile virus in

overwintering *Culex* mosquitos, New York City, 2000. Emerging Infectious Diseases 7:742–744.

NAUGLE, D. E., C. L. ALDRIDGE, B. L. WALKER, K. E. DOHERTY, M. R. MATCHETT, J. MCINTOSH, T. E. CORNISH, AND M. S. BOYCE. 2005. West Nile virus and sage-grouse: what more have we learned? Wildlife Society Bulletin: 33:1–8.

NAUGLE, D. E., C. L. ALDRIDGE, B. L. WALKER, T. E. CORNISH, B. J. MOYNAHAN, M. J. HOLLORAN, K. BROWN, G. D. JOHNSON, E. T. SCHMIDTMANN, R. T. MAYER, C. Y. KATO, M. R. MATCHETT, T. J. CHRISTIANSEN, W. E. COOK, T. CREEKMORE, R. D. FALISE, E. T. RINKES, AND M. S. BOYCE. 2004. West Nile virus: pending crisis for Greater Sage-Grouse. Ecology Letters: 7:704–713.

NEMETH, N. M., AND R. A. BOWEN. 2007. Dynamics of passive immunity to West Nile virus in domestic chickens (*Gallus gallus domesticus*). American Journal of Tropical Medicine and Hygiene 76: 310–317.

NEMETH, N. M., D. GOULD, R. BOWEN, AND N. KOMAR. 2006a. Natural and experimental West Nile virus infection in five raptor species. Journal of Wildlife Diseases 42:1–13.

NEMETH, N. M., D. C. HAHN, D. H. GOULD, AND R. A. BOWEN. 2006b. Experimental West Nile virus infection in Eastern Screech Owls (*Megascops asio*). Avian Diseases 50:252–258.

OWEN, J., F. MOORE, N. PANELLA, E. EDWARDS, R. BRU, M. HUGHES, AND N. KOMAR. 2006. Migrating birds as dispersal vehicles for West Nile virus. EcoHealth 3:79–85.

OYLER-MCCANCE, S. J., S. E. TAYLOR, AND T. W. QUINN. 2005. A multilocus population genetic survey of the Greater Sage-Grouse across their range. Molecular Ecology 14:1293–1310.

PAIGE, C., AND S. A. RITTER. 1999. Birds in a sagebrush sea: managing sagebrush habitats for bird communities. Partners in Flight Western Working Group, Boise, ID.

PETERSON, A. T., D. A. VIEGLAIS, AND J. K. ANDREASEN. 2003. Migratory birds modeled as critical transport agents for West Nile virus in North America. Vector-Borne and Zoonotic Diseases 3:27–37.

PLATT, K. B., B. J. TUCKER, P. G. HALBUR, S. TIAWSIRISUP, B. J. BLITVICH, F. G. FABIOSA, L. C. BARTHOLOMAY, AND W. A. ROWLEY. 2007. West Nile virus viremia in eastern chipmunks (*Tamias striatus*) sufficient for infecting different mosquitoes. Emerging Infectious Diseases 13:831–837.

PLATT, K. B., B. J. TUCKER, P. G. HALBUR, S. TIAWSIRISUP, B. J. BLITVICH, F. G. FABIOSA, K. MULLIN, G. R. PARIKH, P. KITIKOON, L. C. BARTHOLOMAY, AND W. A. ROWLEY. 2008. Fox squirrels (*Sciurus niger*) develop West Nile virus viremias sufficient for infecting select mosquito species. Vector-Borne and Zoonotic Diseases 5:9.

RAPPOLE, J. H., AND Z. HUBÁLEK. 2003. Migratory birds and West Nile virus. Journal of Applied Microbiology 94 (Supplement 1):47–58.

REED, K. D., J. K. MEECE, J. S. HENKEL, AND S. K. SHUKLA. 2003. Birds, migration, and emerging zoonoses: West Nile virus, Lyme disease, influenza A and enteropathogens. Clinical Medicine and Research 1:5–12.

REED, J. M., L. S. MILLS, J. B. DUNNING JR., E. S. MENGES, K. S. MCKELVEY, R. FRYE, S. BEISSINGER, M.-C. ANSTETT, AND P. MILLER. 2002. Emerging issues in population viability analysis. Conservation Biology 16:7–19.

REISEN, W. K., AND A. C. BRAULT. 2007. West Nile virus in North America: perspectives on epidemiology and intervention. Pest Management Science 63:641–646.

REISEN, W. K., Y. FANG, V. M. MARTINEZ. 2006a. Effects of temperature on the transmission of West Nile virus by *Culex tarsalis* (Diptera: Culicidae). Journal of Medical Entomology 43:309–317.

REISEN, W. K., Y. FANG, AND V. M. MARTINEZ. 2007. Is nonviremic transmission of West Nile virus by *Culex* mosquitoes (Diptera: Culicidae) nonviremic? Journal of Medical Entomology 44:299–302.

REISEN, W. K., H. D. LOTHROP, AND B. LOTHROP. 2003. Factors influencing the outcome of mark-release-recapture studies with *Culex tarsalis* (Diptera: Culicidae). Journal of Medical Entomology 40:820–829.

REISEN, W. K., Y. FANG, H. D. LOTHROP, V. M. MARTINEZ, J. WILSON, P. O'CONNOR, R. CARNEY, B. CAHOON-YOUNG, M. SHAFII, AND A. C. BRAULT. 2006b. Overwintering of West Nile virus in southern California. Journal of Medical Entomology 43:344–355.

SAITO, E. K., L. SILEO, D. E. GREEN, C. U. METEYER, G. S. MCLAUGHLIN, K. A. CONVERSE, AND D. E. DOCHERTY. 2007. Raptor mortality due to West Nile virus in the United States, 2002. Journal of Wildlife Diseases 43:206–213.

SARDELIS, M. R., M. J. TURELL, D. J. DOHM, AND M. L. O'GUINN. 2001. Vector competence of selected North American *Culex* and *Coquillettidia* mosquitos for West Nile virus. Emerging Infectious Diseases 7:1018–1022.

SCHROEDER, M. A., C. L. ALDRIDGE, A. D. APA, J. R. BOHNE, C. E. BRAUN, S. D. BUNNELL, J. W. CONNELLY, P. A. DEIBERT, S. C. GARDNER, M. A. HILLIARD, G. D. KOBRIGER, S. M.

MCADAM, C. W. MCCARTHY, J. J. MCCARTHY, D. L. MITCHELL, E. V. RICKERSON, AND S. J. STIVER. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

SCHROEDER, M. A., J. R. YOUNG, AND C. E. BRAUN. 1999. Sage grouse (*Centrocercus urophasianus*). *In* A. Poole, and F. Gill (editors). The Birds of North America, No. 425. The Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union, Washington, DC.

SHAMAN, J., J. F. DAY, AND M. STIEGLITZ. 2005. Drought-induced amplification and epidemic transmission of West Nile virus in southern Florida. Journal of Medical Entomology 42:134–141.

SOVADA, M. A., P. J. PIETZ, K. A. CONVERSE, D. T. KING, E. K. HOFMEISTER, P. SCHERR, H. S. IP. 2008. Impact of West Nile virus and other mortality factors on American White Pelicans at breeding colonies in the northern plains of North America. Biological Conservation 141:1021–1031.

STIVER, S. J., A. D. APA, J. R. BOHNE, S. D. BUNNELL, P. A. DEIBERT, S. C. GARDNER, M. A. HILLIARD, C. W. MCCARTHY, AND M. A. SCHROEDER. 2006. Greater Sage-Grouse comprehensive conservation strategy. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, WY.

STYER, L.M., M. A. MEOLA, AND L. D. KRAMER. 2007a. West Nile virus infection decreases fecundity of *Culex tarsalis* females. Journal of Medical Entomology 44:1074–1085.

STYER, L.M., K.A. KENT, R.G. ALBRIGHT, C. J. BENNETT, L. D. KRAMER, AND K. A. BERNARD. 2007b. Mosquitos inoculate high doses of West Nile virus as they probe and feed on live hosts. PLoS Pathology 3:1262–1270.

MATHWORKS, INC. 2007. MATLAB. Version R2007a. Natick, MA.

TIAWSIRISUP, S., K. B. PLATT, B. J. TUCKER, AND W. A. ROWLEY. 2005. Eastern cottontail rabbits (*Sylvilagus floridanus*) develop West Nile virus viremias sufficient for infecting select mosquito species. Vector-Borne and Zoonotic Diseases 5:342–349.

TIAWSIRISUP, S., J. R. KINLEY, B. J. TUCKER, R. B. EVANS, W. A. ROWLEY, AND K. B. PLATT. 2008. Vector competence of *Aedes vexans* (Diptera: Culicidae) for West Nile virus and potential as an enzootic vector. Journal of Medical Entomoogy 45:452–457.

TURELL, M. J., M. L. O'GUINN, D. J. DOHM, AND J. W. JONES. 2001. Vector competence of North American mosquitos (Diptera: Culicidae) for West Nile virus. Journal of Medical Entomology 38:130–134.

TURELL, M. J., M. L. O'GUINN, AND J. OLIVER. 2000. Potential for New York mosquitoes to transmit West Nile virus. American Journal of Tropical Medicine and Hygiene 62:413–414.

TURELL, M. J., D. J. DOHM, M. R. SARDELIS, M. L. O'GUINN, T. G. ANDREADIS, AND J. A. BLOW. 2005. An update on the potential of North American mosquitos (Diptera: Culicidae) to transmit West Nile virus. Journal of Medical Entomology 42:57–62.

US GEOLOGICAL SURVEY. 2006. West Nile virus in Greater Sage-Grouse. Wildlife health bulletin 06-08. <http://www.nwhc.usgs.gov/publications/wildlife_health_bulletins/WHB_06_08.jsp> (15 October 2008).

VAN DER MEULEN, K. M., M. B. PENSAERT, AND H. J. NAUWYNCK. 2005. West Nile virus in the vertebrate world. Archives of Virology 150:637–657.

WALKER, B. L. 2006. West Nile and sage-grouse update. Sagemap <http://sagemap.wr.usgs.gov/> (15 October 2008).

WALKER, B. L. 2008. Greater Sage-Grouse response to coal-bed natural gas development and West Nile virus in the Powder River Basin, Montana and Wyoming, USA. Ph.D. dissertation, University of Montana, Missoula, MT.

WALKER, B. L., D. E. NAUGLE, AND K. E. DOHERTY. 2007a. Greater Sage-Grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

WALKER, B. L., D. E. NAUGLE, K. E. DOHERTY, AND T. E. CORNISH. 2004. From the field: outbreak of West Nile virus in Greater Sage-Grouse and guidelines for monitoring, handling, and submitting dead birds. Wildlife Society Bulletin 32:1000–1006.

WALKER, B. L., D. E. NAUGLE, K. E. DOHERTY, AND T. E. CORNISH. 2007b. West Nile virus and Greater Sage-Grouse: estimating infection rate in a wild bird population. Avian Diseases 51:691–696.

WARD, M. R., D. E. STALLKNECHT, J. WILLIS, M. J. CONROY, AND W. R. DAVIDSON. 2006. Wild bird mortality and West Nile virus surveillance: biases associated with detection, reporting, and carcass persistence. Journal of Wildlife Diseases 42:92–106.

WHITE, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pp. 288–331 *in* L. Boitani, and T. K. Fuller (editors). Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, NY.

WITHEY, J. C., T. D. BLOXTON, AND J. M. MARZLUFF. 2001. Effects of tagging and location error in wildlife studies. Pp. 43–75 *in* J. J. Millspaugh, and J. M. Marzluff (editors). Radio tracking and animal populations. Academic Press, San Diego, CA.

WISDOM, M. J., L. S. MILLS, AND D. F. DOAK. 2000. Life state simulation analysis: estimating vital rate effects on population growth for species conservation. Ecology 81:628–641.

WÜNSCHMANN, A., AND A. ZIEGLER. 2006. West Nile virus-associated mortality events in domestic Chukar Partridges (*Alectoris chukar*) and domestic Impeyan Pheasants (*Lophophorus impeyanus*). Avian Diseases 50:456–459.

YAREMYCH, S.A., R. E. WARNER, P. C. MANKIN, J. D. BRAWN, A. RAIM, AND R. NOVAK. 2004. West Nile virus and high death rate in American crows. Emerging Infectious Diseases 10:709–711.

ZOU, L., S. N. MILLER, AND E. T. SCHMIDTMANN. 2006a. A GIS tool to estimate West Nile virus risk based on a degree-day model. Environmental Modeling and Assessment (on-line): DOI 10.1007/s10661-006-9373-8

ZOU, L., S. N. MILLER, AND E. T. SCHMIDTMANN. 2006b. Mosquito larval habitat mapping using remote sensing and GIS: implications of coalbed methane development and West Nile virus. Journal of Medical Entomology 43:1034–1041.

TABLE 1. US STATES AND CANADIAN PROVINCES WITH CONFIRMED (+) WEST NILE VIRUS-POSITIVE GREATER SAGE-GROUSE MORTALITIES, 2002–2007. WEST NILE VIRUS WAS DETECTED IN OTHER SPECIES (HORSES, HUMANS, MOSQUITOES, OR SENTINEL SPECIES) IN ALL STATES AND PROVINCES WITHIN SAGE-GROUSE RANGE BY 2002 EXCEPT ALBERTA (2003), NEVADA (2003), UTAH (2003), AND OREGON (2005) (KILPATRICK ET AL. 2007, CDC 2008).

| State or province | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 |
|---|---|---|---|---|---|---|
| California | | | + | + | | |
| Colorado | | | + | | | |
| Idaho | | | | + | | |
| Montana | | + | + | + | + | + |
| Nevada | | | | + | | |
| North Dakota | | | | | + | |
| Oregon | | | | | + | |
| South Dakota | | | | | + | + |
| Utah | | | + | | | |
| Washington | | | | | | |
| Wyoming | + | + | + | + | + | + |
| Alberta | | + | + | + | | |
| Saskatchewan | | | | | | |

TABLE 2. ESTIMATED AVERAGE REDUCTION IN ANNUAL POPULATION GROWTH RATE (FINITE RATE OF INCREASE, λ) UNDER DIFFERENT WEST NILE VIRUS (WNV) IMPACT SCENARIOS RELATIVE TO NO WNV MORTALITY. DATA ARE BASED ON LIFE-STAGE SIMULATION ANALYSES USING VITAL RATES FOR FEMALE GREATER SAGE-GROUSE FROM RANGE-WIDE DATA. RESULTS ARE BASED ON 1,000 LSA SIMULATION REPLICATES. REDUCTIONS IN Λ DUE TO WNV MORTALITY MAY BE MASKED IN ANY GIVEN YEAR BY ANNUAL FLUCTUATIONS IN VITAL RATES INFLUENTIAL FOR POPULATION GROWTH (NEST SUCCESS, CHICK SURVIVAL, JUVENILE SURVIVAL, SURVIVAL OF BREEDING-AGE FEMALES).

| | Correlated[a] | Uncorrelated[b] |
|---|---|---|
| Scenario | Δλ | Δλ |
| No WNV | 0.000 | 0.000 |
| Current WNV | -0.086 | -0.060 |
| Current WNV with increasing resistance | -0.081 | -0.059 |

[a] Simulated vital rates for each replicate accounted for correlations among vital rates.

[b] Simulated vital rates for each replicate were uncorrelated.

FIGURE LEGENDS

FIGURE 1. Distribution of Greater Sage-Grouse and Gunnison Sage-Grouse and locations where birds were monitored or tested for West Nile virus from 2002–2007. Numbered sites include Mono Co., CA (1); Douglas Co., NV (2); Harney Co., OR (3); Malheur Co., OR (4); Washington Co., ID (5); Owyhee Co., ID and Elko Co., NV (6); Twin Falls Co., ID (7); Douglas Co., WA (8); Duchesne Co., UT (9); Moffat Co. (Hiawatha/Cold Springs Mtn.), CO (10); Moffat Co. (Axial Basin), CO (11); Routt Co., CO (12); Gunnison Co., CO (13); Sublette Co. (Pinedale), WY (14); Fremont Co. (Lander), WY (15); Fremont Co. (Wind River Indian Reservation), WY (16); Carbon Co., WY (17); Natrona Co., WY (18); Campbell Co. (Wright), WY (19); Johnson Co., WY (20); Campbell Co. (Spotted Horse), WY (21); Bighorn Co., MT and Sheridan Co., WY (22); Butte Co. and Harding Co., SD, Crook Co., WY, and Carter Co., MT (23); Bowman Co., ND (24); Golden Valley Co. and Musselshell Co., MT (25); Phillips Co., MT (26); Valley Co., MT (27); and southeastern AB (28). Map is based on data reported in Naugle et al. (2004, 2005), Walker et al. (2004), Walker (2006), USGS (2006), Kaczor (2008), Walker (2008), and unpublished data provided by state agencies and researchers.

FIGURE 2. Distribution of simulated annual population growth rates (finite rate of increase, $\lambda$) for female Greater Sage-Grouse based on life-stage simulation analysis using range-wide data, assuming no WNV impacts. Absolute values of range-wide population growth based on simulated data from population models cannot be used to infer range-wide population trends.

FIGURE 3. Variance in finite rate of increase, $\lambda$, explained by vital rates grouped into those affected by different management strategies, based on range-wide vital-rate data for female Greater Sage-Grouse. Simulated data included correlations between vital rates. Values are

coefficients of determination ($r^2$) standardized to 1 (vital rate definitions in Appendix 1).

FIGURE 4. Projected change in resistance to WNV disease of female Greater Sage-Grouse at the start of the breeding season over a 20-yr period based on simulated vital rates in life-stage simulation analyses. Error bars represent 1 SD. The initial value for resistance was set at 0.04 in year 1 (i.e., 4% of the population resistant to WNV).

FIGURE 5. Distribution of WNV mortality among female Greater Sage-Grouse in year 1 (open squares) and year 20 (black circles) of the simulation with increasing resistance over time based on simulated infection rates from range-wide data, assuming no carryover effects of WNV infection.

APPENDIX 1. RANGE-WIDE VITAL RATE SUMMARY.

| Vital Rate[a] | Mean | Variance[b] |
|---|---|---|
| $INIT_{YR1}$ | 0.829 | 0.0166 |
| $INIT_{AD1}$ | 0.930 | 0.0038 |
| $INIT_{YR2}$ | 0.148 | 0.0368 |
| $INIT_{AD2}$ | 0.395 | 0.0599 |
| $INIT_{AD3}$ | 0.074 | 0.0051 |
| $FCLUTCH_{YR1}$ | 3.81 | 0.118 |
| $FCLUTCH_{YR2}$ | 3.29 | 0.316 |
| $FCLUTCH_{AD1}$ | 4.16 | 0.040 |
| $FCLUTCH_{AD2}$ | 3.52 | 0.200 |
| $FCLUTCH_{AD3}$ | 3.02 | 0.200[c] |
| $SUCC_{YR1}$ | 0.481 | 0.0268 |
| $SUCC_{AD1}$ | 0.569 | 0.0183 |
| $SUCC_{YR2}$ | 0.540 | 0.1309 |
| $SUCC_{AD2}$ | 0.553 | 0.0623 |
| HATCH | 0.921 | 0.0018 |
| $CHSURV_{YR}$ | 0.391[d] | 0.0084[d] |
| $CHSURV_{AD}$ | 0.391[d] | 0.0084[d] |
| $JUVSURV_{83}$ | 0.799 | 0.0154 |
| $JUVSURV_{91}$ | 0.782 | 0.0177 |
| $SURV_{YR}$ | 0.684 | 0.0182 |

| | | |
|---|---|---|
| $SURV_{AD}$ | 0.582 | 0.0050 |

[a] Variables defined as: $INIT_{YR1}$ = nest initiation rate of yearlings; $INIT_{AD1}$ = nest initiation rate of adults; $INIT_{YR2}$ = renesting rate of yearlings; $INIT_{AD2}$ = renesting rate of adults; $INIT_{AD3}$ = second renesting rate of adults; $FCLUTCH_{YR1}$ = clutch size (female eggs only) of yearling first nests; $FCLUTCH_{YR2}$ = clutch size (female eggs only) of yearling renests; $FCLUTCH_{AD1}$ = clutch size (female eggs only) of adult first nests; $FCLUTCH_{AD2}$ = clutch size (female eggs only) of adult renests; $FCLUTCH_{AD3}$ = clutch size (female eggs only) of adult second renests; $SUCC_{YR1}$ = nest success of yearling first nests; $SUCC_{AD1}$ = nest success of adult first nests; $SUCC_{YR2}$ = nest success of yearling renests; $SUCC_{AD2}$ = nest success of adult renests (and second nests); HATCH = hatching success; $CHSURV_{YR}$ = survival of chicks from yearling females from hatch to 35 d; $CHSURV_{AD}$ = survival of chicks from adult females from hatch to 35 d of age; $JUVSURV_{83}$ = survival of juveniles from 35 d of age to 10 September for renests; $JUVSURV_{91}$ = survival of juveniles from 35 d of age to 10 September for first nests; $SURV_{YR}$ = annual survival of yearlings; and $SURV_{AD}$ = annual survival of adults.

[b] Process variance estimated following White (2000).

[c] Process variance for clutch size of second renests could not be estimated from range-wide data; the value for clutch size of renests was used.

[d] Mean and process variance for chick survival of yearling and adult females were the same in range-wide data because most previous publications did not present chick survival estimates separately for each stage.

[e] Process variance for juvenile survival could not be estimated from Powder River Basin data; values represent raw variance estimates from range-wide data.

Figure 1.

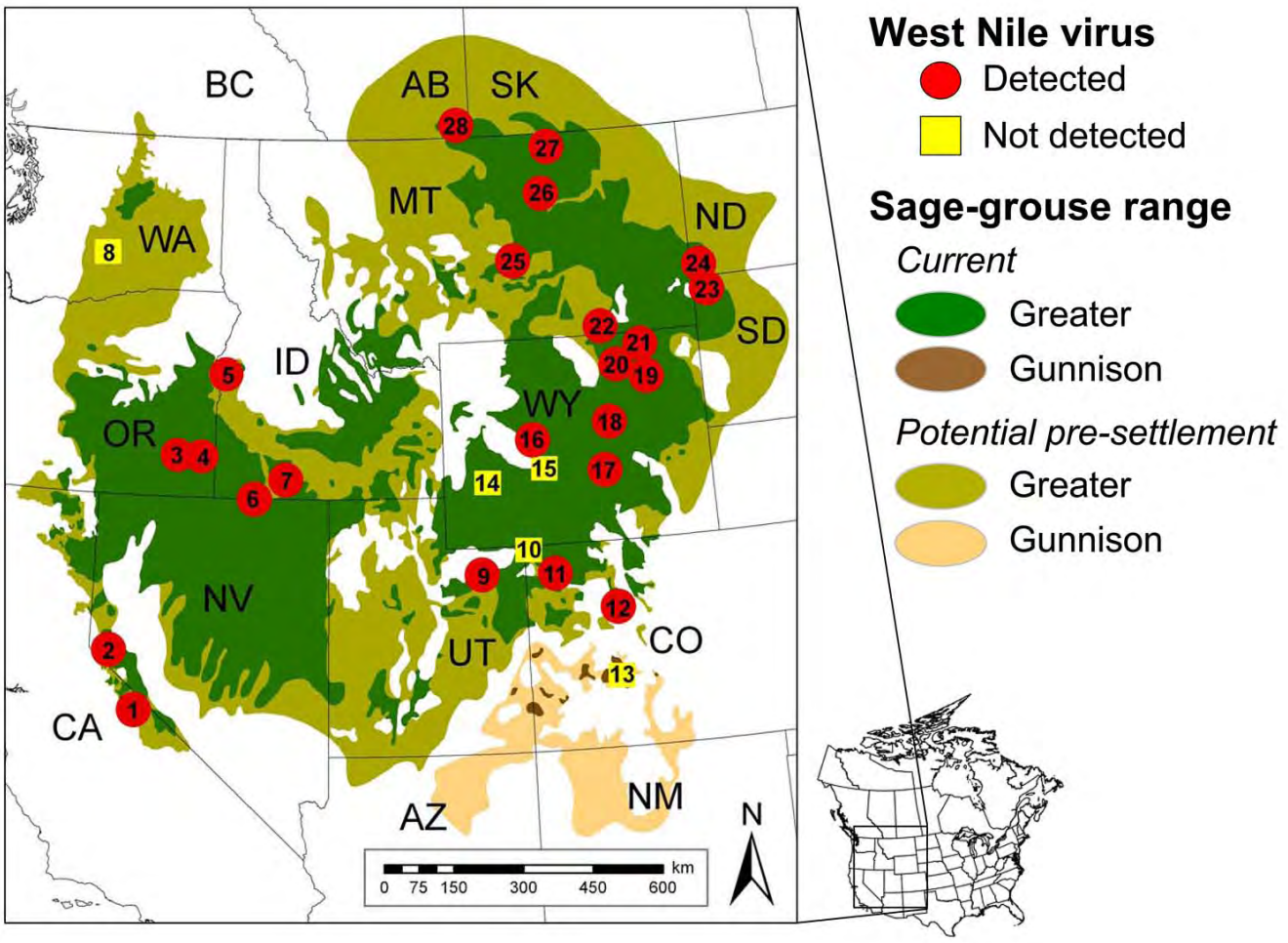

West Nile virus
Detected
Not detected
Sage-grouse range
Current
Greater
Gunnison
Potential pre-settlement
Greater
Gunnison
BC
AB
SK
MT
ND
WA
OR
ID
WY
SD
NV
UT
CO
CA
AZ
NM
N
0 75 150 300 450 600
km

Figure 2.

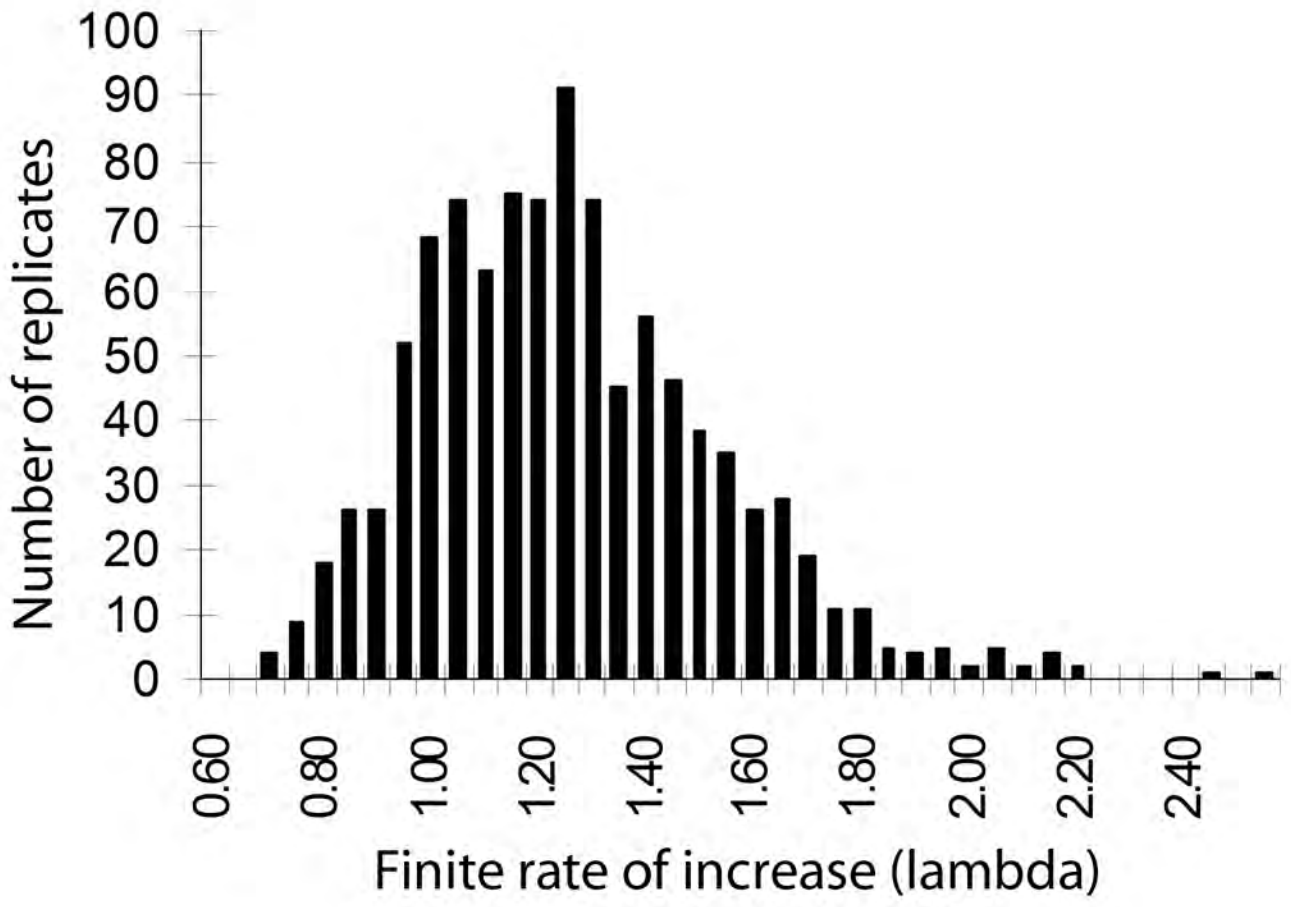

Number of replicates
100
90
80
70
60
50
40
30
20
10
0
0.60
0.80
1.00
1.20
1.40
1.60
1.80
2.00
2.20
2.40
Finite rate of increase (lambda)

Figure 3.

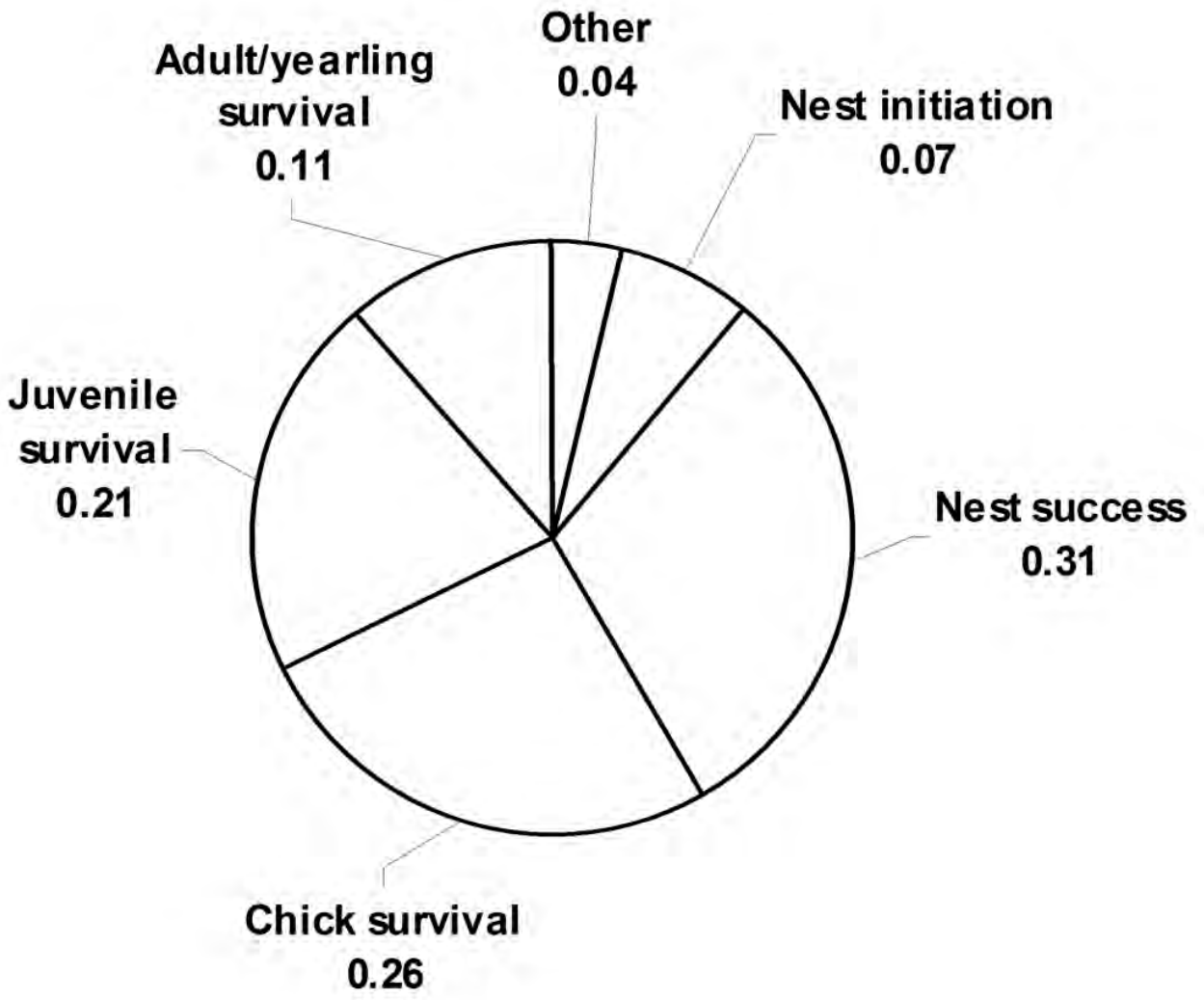

Other
0.04
Adult/yearling
survival
0.11
Nest initiation
0.07
Juvenile
survival
0.21
Nest success
0.31
Chick survival
0.26

Figure 4.

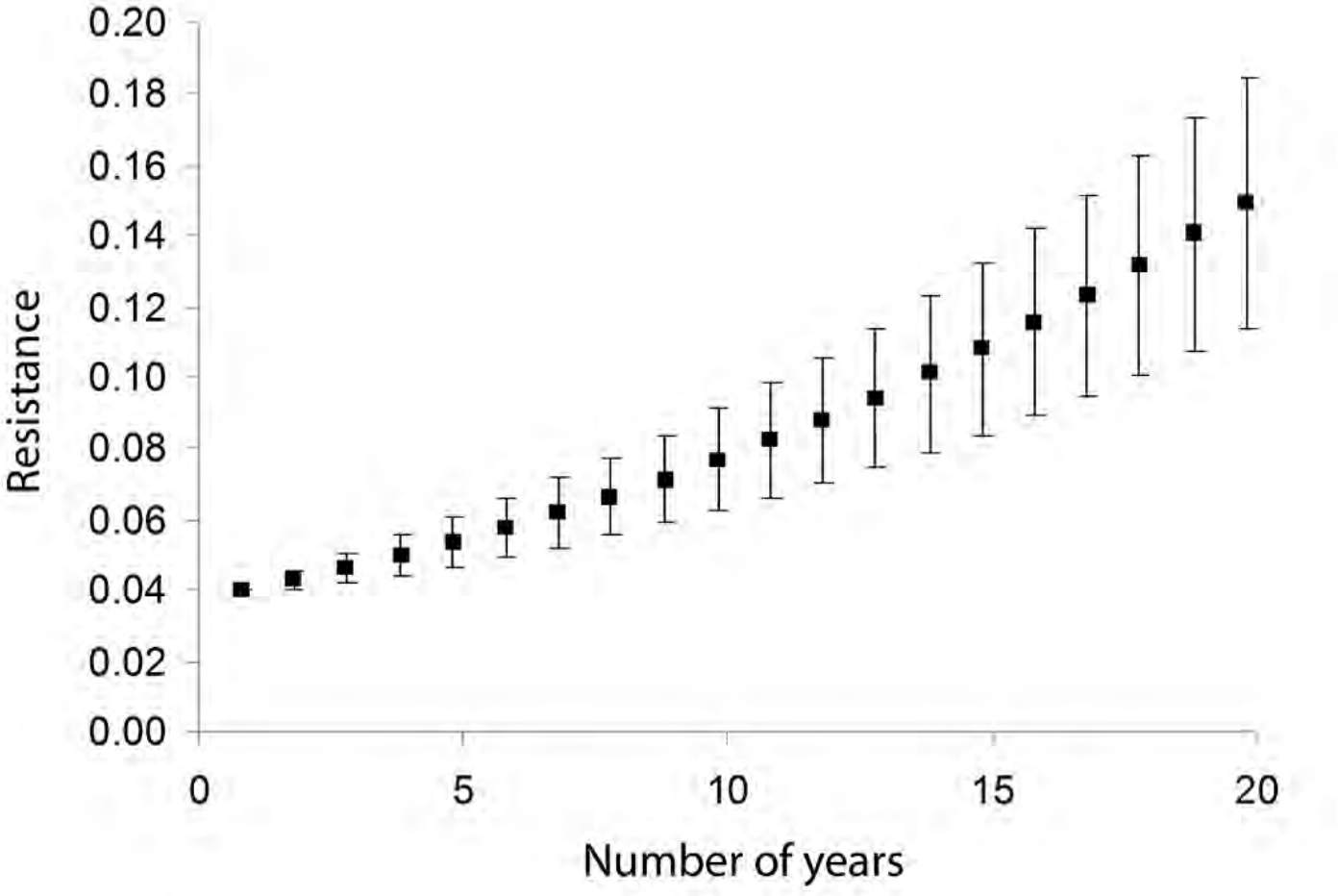
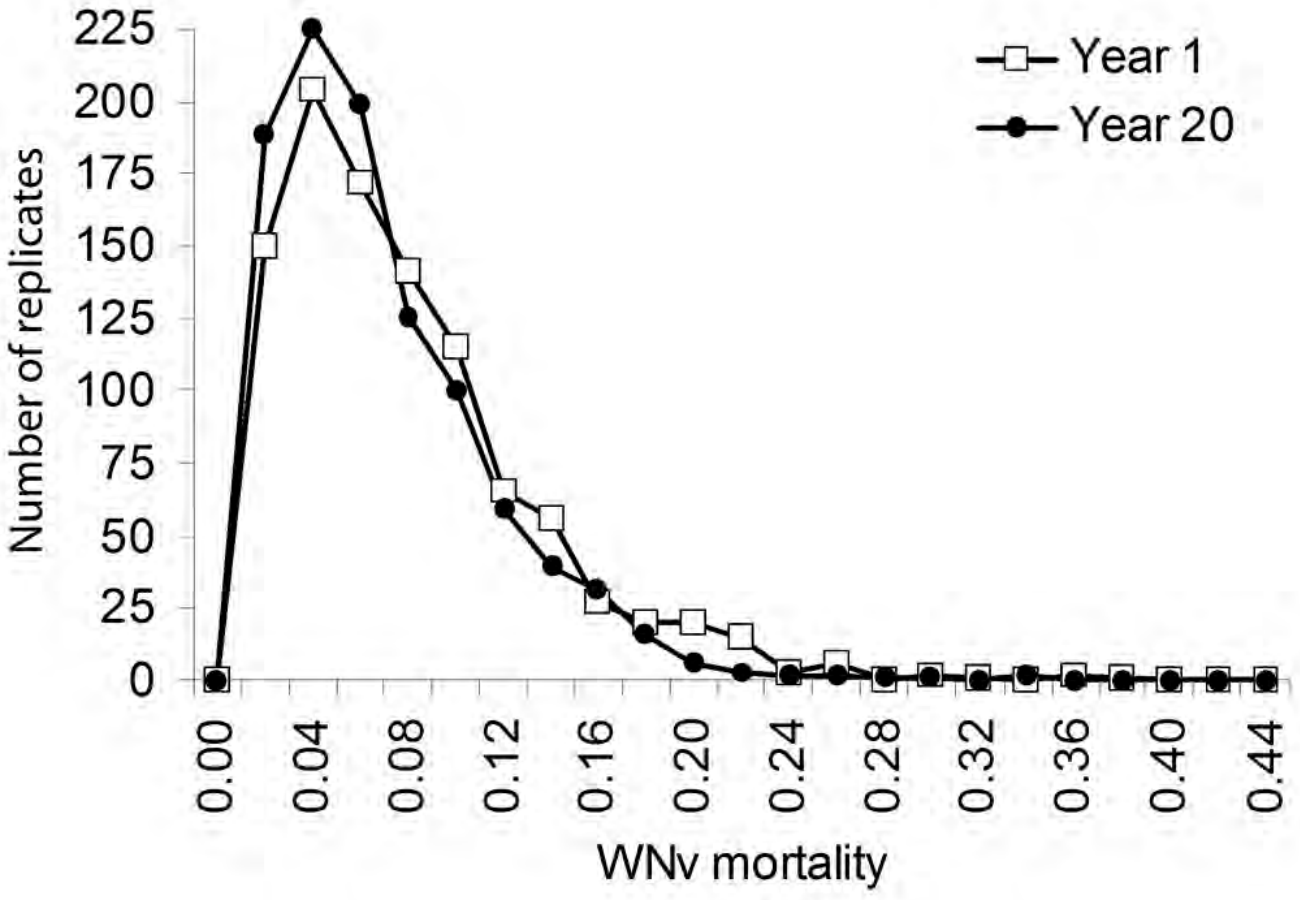

0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Resistance
0
5
10
15
20
Number of years

Figure 5.


Year 1
Year 20
Number of replicates
225
200
175
150
125
100
75
50
25
0
0.00
0.04
0.08
0.12
0.16
0.20
0.24
0.28
0.32
0.36
0.40
0.44
WNv mortality

*Research Article*

# Greater Sage-Grouse Population Response to Energy Development and Habitat Loss

**BRETT L. WALKER,**[1] *Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA*
**DAVID E. NAUGLE,** *Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA*
**KEVIN E. DOHERTY,** *Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA*

**ABSTRACT** Modification of landscapes due to energy development may alter both habitat use and vital rates of sensitive wildlife species. Greater sage-grouse (*Centrocercus urophasianus*) in the Powder River Basin (PRB) of Wyoming and Montana, USA, have experienced rapid, widespread changes to their habitat due to recent coal-bed natural gas (CBNG) development. We analyzed lek-count, habitat, and infrastructure data to assess how CBNG development and other landscape features influenced trends in the numbers of male sage-grouse observed and persistence of leks in the PRB. From 2001 to 2005, the number of males observed on leks in CBNG fields declined more rapidly than leks outside of CBNG. Of leks active in 1997 or later, only 38% of 26 leks in CBNG fields remained active by 2004–2005, compared to 84% of 250 leks outside CBNG fields. By 2005, leks in CBNG fields had 46% fewer males per active lek than leks outside of CBNG. Persistence of 110 leks was positively influenced by the proportion of sagebrush habitat within 6.4 km of the lek. After controlling for habitat, we found support for negative effects of CBNG development within 0.8 km and 3.2 km of the lek and for a time lag between CBNG development and lek disappearance. Current lease stipulations that prohibit development within 0.4 km of sage-grouse leks on federal lands are inadequate to ensure lek persistence and may result in impacts to breeding populations over larger areas. Seasonal restrictions on drilling and construction do not address impacts caused by loss of sagebrush and incursion of infrastructure that can affect populations over long periods of time. Regulatory agencies may need to increase spatial restrictions on development, industry may need to rapidly implement more effective mitigation measures, or both, to reduce impacts of CBNG development on sage-grouse populations in the PRB. (JOURNAL OF WILDLIFE MANAGEMENT 71(8):2644–2654; 2007)

DOI: 10.2193/2006-529

**KEY WORDS** agriculture, *Centrocercus urophasianus*, coal-bed methane, coal-bed natural gas, energy development, greater sage-grouse, lek count, population, Powder River Basin, sagebrush.

Large-scale modification of habitat associated with energy development may alter habitat use or vital rates of sensitive wildlife species. Populations in developed areas may decline if animals avoid specific features of infrastructure such as roads or power lines (Trombulak and Frissell 2000; Nelleman et al. 2001, 2003) or if energy development negatively affects survival or reproduction (Holloran 2005, Aldridge and Boyce 2007). For example, mortality caused by collisions with vehicles and power lines reduces adult and juvenile survival in a variety of wildlife species (reviewed in Bevanger 1998 and Trombulak and Frissell 2000). Indirect effects of energy development on populations are also possible due to changes in predator or parasite communities (Knight and Kawashima 1993, Steenhof et al. 1993, Daszak et al. 2000) or changes in vegetation structure and composition associated with disturbance (Trombulak and Frissell 2000, Gelbard and Belnap 2003). Negative impacts may be exacerbated if features of development that attract animals (e.g., ponds) simultaneously reduce survival and thereby function as ecological traps (Gates and Gysel 1978).

Rapidly expanding coal-bed natural gas (CBNG) development is a concern for conservation of greater sage-grouse (*Centrocercus urophasianus*) in the Powder River Basin (PRB) of northeastern Wyoming and southeastern Montana, USA. The PRB supports an important regional population, with over 500 leks documented between 1967 and 2005 (Connelly et al. 2004). In the past decade, the PRB has also experienced rapidly increasing CBNG development, with impacts on wildlife habitat projected to occur over an area of approximately 24,000 km$^2$ (Bureau of Land Management [BLM] 2003*a*, *b*). Coal-bed natural gas development typically requires construction of 2–7 km of roads and 7–22 km of power lines per square kilometer as well as an extensive network of compressor stations, pipelines, and ponds (BLM 2003*b*). Approximately 10% of surface lands and 75% of mineral reserves in the PRB are federally owned and administered by the BLM (BLM 2003*a*, *b*). Over 50,000 CBNG wells have been authorized for development on federal mineral reserves in northeastern Wyoming, at a density of 1 well per 16–32 ha, and as many as 18,000 wells are anticipated in southeastern Montana (BLM 2003*a*, *b*). According to data from the Wyoming Oil and Gas Conservation Commission and Montana Board of Oil and Gas Conservation, by the beginning of 2005, approximately 28,000 CBNG wells had been drilled on federal (approx. 31%), state (approx. 11%), and private (approx. 58%) mineral holdings in the PRB. Mitigation for sage-grouse on BLM lands typically includes lease stipulations prohibiting surface infrastructure within 0.4 km of sage-grouse leks as well as restrictions on timing of drilling and construction within 3.2 km of documented leks during the 15 March–15 June breeding season and within crucial winter habitat from 1 December–31 March (MT only; BLM 2003*a*, *b*). These restrictions can be modified or waived by BLM, or additional conditions of approval applied, on a case-by-case basis. In contrast, most state

[1] *E-mail: pancaminando@hotmail.com*

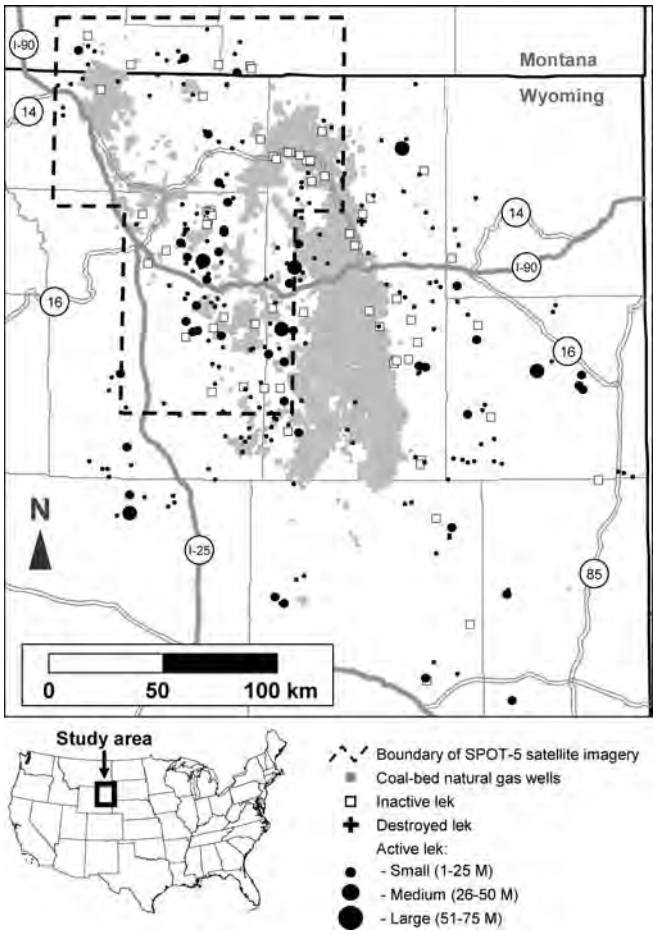



**Figure 1.** Distribution and status of active, inactive, and destroyed greater sage-grouse leks, coal-bed natural gas wells, and major highways in the Powder River Basin, Montana and Wyoming, USA. The dashed line shows the extent of SPOT-5 satellite imagery. This map excludes leks that became inactive or were destroyed prior to 1997 and leks whose status in 2004–2005 was unknown. The status of leks within a lek complex are depicted separately. Dot sizes of active leks represent the final count of displaying males in 2004 or 2005, whichever was the last year surveyed: small = 1–25 males, medium = 26–50 males, large = 51–75 males.

and private minerals have been developed with few or no requirements to mitigate impacts on wildlife.

Coal-bed natural gas development and its associated infrastructure may affect sage-grouse populations via several different mechanisms, and these mechanisms can operate at different scales. For example, males and females may abandon leks if repeatedly disturbed by raptors perching on power lines near leks (Ellis 1984), by vehicle traffic on nearby roads (Lyon and Anderson 2003), or by noise and human activity associated with energy development during the breeding season (Braun et al. 2002, Holloran 2005, Kaiser 2006). Collisions with nearby power lines and vehicles and increased predation by raptors may also increase mortality of birds at leks (Connelly et al. 2000*a*, *b*). Alternatively, roads and power lines may indirectly affect lek persistence by altering productivity of local populations or survival at other times of the year. For example, sage-grouse mortality associated with power lines and roads occurs year-round (Patterson 1952, Beck et al. 2006, Aldridge and Boyce 2007), and ponds created by CBNG development may increase risk of West Nile virus (WNv) mortality in late summer (Walker et al. 2004, Zou et al. 2006, Walker et al. 2007). Loss and degradation of sagebrush habitat can also reduce carrying capacity of local breeding populations (Swenson et al. 1987, Braun 1998, Connelly et al. 2000*b*, Crawford et al. 2004). Alternatively, birds may simply avoid otherwise suitable habitat as the density of roads, power lines, or energy development increases (Lyon and Anderson 2003, Holloran 2005, Kaiser 2006, Doherty et al. 2008).

Understanding how energy development affects sage-grouse populations also requires that we control for other landscape features that affect population size and persistence, including the extent of suitable habitat. Sage-grouse are closely tied to sagebrush habitats throughout their annual cycle, and variation in the amount of sagebrush habitat available for foraging and nesting is likely to influence the size of breeding populations and persistence of leks (Swenson et al. 1987, Ellis et al. 1989, Schroeder et al. 1999, Leonard et al. 2000, Smith et al. 2005). For this reason, it is crucial to quantify and separate the effects of habitat loss from those of energy development.

To assess how CBNG development and habitat loss influence sage-grouse populations in the PRB, we conducted 2 analyses based on region-wide lek-count data. Lek counts are widely used for monitoring sage-grouse populations and, at present, are the only data suitable for examining trends in population size and distribution at this scale (Connelly et al. 2003, 2004). First, we analyzed counts of the numbers of males displaying on leks (lek counts) to assess whether trends in the number of males counted and proportion of active and inactive leks differed between areas with and without CBNG development. Second, we used logistic regression to model lek status (i.e., active or inactive) in relation to landscape features hypothesized to influence sage-grouse demographics and habitat use at 3 spatial scales. The objectives of the lek-status analysis were 1) to identify the scale at which habitat and non-CBNG landscape features influence lek persistence and 2) to evaluate and compare effects of CBNG development at different scales with those of non-CBNG landscape features after controlling for habitat.

## STUDY AREA

We analyzed data from sage-grouse leks within an approximately 50,000-km$^2$ area of northeastern Wyoming and southeastern Montana (Fig. 1). This area included all areas with existing or predicted CBNG development in the PRB (BLM 2003*a*, *b*) as well as surrounding areas without CBNG. Land use in this region was primarily cattle ranching with limited dry-land and irrigated tillage agriculture. Natural vegetation consisted of sagebrush-steppe and mixed-grass prairie interspersed with occasional stands of conifers. Sagebrush-steppe was dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) with an understory of native and nonnative grasses

and forbs. Plains silver sagebrush (*A. cana* ssp. *cana*) and black greasewood (*Sarcobatus vermiculatus*) co-occurred with Wyoming big sagebrush in drainage bottoms.

# METHODS

## Lek-Count Trend Analyses

*Lek-count data.*—We used sage-grouse lek-count data in public databases maintained by Wyoming Game and Fish Department and Montana Department of Fish, Wildlife, and Parks as the foundation for analyses. We augmented databases with lek counts provided by consultants and by the BLM's Miles City field office for 37 leks (36 in MT, 1 in WY) known to have been counted but for which data were missing. We checked for and, when possible, corrected errors in the database after consultation with database managers and regional biologists for each state. We excluded records with known errors, surveys in which lek status was not determined, leks without supporting count data, and duplicate leks prior to analysis.

*Coal-bed natural gas development.*—We obtained data on the type, location, status, drilling date, completion date, and abandonment date of wells from public databases maintained by the Wyoming Oil and Gas Conservation Commission and Montana Board of Oil and Gas Conservation. Because wells are highly correlated with other features of development, such as roads, power lines, and ponds (D. E. Naugle, University of Montana, unpublished data), using well locations is a reliable way to map and measure the extent of CBNG development. We retained only those wells that were clearly in the ground, associated with energy development (gas, oil, stratification test, disposal, injection, monitoring, and water source wells), and likely to have infrastructure. We excluded wells that were plugged and abandoned, wells waiting on permit approval, wells drilled or completed in 2005 or later, and those with status reported as dry hole, expired permit, permit denied, unknown, or no report. We included wells in analyses starting in the year in which they were drilled or completed (i.e., started producing). For active wells without drilling or completion dates, we estimated start year based on approval and completion dates of nearby wells and those in the same unit lease. We included wells with status reported as dormant, temporarily abandoned, or permanently abandoned only until the year prior to when they were first reported as abandoned. Because capped wells (also commonly referred to as shut-in wells) may or may not have associated infrastructure, we included them only in years in which they were surrounded by, or within 1 km of, a producing gas field.

We estimated the extent of CBNG development around each lek in each year. We first approximated the area affected by CBNG development by creating a 350-m buffer around all well locations using ArcInfo 8.2 and dissolving boundaries where buffers overlapped. We then estimated the proportion of the area within 3.2 km of the lek center that was covered by the buffer around wells. At current well density (1 well/32–64 ha), a 350-m buffer around wells estimates the extent of CBNG development more accurately than larger or smaller buffer sizes. This metric is less sensitive to variation in spacing of wells than measures such as well density and therefore more accurate for estimating the total area affected by CBNG development.

*Trends in lek counts.*—We examined lek-count data from 1988 to 2005. In each year, we categorized a lek as in CBNG if $\geq$40% of the area within 3.2 km was developed or if $\geq$25% within 3.2 km was developed and $\geq$1 well was within 350 m of the lek center. We categorized a lek as outside CBNG if $<$40% of the area within 3.2 km was developed and no wells were within 350 m of the lek center. However, because few leks in CBNG were counted in consecutive years prior to 2001, we analyzed trends in lek-counts only from 2001 to 2005. We calculated the rate of increase in the number of males counted on leks for each year-to-year transition by summing count data across leks within each category (in CBNG vs. outside CBNG) according to their stage of development at the end of the first year of each year-to-year transition (Connelly et al. 2004). We summed data across leks to reduce the influence of geographic variation in detectability and used the maximum annual count for each lek to reduce the influence of within-year variation in detectability on the estimated rate of increase. We derived data for each transition only from leks counted in both years and known to be active in at least 1 of the 2 years of the transition. We estimated mean rates of increase in CBNG versus outside CBNG fields based on the slope of a linear regression of interval length versus rate of increase (Morris and Doak 2002). Wells completed between January and March (i.e., before lek counts were conducted) in the second year of each transition may have caused us to underestimate the amount of CBNG development around leks at the time counts were conducted. However, if CBNG development negatively affects populations, this would cause the difference between trends in lek-count data in CBNG and outside CBNG to be underestimated and would produce a conservative estimate of impacts.

*Timing of lek disappearance.*—If CBNG development negatively affects lek persistence, most leks in CBNG fields that became inactive should have done so following CBNG development. To explore this prediction, we examined the timing of lek disappearance in relation to when a lek was first classified as being in a CBNG field (i.e., $\geq$40% development within 3.2 km or $\geq$25% development within 3.2 km and $\geq$1 well within 350 m of the lek center) for leks confirmed active in 1997 or later.

## Lek-Status Analysis

*Definition of leks.*—We defined a lek as a site where multiple males were documented displaying on multiple visits within a single year or over multiple years. We defined a lek complex as multiple leks located $<$2.5 km from the largest and most regularly attended lek in the complex (Connelly et al. 2004). We defined an initial set of lek complexes based on those known prior to 1990. We considered leks discovered in 1990 or later as separate

complexes, even if they occurred <2.5 km from leks discovered in previous years. We did this to avoid problems with the location of already-defined leks and lek complexes shifting as new leks were discovered or if new leks formed in response to nearby CBNG development. We grouped leks discovered within 2.5 km of each other in the same year in the same lek complex. We used lek complexes as the sample unit for calculating proportion of active and inactive leks and in the lek-status analysis, but because the term lek complex can refer either to multiple leks or to a single lek, we hereafter refer to both simply as a lek.

*Lek status.*—We determined the final status of leks by examining count data from 2002 to 2005. We considered a lek active if ≥1 male was counted in 2004 or 2005, whichever was the last year surveyed. To minimize problems with nondetection of males, we considered a lek inactive only if 1) ≥3 consecutive ground or air visits in the last year surveyed failed to detect males or 2) surveys in the last 3 consecutive years the lek was checked (2002–2004 or 2003–2005) failed to detect males. We classified the status of leks that were not surveyed or were inadequately surveyed in 2004 or 2005 as unknown. Survey effort in the PRB increased 5-fold from 1997 to 2005 and included systematic aerial searches for new leks and repeated air and ground counts of known leks within and adjacent to CBNG fields. Therefore, it is unlikely that leks shifted to nearby sites without being detected. Many leks in the PRB disappeared during a region-wide population decline in 1991–1995 (Connelly et al. 2004), well before most CBNG development in the PRB began. To eliminate leks that became inactive for reasons other than CBNG, we calculated proportions of active and inactive leks in CBNG and outside CBNG based only on leks active in 1997 or later.

*Scale.*—We calculated landscape metrics at 3 distances around each lek: 0.8 km (201 ha), 3.2 km (3,217 ha), and 6.4 km (12,868 ha). We selected the 0.8-km scale to represent processes that impact breeding birds at or near leks, while avoiding problems with spatial error in lek locations. We selected the 6.4-km scale to reflect processes that occur at larger scales around the lek, such as loss of nesting habitat, demographic impacts on local breeding populations, or landscape-scale avoidance of CBNG fields. The 3.2-km scale is that at which state and federal agencies apply mitigation for CBNG impacts (e.g., timing restrictions), and it is important to determine the appropriateness of managing at a 3.2-km scale versus at smaller or larger scales.

*Habitat variables.*—Each model represented a distinct hypothesis, or combination of hypotheses, regarding how landscape features influence lek persistence. We included 2 types of habitat variables in the analysis, the proportion of sagebrush habitat and the proportion of tillage agriculture in the landscape around each lek. Because the scale at which habitat most strongly influenced lek persistence was unknown, we considered habitat variables at all 3 scales. We calculated the amount of sagebrush habitat and tillage agriculture around each lek at each scale using ArcInfo 8.2 based on classified SPOT-5 satellite imagery taken in August 2003 over an approximately 15,700-km$^2$ area of the PRB. We restricted the lek-status analysis to leks within the SPOT-5 satellite imagery because the only other type of classified imagery available for this region (Thematic Mapper at 30-m resolution) is unreliable for measuring the extent of sagebrush habitat (Moynahan 2004). We visually identified and manually digitized areas with tillage agriculture from the imagery. Classification accuracy was 83% for sagebrush habitat (i.e., sagebrush-steppe and sagebrush-dominated grassland). We excluded 20 leks for which >10% of classified habitat data were unavailable due to cloud cover or proximity to the edge of the imagery.

*Road, power line, and CBNG variables.*—We hypothesized that infrastructure can affect lek persistence in 3 ways and included different variables to examine each hypothesis. Roads, power lines, and CBNG development may affect lek persistence in proportion to their extent on the landscape. Alternatively, the effects of roads and power lines may depend their distance from the lek, in which case they are expected to drop off rapidly as distance increases. Coal-bed natural gas development may also influence lek status depending on how long the lek has been in a CBNG field. If CBNG increases mortality, it may be several years before local breeding populations are reduced to the point that males no longer attend the lek (Holloran 2005). Avoidance of leks in CBNG fields by young birds (Kaiser 2006) combined with site fidelity of adults to breeding areas (Schroeder et al. 1999) would also result in a time lag between CBNG development and lek disappearance.

We used TIGER/Line® 1995 public-domain road layers for Wyoming and Montana (U.S. Census Bureau 1995) to estimate the proportion of each buffer around each lek within 350 m of a road at each of the 3 scales. We used 1995 data, rather than a more recent version, to represent roads that existed on the landscape prior to CBNG development. We obtained autumn 2005 GIS coverages of power lines directly from utility companies and used this layer to estimate the proportion of each buffer around each lek within 350 m of a power line at each scale. Year-specific power line coverages were not available, so this variable includes both CBNG and non-CNBG power lines. We estimated the extent of CBNG development around each lek at each scale by calculating the proportion of the total buffer area around the lek center covered by a dissolved 350-m buffer around well locations. If a lek was a complex, we first placed a buffer around all lek centers in the complex then dissolved the intersections to create a single buffer. We selected a 350-m buffer around roads, power lines, and CBNG wells for 2 reasons. First, quantitative estimates of the distance at which infrastructure affects habitat use or vital rates of sage-grouse were not available, and 350 m is a reasonable distance over which to expect impacts to occur, such as increased risk of predation near power lines or increased risk of vehicle collisions near roads. Second, we also wished to maintain a consistent relationship between well, road, and power line variables and the amount of area affected by each feature. We measured how long a lek was in

a CBNG field as the number of years prior to 2005 during which the lek had ≥40% CBNG development within 3.2 km (or ≥25% CBNG within 3.2 km and ≥1 well within 350 m of the lek center).

*Analyses.*—We used a hierarchical analysis framework to evaluate how landscape features influenced lek status (i.e., active or inactive). Our first goal was to identify the scale at which habitat, roads, and power lines affected lek persistence. Our second goal was to evaluate and compare effects of CBNG development at different scales with those of roads and power lines after controlling for habitat. In both cases, we used an information-theoretic approach (Burnham and Anderson 2002) to select the most parsimonious model from a set of plausible candidate models. We conducted all analyses using logistic regression in R (version 2.3.1, R Development Core Team 2006). We used a logit-link function to bound persistence estimates within a (0,1) interval. Almost all CBNG development within the extent of the SPOT-5 imagery occurred after 1997, so we restricted our analysis to leks known to have been active in 1997 or later to eliminate those that disappeared for reasons other than CBNG development. We also excluded 4 leks known to have been destroyed by coal mining.

To identify the most relevant scale(s) for each landscape variable, we first allowed univariate models at different scales to compete. Variables assessed for scale effects included 1) proportion sagebrush habitat, 2) proportion tillage agriculture, 3) proportion area affected by power lines, and 4) proportion area affected by non-CBNG roads. We then used the scale for each variable that best predicted lek status to construct the final set of candidate models. We also included models with squared distance to nearest road and squared distance to nearest power line in the final model set. To assess different possible mechanisms of CBNG impacts, we evaluated models with the extent of CBNG development or the number of years since the lek was classified as in CBNG. To assess the scale at which CBNG impacts occur, we included models with CBNG effects at all 3 scales. We also included models with interactions between habitat and CBNG metrics to evaluate whether effects of CBNG development are ameliorated by the amount of sagebrush habitat around the lek. To avoid problems with multicollinearity, we did not allow models with correlated variables (i.e., $r > |0.7|$) in the final model set.

We judged models based on Akaike's Information Criterion adjusted for small sample size ($AIC_c$) and examined beta coefficients and associated standard errors in all models to determine the direction and magnitude of effects. We estimated overdispersion by dividing the deviance of the global model by the deviance degrees of freedom. We conducted goodness-of-fit testing in R following methods described in Hosmer et al. (1997). We used parametric bootstrapping (Efron and Tibshirani 1993) to obtain means, standard errors, and 95% confidence limits for persistence estimates because coefficients of variation for most beta estimates were large (Zhou 2002). Due to model uncertainty, we used model averaging to obtain unconditional parameter estimates and variances (Burnham and Anderson 2002). We compared the relative importance of habitat, CBNG, and infrastructure in determining lek persistence by summing Akaike weights across all models containing each class of variable (Burnham and Anderson 2002). We also calculated evidence ratios to compare the likelihood of the best approximating habitat-plus-CBNG model versus the best approximating habitat-plus-infrastructure and habitat-only models.

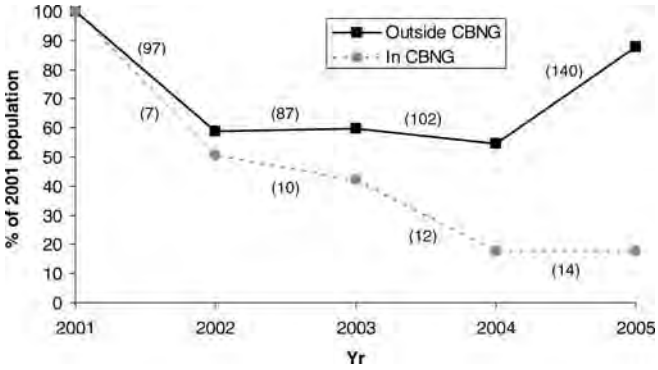



**Figure 2.** Population indices based on male lek attendance for greater sage-grouse in the Powder River Basin, Montana and Wyoming, USA, 2001–2005 for leks categorized as in coal-bed natural gas fields or outside coal-bed natural gas (CBNG) fields on a year-by-year basis. Sample sizes in parentheses next to each year-to-year transition indicate the number of leks available for calculating rates of increase for that transition.

To assess whether a known WNv outbreak or habitat loss associated with tillage agriculture disproportionately influenced model selection and interpretation, we also reanalyzed the dataset after removing specific leks. The first analysis excluded 4 leks near Spotted Horse, Wyoming, known to have disappeared after 2003 likely due to WNv-related mortality (Walker et al. 2004). The second analysis excluded 20 leks that had ≥5% agriculture at ≥1 of the 3 scales examined.

To evaluate the effectiveness of the stipulation for no surface infrastructure within 0.4 km of a lek, we examined the estimated probability of lek persistence without development versus that under full CBNG development with a 0.4-km buffer.

## RESULTS

*Trends in lek counts.*—From 2001 to 2005, lek-count indices in CBNG fields declined by 82%, at a rate of 35% per year ($\bar{x}$ rate of increase in CBNG = 0.65, 95% CI: 0.34–1.25) whereas indices outside CBNG declined by 12%, at a rate of 3% per year ($\bar{x}$ rate of increase outside CBNG = 0.97, 95% CI: 0.50–1.87; Fig. 2). The mean number of males per active lek was similar for leks in CBNG and outside CBNG in 2001, but averaged 46 ± 8% ($\bar{x}$ ± SE; range 33–55%) lower for leks in CBNG from 2002 to 2005 (Fig. 3).

*Lek status.*—Among leks active in 1997 or later, fewer leks remained active by 2004–2005 in CBNG fields (38%) than outside CBNG fields (84%; Table 1). Of the 10

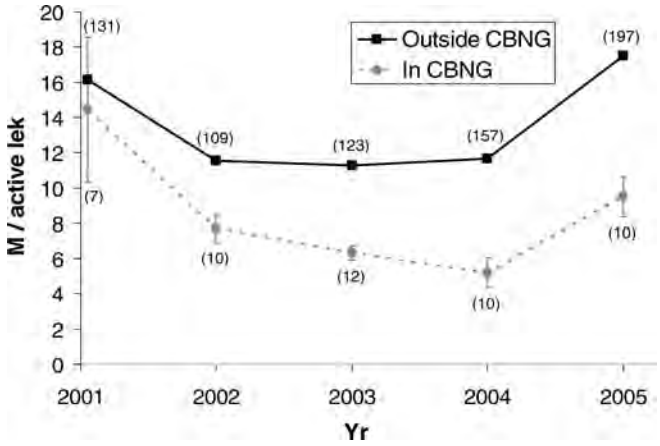



**Figure 3.** Number of male sage-grouse per active lek in coal-bed natural gas (CBNG) fields (gray) and outside (black) CBNG fields in the Powder River Basin, Montana and Wyoming, USA, 2001–2005. Error bars represent 95% confidence intervals (error bars for leks outside CBNG are too small to be visible). Sample sizes in parentheses above each index indicate the number of active leks available for calculating males per active lek in each year.

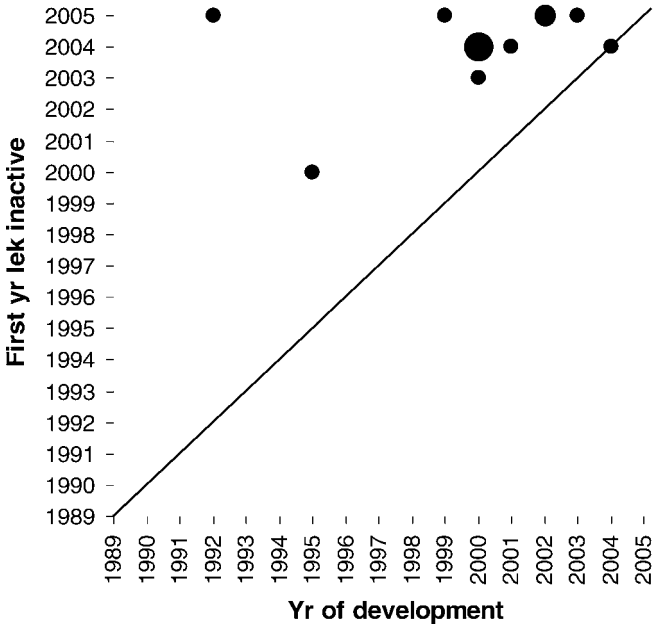



**Figure 4.** Timing of greater sage-grouse lek disappearance relative to coal-bed natural gas (CBNG) development in the Powder River Basin, Montana and Wyoming, USA, for leks confirmed active in 1997 or later. Leks above the diagonal line became inactive after CBNG development reached ≥40% within 3.2 km (or >25% development within 3.2 km and ≥1 well within 350 m of the lek center). Small dot = 1 lek, medium dot = 2 leks, large dot = 3 leks.

remaining active leks in CBNG fields, all were classified as being in CBNG in 2000 or later.

*Timing of lek disappearance.*—Of 12 leks in CBNG fields monitored intensively enough to determine the year when they disappeared, 12 became inactive after or in the same year that development occurred (Fig. 4). The average time between CBNG development and lek disappearance for these leks was 4.1 ± 0.9 years ($\bar{x}$ ± SE).

*Lek-status analysis.*—We analyzed data from 110 leks of known status within the SPOT-5 imagery that were confirmed active in 1997 or later. Proportion sagebrush habitat and proportion tillage agriculture best explained lek persistence at the 6.4-km scale (Table 2). Proportion power lines also best explained lek persistence at the 6.4-km scale (although power line effects at the 3.2-km scale were also supported), whereas proportion roads best explained lek persistence at the 3.2-km scale.

The final model set consisted of 19 models: 2 models based on habitat only (i.e., sagebrush, sagebrush plus tillage agriculture), 4 models with habitat plus power line variables, 4 models with habitat plus road variables, and 9 models with habitat plus CBNG variables (Table 3). Goodness-of-fit testing using the global model revealed no evidence of lack of fit ($P = 0.49$). Our estimate of the variance inflation factor based on the global model ($\hat{c} = 0.96$) indicated no evidence of overdispersion, so we based model selection on $AIC_c$ values (Burnham and Anderson 2002).

Despite substantial model uncertainty, the top 8 of 19 models all included a moderate to strong positive effect of sagebrush habitat on lek persistence and a strong negative effect of CBNG development, measured either as proportion CBNG development within 0.8 km, proportion CBNG development within 3.2 km, or number of years in a CBNG field. These 8 models were well supported, with a combined Akaike weight of 0.96. Five of the 8 models were within 2 $\Delta AIC_c$ units of the best approximating model, whereas all habitat-plus-infrastructure and habitat-only models showed considerably less support (>6 $\Delta AIC_c$ units lower). Evidence ratios indicate that the best habitat-plus-CBNG model was 28 times more likely to explain patterns of lek persistence than the best habitat-plus-infrastructure model and 50 times more likely than the best habitat-only model. Models 1 and 2 both included a negative effect of proportion CBNG development within 0.8 km. Models with a negative effect of number of years in CBNG (model 3) or proportion CBNG development within 3.2 km (model 4) also had considerable support. Although regression coefficients suggested that CBNG within 6.4 km also had a negative impact on lek persistence (Table 4), models with CBNG at

**Table 1.** Status of greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, USA, as of 2004–2005, including only leks confirmed active in 1997 or later.[a]

| | In CBNG | | Outside CBNG | |
|---|---|---|---|---|
| Lek status | No. | % | No. | % |
| Active | 10 | 38 | 211 | 84 |
| Inactive | 16 | 62 | 39 | 16 |
| Unknown | 1 | | 43 | |
| Total active + inactive | 26 | | 250 | |

[a] Leks in coal-bed natural gas (CBNG) nad ≥40% development within 3.2 km or ≥25% development and ≥1 well within 350 m of the lek center. Leks outside CBNG development had <40% CBNG development and no wells within 350 m of the lek center. Each lek complex counted as one lek. We calculated percentages based only on the total number of active and inactive leks.

**Table 2.** Univariate model selection summary for different classes of landscape variables influencing greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, USA, 1997–2005.[a]

| Model | LL | *K* | *n* | $\Delta AIC_c$ | $w_i$ | β | SE |
|---|---|---|---|---|---|---|---|
| Sagebrush | | | | | | | |
| 6.4 km | −60.05 | 2 | 110 | 0.00 | 0.70 | 5.20 | 1.68 |
| 3.2 km | −60.95 | 2 | 110 | 1.81 | 0.28 | 4.38 | 1.53 |
| 0.8 km | −63.43 | 2 | 110 | 6.77 | 0.02 | 2.26 | 1.15 |
| Tillage agriculture | | | | | | | |
| 6.4 km | −55.52 | 2 | 110 | 0.00 | 0.79 | −20.98 | 6.02 |
| 3.2 km | −56.83 | 2 | 110 | 2.63 | 0.21 | −19.31 | 6.30 |
| 0.8 km | −60.92 | 2 | 110 | 10.81 | 0.00 | −10.44 | 4.59 |
| Power lines | | | | | | | |
| 6.4 km | −58.69 | 2 | 110 | 0.00 | 0.52 | −6.06 | 1.76 |
| 3.2 km | −58.81 | 2 | 110 | 0.24 | 0.46 | −4.92 | 1.43 |
| 0.8 km | −62.12 | 2 | 110 | 6.84 | 0.02 | −2.51 | 0.99 |
| Roads | | | | | | | |
| 3.2 km | −64.59 | 2 | 110 | 0.00 | 0.50 | −2.50 | 1.99 |
| 6.4 km | −65.20 | 2 | 110 | 1.21 | 0.27 | −1.52 | 2.35 |
| 0.8 km | −65.41 | 2 | 110 | 1.63 | 0.22 | −0.08 | 0.87 |

[a] We present max. log-likelihood (LL), no. of parameters (*K*), sample size (*n*), relative Akaike's Information Criterion adjusted for small sample size ($\Delta AIC_c$ values), $AIC_c$ wt ($w_i$), estimated regression coeff. (β), and SE for each model in each class in order of decreasing max. log-likelihood.

6.4 km showed considerably less support (approx. 5–7 $\Delta AIC_c$ units lower). Tillage agriculture appeared in one well-supported model (model 2), and the coefficient suggested that tillage agriculture had a strong negative effect on lek persistence. However, this effect was poorly estimated, and the same model without tillage agriculture (model 1) was more parsimonious. Regression coefficients suggested negative effects of proximity to power lines and of proportion power line development within 6.4 km (Table 4), but models with power line effects were only weakly supported (approx. 6–8 $\Delta AIC_c$ units lower; Table 3). Models containing effects of roads unrelated to CBNG development received little or no support. Coefficients for interaction terms did not support an interaction between habitat and CBNG variables. The best approximating model accurately predicted the status of 79% of 79 active leks and 47% of 31 inactive leks. The summed Akaike weight for CBNG variables (0.97) was almost as large as that of sagebrush habitat (1.00) and greater than that for the effects of tillage agriculture (0.26), power lines (0.02), or non-CBNG roads (0.01). Unconditional, model-averaged estimates and 95% confidence limits for beta estimates and

**Table 3.** Model selection summary for hypotheses to explain greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, USA, 1997–2005.[a]

| No. | Model[b] | LL | *K* | *n* | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|---|---|
| 1 | Sagebrush 6.4 + CBNG 0.8 | −51.16 | 3 | 110 | 0.00 | 0.24 |
| 2 | Sagebrush 6.4 + Agriculture 6.4 + CBNG 0.8 | −50.48 | 4 | 110 | 0.80 | 0.16 |
| 3 | Sagebrush 6.4 + Years in CBNG | −51.56 | 3 | 110 | 0.80 | 0.16 |
| 4 | Sagebrush 6.4 + CBNG 3.2 | −51.70 | 3 | 110 | 1.09 | 0.14 |
| 5 | Sagebrush 6.4 * CBNG 0.8 | −50.98 | 4 | 110 | 1.81 | 0.10 |
| 6 | Sagebrush 6.4 * Years in CBNG | −51.32 | 4 | 110 | 2.48 | 0.07 |
| 7 | Sagebrush 6.4 + Agriculture 6.4 + CBNG 3.2 | −51.52 | 4 | 110 | 2.88 | 0.06 |
| 8 | Sagebrush 6.4 + CBNG 6.4 | −53.69 | 3 | 110 | 5.07 | 0.02 |
| 9 | Sagebrush 6.4 + Agriculture 6.4 + Dist. power line$^2$ | −53.39 | 4 | 110 | 6.63 | 0.01 |
| 10 | Sagebrush 6.4 + Agriculture 6.4 + CBNG 6.4 | −53.48 | 4 | 110 | 6.81 | 0.01 |
| 11 | Sagebrush 6.4 + Agriculture 6.4 | −55.08 | 3 | 110 | 7.84 | 0.00 |
| 12 | Sagebrush 6.4 + Power lines 6.4 | −55.08 | 3 | 110 | 7.84 | 0.00 |
| 13 | Sagebrush 6.4 + Agriculture 6.4 + Power lines 6.4 | −54.07 | 4 | 110 | 7.99 | 0.00 |
| 14 | Sagebrush 6.4 + Agriculture 6.4 + Dist. road$^2$ | −54.47 | 4 | 110 | 8.78 | 0.00 |
| 15 | Sagebrush 6.4 + Agriculture 6.4 + Roads 3.2 | −54.49 | 4 | 110 | 8.83 | 0.00 |
| 16 | Sagebrush 6.4 + Dist. power line$^2$ | −57.36 | 3 | 110 | 12.41 | 0.00 |
| 17 | Sagebrush 6.4 | −60.05 | 2 | 110 | 15.67 | 0.00 |
| 18 | Sagebrush 6.4 + Roads 3.2 | −59.39 | 3 | 110 | 16.46 | 0.00 |
| 19 | Sagebrush 6.4 + Dist. road$^2$ | −59.46 | 3 | 110 | 16.62 | 0.00 |

[a] We present max. log-likelihood (LL), no. of parameters (*K*), sample size (*n*), relative Akaike's Information Criterion adjusted for small sample size ($\Delta AIC_c$ values), and $AIC_c$ wt ($w_i$) for each model in order of increasing $\Delta AIC_c$ units, starting with the best approximating model. The $AIC_c$ value of the best approximating model in the analysis was 108.54.

[b] CBNG = coal-bed natural gas development. Numbers refer to the radius (km) around the lek at which the variable was measured.

**Table 4.** Model-averaged estimates of regression coefficients (β) and standard errors, odds ratios, and lower and upper 95% confidence limits on odds ratios for effects of landscape variables on greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, USA, 1997–2005.

| Variable[a] | β | SE | Odds ratio | Lower CL | Upper CL |
|---|---|---|---|---|---|
| Intercept | −1.25 | 1.40 | | | |
| Sagebrush | 4.06 | 2.03 | 58.241 | 1.083 | 3131.682 |
| Agriculture | −8.76 | 8.73 | $1.57 \times 10^{-4}$ | $5.81 \times 10^{-12}$ | $4.22 \times 10^{3}$ |
| Dist. power line$^2$ | 1.72 | 1.27 | 5.603 | 0.462 | 67.925 |
| Power lines | −4.52 | 2.40 | 0.011 | 0.0001 | 1.203 |
| Dist. road$^2$ | 0.62 | 0.67 | 1.86 | 0.505 | 6.859 |
| Roads | −2.38 | 2.23 | 0.092 | 0.001 | 7.331 |
| CBNG 0.8 km | −3.67 | 1.18 | 0.026 | 0.003 | 0.257 |
| CBNG 3.2 km | −4.72 | 1.50 | 0.009 | 0.001 | 0.169 |
| CBNG 6.4 km | −5.11 | 2.04 | 0.006 | 0.0001 | 0.328 |
| Years in CBNG | −1.41 | 0.58 | 0.244 | 0.078 | 0.761 |

[a] CBNG = coal-bed natural gas development. The estimated regression coeff. for Years in CBNG could only be derived from one model.

odds ratios show that loss of sagebrush habitat and addition of CBNG development around leks had effects of similar magnitude (Table 4).

The model-averaged estimate for the effect of CBNG within 0.8 km was close to that of the best approximating model (model 1, $\beta_{\text{CBNG 0.8 km}} = -3.91 \pm 1.11$ SE; Table 4). Thus, we illustrate the effects CBNG within 0.8 km on lek persistence using estimates from that model (Fig. 5a). We also illustrate results from model 3, which indicated that leks disappeared, on average, within 3–4 years of CBNG development (Fig. 5b).

The current 0.4-km stipulation for no surface infrastructure leaves 75% of the landscape within 0.8 km and 98% of the landscape within 3.2 km open to CBNG development. In an average landscape around a lek (i.e., 74% sagebrush habitat, 26% other land cover types), 75% CBNG development within 0.8 km would drop the probability of lek persistence from 86% to 24% (Fig. 5a). Similarly, 98% CBNG development within 3.2 km would drop the average probability of lek persistence from 87% to 5%.

*Secondary analyses.*—Analysis of reduced datasets did not meaningfully change model fit, model selection, or interpretation, nor did it alter the magnitude or direction of estimated CBNG effects. After excluding leks affected by WNv, the top 8 of 19 models and all 3 models within 2 $\Delta AIC_c$ units included a positive effect of sagebrush within 6.4 km and a negative effect of CBNG development. Model-averaged estimates of CBNG effects were similar to those from the original analysis ($\beta_{\text{Sagebrush 6.4 km}} = 3.96 \pm 1.97$ SE; $\beta_{\text{CBNG 0.8 km}} = -3.48 \pm 1.15$ SE; $\beta_{\text{CBNG 3.2 km}} = -4.39 \pm 1.52$ SE; $\beta_{\text{CBNG 6.4 km}} = -4.57 \pm 2.06$ SE; $\beta_{\text{Years in CBNG}} = -1.30 \pm 0.61$ SE). After excluding leks with ≥5% tillage agriculture, the top 4 of 11 models and 4 of 5 models within 2 $\Delta AIC_c$ units included a positive effect of sagebrush within 6.4 km and a negative effect of CBNG development. Estimates of CBNG effects were again similar to the original model-averaged values ($\beta_{\text{Sagebrush 6.4 km}} = 4.03 \pm 2.29$ SE; $\beta_{\text{CBNG 0.8 km}} = -3.34 \pm 1.41$ SE; $\beta_{\text{CBNG 3.2 km}} = -4.83 \pm 2.06$ SE; $\beta_{\text{CBNG 6.4 km}} = -4.76 \pm 3.21$ SE; $\beta_{\text{Years in CBNG}} = -2.44 \pm 1.25$ SE).

# DISCUSSION

Coal-bed natural gas development appeared to have substantial negative effects on sage-grouse breeding populations as indexed by male lek attendance and lek persistence. Although the small number of transitions ($n = 4$) in the trend analysis limited our ability to detect differences between trends, effect sizes were nonetheless large and suggest more rapidly declining breeding populations in CBNG fields. Effects of CBNG development explained lek persistence better than effects of power lines, preexisting roads, WNv mortality, or tillage agriculture, even after controlling for availability of sagebrush habitat. Strong support for models with negative effects of CBNG at both the 0.8-km and 3.2-km scales indicate that the current restriction on surface infrastructure within 0.4 km is insufficient to protect breeding populations. Moreover, support for a lag time between CBNG development and lek disappearance suggests that monitoring effects of a landscape-level change like CBNG may require several years before changes in lek status are detected.

Although CBNG development was clearly associated with population declines, the relative contribution of different components of infrastructure to overall population impacts remains unclear. Models with power line effects were weakly supported compared to models with CBNG, but coefficients nonetheless suggested that power lines (including those associated with CBNG) had a negative effect on lek persistence. In our study, non-CBNG roads did not appear to influence lek persistence, even though collisions with vehicles and disturbance of leks near roads can have negative impacts on sage-grouse (Lyon and Anderson 2003, Holloran 2005). This may be because most roads in sage-grouse habitat in the PRB prior to CBNG development were rarely traveled dirt tracks rather than the more heavily traveled, all-weather roads associated with CBNG development. West Nile virus has also contributed to local lek extirpations in the PRB (Walker et al. 2004). However, unless CBNG development facilitates the spread of WNv into sage-grouse habitat, impacts of the virus should be similar in areas with and without CBNG. Thus, the impact of WNv by itself cannot explain declining breeding populations in CBNG. Rather, increased WNv-related

mortality may be an indirect effect of CBNG development (Zou et al. 2006). Other indirect effects, such as changes in livestock grazing due to newly available CBNG water or changes in predator abundance caused by addition of ponds or power lines, may also contribute to the cumulative effect of CBNG development on sage-grouse populations.

Although CBNG development and loss of sagebrush habitat both contributed to declines in lek persistence, more of the landscape in the PRB has potential for CBNG than for tillage agriculture, which suggests that CBNG may eventually have a greater impact on region-wide populations. In our analyses, we were unable to distinguish between conversion of sagebrush to cropland that would have occurred without CBNG development and that which occurred because CBNG water became available for irrigation following development. Although sage-grouse sometimes use agricultural fields during brood-rearing (Schroeder et al. 1999, Connelly et al. 2000*b*), conversion of sagebrush habitat to irrigated cropland in conjunction with CBNG development may be detrimental (Swenson et al. 1987, Leonard et al. 2000, Smith et al. 2005), particularly if birds in agricultural areas experience elevated mortality due to mowing, pesticides, or WNv (Patterson 1952, Connelly et al. 2000*b*, Naugle et al. 2004).

Accumulated evidence across studies suggests that sage-grouse populations typically decline following energy development (Braun 1986, Remington and Braun 1991, Braun et al. 2002, Holloran 2005), but our study is the first to quantify and separate effects of energy development from those of habitat loss. Our results are similar to those of Holloran (2005:49), who found that "natural gas field development within 3–5 km of an active greater sage-grouse lek will lead to dramatic declines in breeding populations," leks heavily impacted by development typically became inactive within 3–4 years, and energy development within 6.2 km of leks decreased male attendance. As in other parts of their range, sage-grouse populations in the PRB likely have declined due to cumulative impacts of habitat loss combined with numerous other known and unknown stressors. New threats, such as WNv, have also emerged (Naugle et al. 2004, Walker et al. 2007). Nonetheless, our analysis indicates that energy development has contributed to recent localized population declines in the PRB. More importantly, the scale of future development in the PRB suggests that, without more effective mitigation, CBNG will continue to impact populations over an even larger area.

It is unclear whether declines in lek attendance within CBNG fields were caused by impacts to breeding birds at the lek, reduced survival or productivity of birds in the surrounding area, avoidance of developed areas, or some combination thereof. We simultaneously observed less support for models with CBNG effects and increasing magnitude of those effects at larger scales around leks, but model uncertainty precluded identification of a specific mechanism underlying impacts. Experimental research using a before–after, control–impact design with radio-marked birds would be required to rigorously evaluate these hypotheses. Although this would allow us to identify mechanisms underlying declines, based on our findings and those of others (e.g., Holloran 2005, Aldridge and Boyce 2007, Doherty et al. 2008), such an experiment would

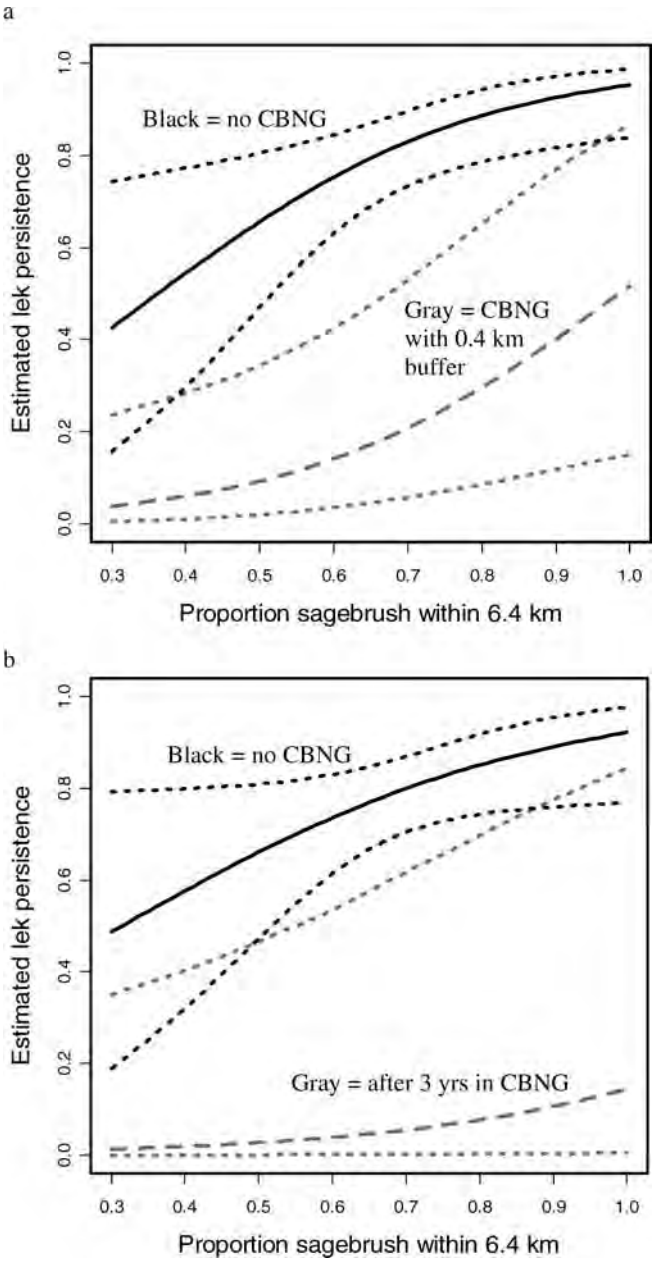



**Figure 5.** Estimated lek persistence as a function of proportion sagebrush habitat within 6.4 km and either (a) proportion coal-bed natural gas (CBNG) development within 0.8 km or (b) number of years within a CBNG field for greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, USA, 1997–2005. Means and 95% confidence intervals (dashed lines) are based on parametric bootstrapping. In (a), black lines are estimated lek persistence with no CBNG development, and gray lines are estimated lek persistence with 75% CBNG development within 0.8 km. Seventy-five percent CBNG development within 0.8 km is equivalent to full development under the Bureau of Land Management's current restriction on surface infrastructure within 0.4 km of active sage-grouse leks. In (b), black lines are estimated lek persistence prior to CBNG development, and gray lines are estimated lek persistence after 3 years in a developed CBNG field (i.e., $\geq$40% CBNG within 3.2 km or $\geq$25% CBNG within 3.2 km and $\geq$1 well within 350 m of the lek center).

likely be detrimental to the affected populations. Nonetheless, ongoing development provides an opportunity to test mitigation measures in an adaptive management framework, with the ultimate goal of determining how to maintain robust sage-grouse populations in areas with CBNG development.

## MANAGEMENT IMPLICATIONS

Our analysis indicates that maintaining extensive stands of sagebrush habitat over large areas (6.4 km or more) around leks is required for sage-grouse breeding populations to persist. This recommendation matches those of all major reviews of sage-grouse habitat requirements (Schroeder et al. 1999; Connelly et al. 2000*b*, 2004; Crawford et al. 2004; Rowland 2004). Our findings also refute the idea that prohibiting surface infrastructure within 0.4 km of the lek is sufficient to protect breeding populations and indicate that increasing the size of no-development zones around leks would increase the probability of lek persistence. The buffer size required would depend on the amount of suitable habitat around the lek and the level of population impact deemed acceptable. Timing restrictions on construction and drilling during the breeding season do not prevent impacts of infrastructure (e.g., avoidance, collisions, raptor predation) at other times of the year, during the production phase (which may last a decade or more), or in other seasonal habitats that may be crucial for population persistence (e.g., winter). Previous research suggests that a more effective mitigation strategy would also include, at minimum, burying power lines (Connelly et al. 2000*b*); minimizing road and well pad construction, vehicle traffic, and industrial noise (Lyon and Anderson 2003, Holloran 2005); and managing water produced by CBNG to prevent the spread of mosquitoes that vector WNv in sage-grouse habitat (Zou et al. 2006, Walker et al. 2007). The current pace and scale of CBNG development suggest that effective mitigation measures should be implemented quickly to prevent impacts from becoming more widespread.

## ACKNOWLEDGMENTS

We thank D. J. Thiele, T. P. Thomas, J. Binfet, J. M. Sandrini, and B. A. Jellison of the Wyoming Game and Fish Department; B. J. Baker of Montana BLM; and R. D. Northrup of Montana Fish, Wildlife, and Parks for providing lek-count data and checking lek databases. J. D. Berry of Western Water Consultants Engineering and K. M. Clayton of Thunderbird Wildlife Consulting provided supplemental lek-count data. The University of Montana Wildlife Spatial Analysis Laboratory processed and analyzed Geographic Information System data. J. J. Rotella of Montana State University provided R code, and J. M. Graham of the University of Montana provided advice on statistical analyses. The BLM, United States Department of Energy, Montana Department of Fish, Wildlife and Parks, Wyoming Game and Fish Department, Wolf Creek Charitable Foundation, National Fish and Wildlife Foundation, Petroleum Association of Wyoming, Western Gas Resources, Incorporated, Anheuser-Busch Companies, Incorporated, and the University of Montana provided funding for the project. We also thank numerous private landowners in the PRB for providing access to leks. J. W. Hupp, J. L. Beck, and M. A. Gregg provided valuable feedback on the original manuscript.

## LITERATURE CITED

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: a habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070–1078.

Bevanger, K. 1998. Biological and conservation aspects of bird mortality caused by electricity power lines: a review. Biological Conservation 86: 67–76.

Braun, C. E. 1986. Changes in sage-grouse lek counts with advent of surface coal mining. Proceedings: Issues and Technology in the Management of Impacted Western Wildlife, Thorne Ecological Institute 2:227–231.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139–156.

Braun, C. E., O. O. Oedekoven, and C. L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage grouse. Transactions of the North American Wildlife and Natural Resources Conference 67: 337–349.

Bureau of Land Management [BLM]. 2003*a*. Final Environmental Impact Statement and Proposed Plan Amendment for the Powder River Basin Oil and Gas Project. <http://www.blm.gov/wy/st/en/info/NEPA/bfodocs/prb_feis.html>. Accessed 18 Mar 2007.

Bureau of Land Management [BLM]. 2003*b*. Montana Final Statewide Oil and Gas Environmental Impact Statement and Proposed Amendment of the Powder River and Billings Resource Management Plans. <http://www.mt.blm.gov/mcfo/cbm/eis/index.html>. Accessed 18 Mar 2007.

Burnham, K. P, and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Connelly, J. W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000*a*. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. Wildlife Biology 6:227–232.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. Station Bulletin 80. University of Idaho College of Natural Resources Experiment Station, Moscow, USA.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000*b*. Guidelines to manage sage-grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Moseley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2–19.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife—threats to biodiversity and human health. Science 287:443–449.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:in press.

Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York, New York, USA.

Ellis, K. L. 1984. Behavior of lekking sage grouse in response to a perched golden eagle. Western Birds 15:37–38.

Ellis, K. L., J. R. Parish, J. R. Murphy, and G. H. Richins. 1989. Habitat

use by breeding male sage grouse: a management approach. Great Basin Naturalist 49:404–407.
Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871–883.
Gelbard, J. L., and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology 17:420–432.
Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.
Hosmer, D. W., T. Hosmer, S. le Cessie, and S. Lemeshow. 1997. A comparison of goodness-of-fit tests for the logistic regression model. Statistics in Medicine 16:965–980.
Kaiser, R. C. 2006. Recruitment by greater sage-grouse in association with natural gas development in western Wyoming. Thesis, University of Wyoming, Laramie, USA.
Knight, R. L., and J. Y. Kawashima. 1993. Responses of raven and red-tailed hawk populations to linear right-of-ways. Journal of Wildlife Management 57:266–271.
Leonard, K. M., K. P. Reese, and J. W. Connelly. 2000. Distribution, movements and habitats of sage grouse, *Centrocercus urophasianus,* on the Upper Snake River Plain of Idaho: changes from the 1950's to the 1990's. Wildlife Biology 6:265–270.
Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage-grouse nest initiation and movement. Wildlife Society Bulletin 31:486–491.
Morris, W., and D. F. Doak. 2002. Quantitative conservation biology. Sinauer, Sunderland, Massachusetts, USA.
Moynahan, B. J. 2004. Landscape-scale factors affecting population dynamics of greater sage-grouse (*Centrocercus urophasianus*) in north-central Montana, 2001–2004. Dissertation, University of Montana, Missoula, USA.
Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: pending crisis for greater sage-grouse. Ecology Letters 7:704–713.
Nelleman, C., I. Vistnes, P. Jordhøy, and O. Strand. 2001. Winter distribution of wild reindeer in relation to power lines, roads, and resorts. Biological Conservation 101:351–360.
Nelleman, C. I., I. Vistnes, P. Jordhøy, O. Strand, and A. Newton. 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. Biological Conservation 113:307–317.
Patterson, R. L. 1952. The sage grouse in Wyoming. Wyoming Game and Fish Commission and Sage, Denver, Colorado, USA.
R Development Core Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. Accessed 3 Feb 2006.
Remington, T. E., and C. E. Braun. 1991. How surface coal mining affects sage grouse, North Park, Colorado. Proceedings: issues and technology in the management of impacted western wildlife. Thorne Ecological Institute 5:128–132.
Rowland, M. M. 2004. Effects of management practices on grassland birds: greater sage-grouse. Version 12AUG2004. Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA. Northern Prairie Wildlife Research Center Online. <http://www.npwrc.usgs.gov/resource/literatr/grasbird/grsg/grsg.htm>. Accessed 14 Feb 2007.
Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage-grouse (*Centrocercus urophasianus*). Account 425 *in* A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.
Smith, J. T., L. D. Flake, K. F. Higgins, G. D. Kobriger, and C. G. Homer. 2005. Evaluating lek occupancy of greater sage-grouse in relation to landscape cultivation in the Dakotas. Western North American Naturalist 65:310–320.
Steenhof, K., M. N. Kochert, and J. A. Roppe. 1993. Nesting by raptors and common ravens on electrical transmission line towers. Journal of Wildlife Management 57:272–281.
Swenson, J. E., C. A. Simmons, and C. D. Eustace. 1987. Decrease of sage grouse *Centrocercus urophasianus* after ploughing of sagebrush steppe. Biological Conservation 41:125–132.
Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14: 18–30.
U.S. Census Bureau. 1995. TIGER/Line® 1995 data. Available from the Wyoming Natural Resources Data Clearinghouse. <http://www.sdvc.uwyo.edu/24k/road.html>. Accessed 3 Aug 2006.
Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2004. Outbreak of West Nile virus in greater sage-grouse and guidelines for monitoring, handling, and submitting dead birds. Wildlife Society Bulletin 32:1000–1006.
Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2007. West Nile virus and greater sage-grouse: estimating infection rate in a wild population. Avian Diseases 51:691–696.
Zhou, S. 2002. Estimating parameters of derived random variables: comparison of the Delta and parametric bootstrap methods. Transactions of the American Fisheries Society 131:667–675.
Zou, L., S. Miller, and E. Schmidtmann. 2006. Mosquito larval habitat mapping using remote sensing and GIS: implications of coal-bed methane development and West Nile virus. Journal of Medical Entomology 43:1034–1041.

*Associate Editor: Hupp.*

This manuscript contains unpublished, peer-reviewed, scientific information. It has been accepted for future publication in a special volume of the Cooper Ornithological Society scientific series "Studies in Avian Biology." No waiver of proprietary rights to the information is granted by this release on the part of the Cooper Ornithological Society and its publisher, the USGS, or the author(s) of the manuscript.

## Document cover Sheet—Studies in Avian Biology

**Title:** FACTORS ASSOCIATED WITH EXTIRPATION OF SAGE-GROUSE

**File name**: wisdom et al.doc

**RH:** SAGE-GROUSE EXTIRPATION—*Wisdom et al.*

**Number of figures:** 5

**Number of tables:** 4

**Author to receive correspondence:**
Michael J. Wisdom
USDA Forest Service
Pacific Northwest Research Station
1401 Gekeler Lane
La Grande, OR 97850
Phone: (541) 962-6532
Email: mwisdom@fs.fed.us

Carl D. Marti, Editor
Studies in Avian Biology
1310 E Jefferson St.
Boise, ID 83712 USA
Tel: 208-426-8996
Email: sab@boisestate.edu

# FACTORS ASSOCIATED WITH EXTIRPATION OF SAGE-GROUSE

MICHAEL J. WISDOM, CARA W. MEINKE, STEVEN T. KNICK, AND MICHAEL A. SCHROEDER

Abstract. Geographic ranges of Greater Sage-Grouse (*Centrocercus urophasianus*) and Gunnison Sage-Grouse (*Centrocercus minimus*) have contracted across large areas in response to habitat loss and detrimental land uses. However, quantitative analyses of the environmental factors most closely associated with range contraction have been lacking, results of which could be highly relevant to conservation planning. Consequently, we analyzed differences in 22 environmental variables between areas of former range (extirpated range), and areas still occupied by the two species (occupied range). Fifteen of the 22 variables, representing a broad spectrum of biotic, abiotic, and anthropogenic conditions, had mean values that were significantly different between extirpated and occupied ranges. Best discrimination between extirpated and occupied ranges, using discriminant function analysis (DFA), was provided by 5 of these variables: sagebrush (*Artemisia* spp.) area; elevation; distance to transmission lines; distance to cellular towers; and land ownership. A DFA model containing these 5 variables correctly classified >80% of sage-grouse historical locations to extirpated and occupied ranges. We used this model to estimate the similarity between areas of occupied range with areas where extirpation has occurred. Areas currently occupied by sage-grouse, but with high similarity to extirpated range, may not support persistent populations. Model estimates showed that areas of highest similarity were concentrated in the smallest, disjunct portions of occupied range and along range peripheries. Large areas in the eastern portion of occupied range also had high similarity with extirpated range. By contrast, areas of lowest similarity with extirpated range were concentrated in the largest, most contiguous portions of occupied range that dominate Oregon, Idaho, Nevada, and western Wyoming. Our results have direct relevance to conservation

planning. We describe how results can be used to identify strongholds and spatial priorities for effective landscape management of sage-grouse.

*Key words*: *Centrocercus minimus, Centrocercus urophasianus,* extirpation, extirpated range, range contraction, Greater Sage-Grouse, Gunnison Sage-Grouse, sagebrush

FACTORES ASOCIADOS A LA EXTIRPACION DEL SAGE-GROUSE

*Resumen*. Las distribuciones geográficas del Greater Sage-Grouse (*Centrocercus urophasianus*) y el Gunnison Sage-Grouse (*Centrocercus minimus*) se han contraído a través de extensas áreas en respuesta a la pérdida de hábitat y a usos perjudiciales del suelo. Sin embargo, se carece de análisis cuantitativos de los factores ambientales que más se asocian a la contracción del territorio, cuyos resultados podrían ser altamente relevantes al planeamiento de la conservación. Por lo tanto, analizamos diferencias en 22 variables ambientales entre las áreas del territorio original (territorio extirpado), y las áreas todavía ocupadas por las dos especies (territorio ocupado). Quince de las 22 variables, representando un amplio espectro de condiciones bióticas, abióticas, y antropogénicas, tuvieron valores medios que resultaron significativamente diferentes entre los territorios extirpados y ocupados. La mejor discriminación entre los territorios extirpados y ocupados, usando el análisis de función discriminante (DFA), fue proporcionada por cinco de estas variables: área del sagebrush (*Artemisia* spp.); elevación; distancia a las líneas de transmisión; distancia a las torres celulares; y propiedad del terreno. Un modelo de DFA que contenía estas 5 variables clasificó correctamente > 80% de las ubicaciones históricas del sage-grouse como territorios extirpados y ocupados. Utilizamos este modelo para estimar la semejanza entre las áreas del territorio ocupado con las áreas donde ha ocurrido la extirpación. Las áreas ocupadas actualmente por sage-grouse, pero con alta semejanza al territorio extirpado, pueden no ser capaces de sostener a las poblaciones persistentes. Las

estimaciones del modelo demostraron que las áreas de mayor semejanza están concentradas en las porciones más pequeñas y divididas del territorio ocupado, y a lo largo de las periferias del territorio. Extensas áreas en la porción este del territorio ocupado también tuvieron gran semejanza con el territorio extirpado. Por el contrario, las áreas de menor semejanza con el territorio extirpado están concentradas en las porciones más grandes y más contiguas del territorio ocupado que dominan Oregon, Idaho, Nevada, y Wyoming occidental. Nuestros resultados tienen relevancia directa al planeamiento de la conservación. Describimos cómo los resultados pueden utilizarse para identificar baluartes y prioridades espaciales para el eficaz manejo del paisaje de sage-grouse.

Species across the world are threatened by human activities that degrade and eliminate habitats at a massive scale. The World Conservation Union estimates that >12,000 species are at risk of extinction from the pervasive and accelerating effects of human-associated causes of habitat loss (Baillie et al. 2004). Habitat loss is reflected in range contraction for many widely distributed species. Large, contiguous ranges of many terrestrial species have become smaller and fragmented, resulting in population isolation and increased vulnerability to extirpation and extinction. In western North America, a myriad of widely distributed birds and mammals have experienced large contractions in their historical ranges in response to habitat loss and detrimental human activities (Wisdom et al. 2000, Laliberte and Ripple 2004).

Range contraction for many species is well documented and the causes generally accepted. However, the specific changes in environmental conditions associated with contraction often are not well studied and thus poorly quantified. Consequently, specific factors and their threshold values associated with range contraction, or regional extirpation of a species, have

rarely been documented (see Laliberte and Ripple 2004 as an exception). The advent of continuous coverage spatial data now allows environmental conditions to be summarized across vast areas, encompassing extirpated and occupied portions of a species historical range. These spatial data provide novel and compelling opportunities for formal analysis of conditions associated with extirpation in areas where species ranges have contracted (Aldridge et al. 2008). Differences in environmental conditions between extirpated and occupied portions of a species historical range could provide important insights for conservation planning and recovery. This is particularly true for many species whose populations are declining and considered imperiled, yet data are insufficient to conduct a formal population viability analysis (Morris and Doak 2002).

Greater Sage-Grouse (*Centrocercus urophasianus*) and Gunnison Sage-Grouse (*Centrocercus minimus*) (collectively referred to as sage-grouse) are typical of many widely distributed species whose ranges have contracted in response to habitat loss and detrimental land uses. Habitats and populations have declined steadily, over long periods, and across large areas (Connelly and Braun 1997, Braun 1998, Schroeder et al. 1999, Connelly et al. 2004. Aldridge et al. 2008) resulting in widespread range contraction (Schroeder et al. 2004). Notably, sage-grouse are strongly associated with sagebrush (*Artemisia* spp.), and like many other sagebrush-associated vertebrates, are highly vulnerable to regional extirpation because of extensive habitat loss and degradation (Raphael et al. 2001).

Our goal was to identify environmental factors associated with regional extirpation of sage-grouse. Our specific objectives were to (1) identify spatially explicit environmental factors most strongly associated with, and providing the best discrimination between, currently occupied versus extirpated ranges of sage-grouse, (2) use these factors in a spatially explicit model to estimate the similarity of remaining areas of occupied range with areas where extirpation has

occurred as a means of identifying areas where sage-grouse may be vulnerable to extirpation, (3) interpret results for conservation planning at regional and range-wide spatial extents, and (4) describe data deficiencies and research needs to enhance knowledge about environmental conditions that potentially contribute to sage-grouse extirpation at regional extents.

## METHODS

We used six steps to meet our objectives: (1) delineate boundaries of currently occupied versus extirpated portions of sage-grouse historical range, (2) obtain or derive continuous coverage spatial layers for all environmental variables likely to differ between occupied and extirpated ranges based on known or hypothesized environmental associations with sage-grouse at landscape scales, (3) develop an unbiased system of sampling or census of these environmental variables in occupied versus extirpated ranges at a spatial extent compatible with that used by sage-grouse populations to meet year-round needs, and consequently, the extent at which regional extirpation may occur, (4) use the system to analyze patterns and differences in environmental variables between occupied and extirpated ranges, (5) build and validate spatial models based on these patterns and differences that best discriminate between occupied and extirpated ranges, and (6) apply the best-performing model to different regions of occupied range to estimate each region's similarity with areas where extirpation has occurred.

### STEP 1—RANGE DELINEATION

We used the range map for Greater and Gunnison Sage-Grouse (Schroeder et al. 2004) as the basis for identifying their occupied and extirpated ranges. The historical ranges of the two species could not always be distinguished. Until recently, the two species were considered one, and historical records often were identified simply as sage-grouse (Schroeder et al. 2004). As a result, our analysis combines both species, recognizing that most areas of their collective ranges

were and continue to be dominated by Greater Sage-Grouse (Schroeder et al. 2004). Both species have similar environmental requirements and respond similarly to habitat loss from human activities, and both have undergone substantial range contractions in response to habitat loss (Oyler-McCance et al. 2001, Rowland 2004).

The range map of Schroeder et al. (2004) depicts the potential pre-settlement and the current range of sage-grouse. Potential pre-settlement was defined as the range before 1800 when settlement of western North America by large numbers of EuroAmericans had not yet occurred. We assumed that the potential pre-settlement range not currently occupied represented areas where sage-grouse once existed but now are extirpated. This assumption is supported by the large number of sage-grouse collected or observed during the latter phases of EuroAmerican settlement (late 1800s and early 1900s) in areas where sage-grouse no longer exist. Collected specimens or unambiguous observations of sage-grouse provided clear evidence of areas where sage-grouse occurred historically, although collections and observations were not systematic across the range and exact locations not always documented. Given this background information, we assumed that potential pre-settlement range, minus the current range, represented the best estimate of areas where sage-grouse have been extirpated. We refer to current range as "occupied" and to potential pre-settlement range, excluding current range, as extirpated.

### STEP 2—ENVIRONMENTAL VARIABLES

We identified 22 environmental variables relevant to sage-grouse or sagebrush landscapes whose values likely differed between occupied and extirpated ranges (Table 1). Most variables were identified from earlier research as being associated with sage-grouse extirpation at large spatial extents (>100,000 ha; Oyler-McCance et al. 2001, Wisdom et al. 2002a, Aldridge and Boyce 2007, Aldridge et al. 2008), or that have modified sagebrush habitats across large

areas of sage-grouse range (Schroeder et al. 1999, Rowland 2004). Other variables represented common landscape features potentially helpful for accurate discrimination between occupied and extirpated ranges. Inclusion of these additional variables was important because of the paucity of prior landscape research on sage-grouse-environmental relations and our objective to identify the best discriminators between occupied and extirpated ranges, regardless of whether such variables had previously been evaluated as causal factors of extirpation.

Nine of the 22 variables were biological measures such as area, patch size, and fragmentation of sagebrush. Five variables were abiotic measures including precipitation, elevation, and soil characteristics. Eight variables were anthropogenic measures such as distance to roads, area in agriculture, and human population density. Of the 22 variables, 16 were raster-based and 6 were vector-based (polygon- or contour-based) estimates (Table 1).

Map resolution (cell size, polygon size, or contour interval) differed by variable, but most raster-based estimates used a 90-m cell size, and contour-based estimates used a resolution as fine as 10 m (Table 1). Variables also had to be available as continuous coverage layers in a geographic information system (GIS) and encompass most areas of pre-settlement range. Some fringes of pre-settlement range in the US and in Canada could not be analyzed because variables were not available in continuous coverage or in compatible GIS formats. These small areas not included in our analysis composed <2% of sage-grouse pre-settlement range. Estimates of variables were made for 2000–2004, and thus were compatible with the timeframe in which sage-grouse ranges were delineated (Schroeder et al. 2004).

Variables used in our analysis were assumed to affect or be associated with changes in sage-grouse habitats or populations at regional spatial extents (≥100,000 ha). Analysis at regional extents was purposefully different than more typical analyses conducted at smaller spatial extents

(<100,000 ha) such as evaluation of factors within a seasonal range or a specific use area, e.g., evaluating a lekking, nesting, brood-rearing, or wintering area used by individual sage-grouse or a sub-population. Consequently, variables included in our analysis did not include all factors associated with smaller areas of fine-scale habitat use or sub-population dynamics (Connelly et al. 2000; Connelly et al., *this volume*). In addition, some variables potentially associated with population dynamics of sage-grouse at regional extents, such as livestock stocking rates and grazing systems, were not available in continuous coverage formats, and thus could not be considered for analysis.

### STEP 3—SAMPLING DESIGN

We used historical locations of sage-grouse for analyzing differences in environmental variables between occupied and extirpated ranges. Historical locations came from two sources (Schroeder et al. 2004): museum specimens collected mostly during the early 1900s and published observations documented for this period. Historical locations represent documented areas of occurrence in pre-settlement range (Schroeder et al. 2004).

We used 375 of >1,300 historical locations after eliminating multiple collections or observations from the same locations, and by excluding locations or observations clearly outside the established pre-settlement range where individual birds may have occasionally occurred (Schroeder et al. 2004). Use of historical locations focused our analysis on documented areas of species occurrence before and during European settlement, in contrast to an analysis of randomly selected areas within pre-settlement range that might include regions not having direct physical evidence of species occurrence.

Each historical location was classified as occupied or extirpated range. A circle with an 18-km radius, encompassing an area of 101,740 ha, was then centered on each historical location

(Fig. 1). Of the 375 historical locations, 239 were in occupied range and 136 were in extirpated range. Portions of some of the associated circles overlapped the boundary between occupied and extirpated ranges. We retained these locations for analysis because (1) the majority of area in the circle was always in the same portion of range as its historical location, and (2) we wanted to include the full spectrum of environmental conditions across areas far from, and close to, the occupied-extirpated range boundary.

### Step 4—Environmental Conditions

We used each historical location and associated 18-km radius as our unit of observation to analyze conditions for each environmental variable in occupied versus extirpated range (Table 1). For this analysis, we first calculated the composite value of each environmental variable within each circle. The composite value was the average of all values for a variable that composed the cells, polygons, or contours within the circle. We then calculated the mean and associated 95% confidence interval (ci) for the composite values among all circles associated with occupied (N = 239) and extirpated range (N = 136) (Fig. 1).

We treated each circle as a sample unit although most (279 of 375) circles overlapped one another on their outer edges. However, most of the area within circles did not overlap other circles ($\bar{x}$overlap = 22%). Moreover, circle overlap occurred most often along the occupied-extirpated range boundary, where we chose to retain circles because of their contribution to the occupied-extirpated gradient.

### Step 5—Discriminant Analysis

We used discriminant function analysis (DFA; SAS Inc. 1990) to identify which environmental variables discriminated best between historical locations in occupied versus extirpated range. Discriminant function analysis is an appropriate method for discriminating

between two or more groups when variables used for discrimination are quantitative and normally distributed (Hair et al. 1992). When these assumptions are met, DFA generally has more discriminatory power than analogues such as logistic regression (Efron 1975). Prior probabilities of classification were set proportional to sample sizes in occupied and extirpated ranges. Variance-covariance structure for the two classification groups were not pooled (i.e., we used quadratic discriminant functions), as recommended when equal variances between groups is not assured (SAS Inc. 1990, Hair et al. 1992). Examination of the frequency distributions of each variable showed that data were normally distributed for all variables within both classification groups, thus meeting this assumption. Discriminatory variables also should not be highly correlated if stepwise procedures are used. Correlation coefficients among all discriminatory variables were <0.35, positive or negative, indicating that stepwise procedures could be used.

Results from the discriminant function analysis were used in cross-validation analysis by withholding data for a different circle for each run to jackknife the assessment of classification accuracy of each combination of discriminatory variables in a given model (SAS Inc. 1990, Hair et al. 1992). Results were expressed as the percentage of locations correctly classified to occupied range, to extirpated range, and incorrectly classified to each (SAS Inc. 1990).

We used cross-validation results to rank model performance. First, we summed the percentage of historical locations correctly classified to occupied or extirpated range, to obtain a cumulative percentage of correct classifications (Table 2). For a model to perform perfectly, the cumulative percentage would be 200%—100% of locations correctly classified to occupied range and to extirpated range. Second, we subtracted the percentage of locations correctly classified to occupied range from the percentage correctly classified to extirpated range. This absolute difference measured the evenness of correct classifications between occupied and

extirpated ranges. The best evenness value would be 0, indicating that a model was equally consistent in correct classifications between occupied and extirpated ranges. Third, we subtracted the evenness value from the cumulative percentage of correct classifications. This difference, or performance value, provided an overall measure of model performance, considering both accuracy and evenness of classifications (Table 2). For example, a given model might correctly classify 100% of locations associated with occupied range but only 75% of locations associated with extirpated range, yielding a cumulative percentage of 175, an evenness of 25, and an overall performance value of 150. By contrast, a second model that correctly classified 90% of locations to occupied range and 85% of locations to extirpated range also results in a cumulative percentage of 175, but an evenness of 5, and an overall performance value of 170. The second model has a higher performance value, owing to its superior capability to correctly classify locations to both occupied and extirpated ranges.

We used this process to evaluate DFA models containing different combinations of the 22 discriminatory variables. The combinations included evaluation of: (1) each environmental variable individually, (2) biotic variables as a group, (3) abiotic variables as a group; (4) anthropogenic variables as a group, (3) all combinations of the three groups of biotic, abiotic, and anthropogenic variables, (4) all variables that had non-overlapping 95% confidence intervals between their mean values for occupied versus extirpated ranges, (5) all groups of variables whose individual performance values were $\geq$75 and $\geq$100, and (6) all variables identified in forward stepwise DFA (Hair et al. 1992) as statistically significant ($P < 0.05$) discriminators. All of these DFA models were identified a priori of any modeling results.

### STEP 6—SPATIAL MODELING

The combination of variables with highest performance value in discriminating between extirpated and occupied ranges was used in a predictive DFA to estimate the probability that different regions of occupied range had environmental conditions similar to conditions in extirpated range. Our purpose was to identify and map areas of occupied range where environmental conditions indicated that sage-grouse may be at higher risk of regional extirpation, versus areas with conditions likely to serve as regional "strongholds" for population persistence.

We first subdivided the occupied range into 100,000-ha blocks. These block were compatible in size with the circular areas used to evaluate performance of various models at historical locations, and likewise compatible with regional effects on sage-grouse. We then applied the model to each of 2,661 blocks that encompassed occupied range. Results were expressed as the probability of environmental similarity of a given block of occupied range with conditions in extirpated range.

The probability of similarity for each block was placed in one of six categories: 0.0–0.10, >0.10–0.25, >0.25–0.50, >0.50–0.75, >0.75–<0.90, and 0.90–1.0. These categories were most narrow for the lowest and highest probabilities because these values represent extreme conditions where similarity to extirpated range is either highly probable or improbable. Categories for intermediate probability values were wider, reflecting higher uncertainty about environmental differences between occupied and extirpated ranges. We summarized results by these categories across occupied range within each sage-grouse management zone (Stiver et al. 2006). We also mapped similarity values as a continuous variable by state and management zone to compare and contrast these results with values summarized by categories.

RESULTS

## Differences Between Extirpated and Occupied Ranges

Fifteen of the 22 environmental variables had mean values with non-overlapping 95% ci between extirpated and occupied ranges (Figs. 2–4). These variables included five biotic, three abiotic, and seven anthropogenic variables.

The five significant biotic variables were sagebrush area, patch size of sagebrush, proximity of sagebrush patches, size of sagebrush core areas, and distance to the boundary between occupied and extirpated ranges. Historical locations in occupied range contained almost twice as much area in sagebrush as those in extirpated range (Fig. 2). Mean patch size of sagebrush was >9 times larger, and mean core areas >11 times larger, in occupied versus extirpated range (Fig. 2). Sagebrush patches also were substantially closer to one another in occupied range (Fig. 2). In addition, historical locations in occupied range were closer to the boundary between occupied and extirpated ranges than locations in extirpated range (Fig. 2).

The three significant abiotic variables were elevation, soil water capacity, and soil salinity. Elevation was almost 50% higher in occupied range than in extirpated range (Fig. 3). Occupied range had lower soil water capacity and higher soil salinity (Fig. 3).

The seven significant anthropogenic variables were area in agriculture, human density, road density, distance to highways, distance to electric transmission lines, distance to cellular towers, and land ownership. Area in agriculture was almost three times lower and mean human density was 26 times lower in occupied than in extirpated range (Fig. 4). Road density also was lower and highways substantially farther from historical locations in occupied range (Fig. 4). Mean distance to electric transmission lines was >two times farther in occupied range than in extirpated range (Fig. 4). The distance to cellular towers averaged almost twice as far in occupied range (Fig. 4). Occupied range also had substantially more public ownership (Fig. 4);

64% of circles encompassing historical locations in occupied range were dominated by public ownership compared to 26% in extirpated range.

## Environmental Discrimination Between Extirpated and Occupied Ranges

### *Individual variables and biotic, abiotic, and anthropogenic groups*

We first evaluated performance of DFA models containing individual discriminatory variables and those containing all combinations of biotic, abiotic, and anthropogenic groups of variables (Table 1). The best-performing of these models contained all biotic and anthropogenic variables, which correctly classified 72% of historical locations to occupied range and 80% to extirpated range (Table 2). The second-best model contained just one variable, sagebrush area, which correctly classified 76% of historical locations to occupied range and 65% to extirpated range. The land ownership model had third-best performance, followed by models containing distance to transmission lines; all biotic and abiotic variables; distance to cellular towers; elevation; all biotic variables; and all anthropogenic and abiotic variables (Table 2). Additional models containing the remaining individual variables performed poorly as discriminators between occupied and extirpated ranges (Table 2).

### *Best-performing combinations of variables*

We evaluated four additional models that contained combinations of variables with potential for high classification accuracy (Table 3), based on our a priori modeling approaches described in step 5 of Methods. The best-performing model, model 2, contained just five variables: sagebrush area, elevation, distance to transmission lines, distance to cellular towers, and land ownership (Table 3). This model correctly classified 85% of locations to occupied range and 83% to extirpated range (performance value 166, Table 3). Model 4, which contained the 15 variables with non-overlapping confidence intervals between mean values in occupied and

extirpated ranges, performed slightly worse than model 2 (performance value 154) and substantially better than models 1 and 3 (Table 3). Both models 2 and 4 out-performed all single-variable models and all models based on biotic, abiotic, and anthropogenic groups of variables (Tables 2, 3).

Nearly all errors in correctly classifying historical locations to occupied and extirpated ranges with model 2, our best-performing model, occurred under two conditions: (1) they were located in the Great Plains management zone (N = 17); or (2) they were substantially closer to the boundary between occupied and extirpated ranges (N = 41) (Fig. 1). Locations incorrectly classified to occupied and extirpated ranges and not within the Great Plains were <10 km from the boundary between occupied and extirpated ranges. By contrast, >80% of correctly classified locations were >20 km from the boundary between occupied and extirpated ranges. Incorrectly classified locations close to the occupied-extirpated range boundary had large portions of the associated circles that overlapped both occupied and extirpated ranges. Thus, locations associated with these circles represented a mix of conditions from both ranges. As a result, performance of model 2 was diminished with the inclusion of these circles that overlapped both classification groups (occupied versus extirpated ranges). However, classification accuracy was high for model 2 (>80%, Table 3) despite the inclusion of these circles along the occupied-extirpated range boundary.

*Similarity of occupied range with extirpated range*

Estimates based on application of model 2 to all 100,000-ha blocks of occupied range showed that similarity to extirpated range was highest along most range peripheries (Fig. 5). Similarity to extirpated range also was highest in the smaller, disjunct areas of occupied range in

Washington, southwest Oregon, northeast California, Idaho, northeast Utah, southern Montana, and in larger areas of east-central Montana and eastern and north-central Wyoming (Fig. 5).

Environmental similarity to extirpated range was lowest in the expansive area of occupied range in southeast Oregon, southwest Idaho, northern and east-central Nevada, and west-central and southwest Wyoming (Fig. 5); these areas compose the largest, most contiguous blocks of occupied range of Greater Sage-Grouse. By contrast, the small, disjunct areas occupied by Gunnison Sage-Grouse in southeast Utah and southern Colorado had similarity values that were mostly intermediate with those of extirpated range (Fig. 5).

The Columbia Basin had the highest percentage of environmental similarity with extirpated range: 65% of the zone was in the two highest similarity classes (probabilities >0.75) and mostly in the highest class (0.90–1.0; Fig. 5, Table 4). The Great Plains had the next-highest percentage of occupied range in the two highest similarity classes (37%), followed by Colorado Plateau at 10% (Table 5). Management zones with lowest similarity to extirpated range were Northern Great Basin, Southern Great Basin, Snake River Plain, and Wyoming Basins. The large majority of occupied range in these four Management Zones had probabilities of similarity of ≤0.10. All four, however, had high similarity with extirpated range along range peripheries or in smaller, disjunct areas (Fig. 5).

## DISCUSSION

### FACTORS ASSOCIATED WITH EXTIRPATION

#### *Biotic variables*

Sage-grouse occupation versus extirpation was strongly associated with measures of sagebrush abundance and distribution, including sagebrush area, patch size, proximity of patches, and size of core areas. These results support past studies that identified sage-grouse as a

sagebrush obligate, dependent on sagebrush for persistence (Braun et al. 1976, Schroeder et al. 1999, Rowland 2004).

Sagebrush area was the single-best discriminator between occupied and extirpated ranges among the 22 variables evaluated. The DFA model containing this single variable was one of the top performing models. These results agree with recent findings that sagebrush area is one of the best landscape predictors of sage-grouse persistence (Wisdom et al. 2002a,b; Walker et al. 2007, Doherty et al. 2008, Aldridge et al. 2008).

The upper 95% ci for sagebrush area in extirpated range was 27%. Landscapes occupied by sage-grouse with sagebrush <27% would thus have a >97.5% probability of being no different than a random sample of extirpated ranges, suggesting that associated populations in these occupied ranges could be more vulnerable to extirpation. Similarly, the lower 95% ci for sagebrush area in occupied range was 50%. Landscapes occupied by sage-grouse with values above this lower bound thus have a >97.5% probability of being no different than a random sample of occupied ranges, suggesting a higher capability to support persistent populations.

Recent landscape studies of Greater Sage-Grouse identified similar threshold values for sagebrush area to maintain population persistence. Aldridge et al. (2008:990), using a 30.77-km radius around sampling locations, estimated that at least 25% and preferably 65% of the landscape needed to be dominated by sagebrush for long-term sage-grouse persistence. These estimates mirror our values of 27% and 50% for sagebrush area, with values <27% indicating a high risk of extirpation, and values above 50% indicating a high probability of persistence. Our estimates also are for large landscapes, based on the 18-km radius circles that we analyzed. Similarly, Walker et al. (2007) estimated that the lowest probability of lek persistence, approximately 40–50%, occurred for landscapes with <30% area in sagebrush within 6.4 km of a

lek center. These probabilities declined even more for landscapes with <30% sagebrush that were subjected to energy development (see Fig. 5 in Walker et al. 2007).

*Abiotic variables*

Three abiotic variables, elevation, soil salinity, and soil water capacity, also differed between occupied and extirpated ranges. Elevation was a good discriminator, probably because most sagebrush loss has occurred disproportionately at lower elevations where human activities and developments have been concentrated (Hann et al. 1997; Leu and Hanser, *this volume*;, Knick et al., *this volume*), and where invasive grasses have displaced large areas of sagebrush (Suring et al. 2005, Meinke et al. 2008). Lower soil salinity and higher soil water capacity in extirpated range also indicate a higher suitability for agricultural development (Knick, this volume), which also was associated with sage-grouse extirpation.

*Anthropogenic variables*

Seven of the eight anthropogenic variables differed between occupied and extirpated ranges. The number of these variables, their diversity, and strength of differences between occupied and extirpated ranges suggest that a variety of human activities and land uses have contributed to or been associated with sage-grouse extirpation. This inference agrees with findings from recent landscape studies that documented negative effects of anthropogenic variables on sage-grouse populations, including human density and percent agriculture (Aldridge et al. 2008), roads and traffic (Lyon and Anderson 2003, Holloran 2005), and energy development (Holloran 2005, Aldridge et al. 2007, Walker et al. 2007, Doherty et al. 2008; Naugle et al., *this volume*). We did not specifically evaluate energy development. However, extirpated range contained almost 27 times the human density, had almost 3 times more area in agriculture, was 60% closer to highways, and had 25% higher density of roads, in contrast to

occupied range. These patterns agree with research cited above that evaluated these or similar variables. Moreover, the four variables of human density, area in agriculture, distance to highways, and road density were part of model 4 that out-performed all models except the top-ranked model 2.

Three additional anthropogenic variables, distance to transmission lines, distance to cellular towers, and land ownership also differed between occupied and extirpated ranges. These variables were the best discriminators among the eight anthropogenic variables considered, and ranked among the best of all individual variables. These variables have received little attention in landscape research on sage-grouse—only transmission lines has been formally evaluated (Connelly et al. 2000, Aldridge and Boyce 2007, Walker et al. 2007). Transmission lines can cause sage-grouse mortality via bird collisions with lines (Beck et al. 2006, Aldridge and Boyce 2007) and facilitate raptor predation of sage-grouse (Connelly et al. 2000). In addition, the electromagnetic radiation emitted from transmission lines has a variety of negative effects on other bird species using areas on or near lines (Fernie and Reynolds 2005). Moreover, transmission lines convert habitat to non-habitat and fragment the remaining habitat, similar to roads (Naugle et al., this volume).

The strong association between distance to cellular towers and sage-grouse extirpation was an especially intriguing result, given that no previous studies of sage-grouse have evaluated this variable. Whether cellular towers function in a cause-effect manner or simply are aligned with other detrimental factors cannot be addressed without additional research. Recent studies, however, suggest possible cause-effect relationships between high levels of electromagnetic radiation within 500 m of cellular towers and reduced population or reproductive performance of a limited number of bird and amphibian species (Balmori 2005, 2006; Balmori and Hallberg

2007, Everaert and Bauwens 2007). These negative effects are similar to those documented for bird species exposed to electromagnetic radiation generated by power lines (Fernie and Reynolds 2005). Cellular towers also are likely to cause sage-grouse mortality via collisions with these structures or influence movements by visual obstruction, but no research has investigated these issues.

Distance to cellular towers may also indicate the most intensive human developments and uses, given that cellular towers are concentrated along major highways and within and near larger towns and cities across the range of sage-grouse. Although correlation coefficients between this and the other environmental variables were low, cellular towers represent discrete points within areas of high human use. Consequently, distance to cellular towers may serve as a finely-measured indicator of more concentrated human uses, in contrast to other anthropogenic variables that reflect more general landscape measures of human uses. This pattern would explain the variable's low correlation with other anthropogenic variables yet its high discriminatory performance.

Land ownership also was an ideal indicator of underlying causes of sage-grouse extirpation, given that many private lands have been converted from sagebrush to other land uses (Vander Haegen 2007; Knick et al., *this volume*). In addition, the conversion of private lands to non-sagebrush land uses has fragmented remaining sagebrush habitats nearby (Vander Haegen et al. 2000) and facilitated the spread of exotic plants in sagebrush habitats near such conversions (Hann et al. 1997, Wisdom et al. 2005a,b).

*Combinations of biotic, abiotic, and anthropogenic variables*

Performance of the many discriminant function models, each containing different combinations of environmental variables, largely reflected differences in individual variables

between occupied and extirpated ranges. Models that performed best either contained all 15 variables whose mean values had non-overlapping confidence intervals between occupied and extirpated ranges—model 4—or contained a subset of 5 of those variables (sagebrush area, elevation, distance to transmission lines, distance to cellular towers, and land ownership) that provided highly distinct and precise differences between ranges—model 2. The superior performance of models 2 and 4 suggests that different combinations of the 15 environmental variables could be used as effective predictors of sage-grouse vulnerability to extirpation for current or projected landscape conditions. These results also clearly demonstrate that sage-grouse extirpation is associated with a varied combination of biotic, abiotic, and anthropogenic influences, and that holistic consideration of these many environmental factors in land management appears important to maintain persistent populations at large landscape extents like those studied here.

### Geographic Patterns of Environmental Similarity with Extirpated Range

Our estimates of environmental similarity of areas occupied by sage-grouse to areas where extirpation has occurred have direct implications for range-wide conservation planning. First, populations along the peripheries of occupied range may have a higher risk of extirpation. This higher risk is an expected extension of past extirpation patterns that have largely occurred from the outside inward.That is, sage-grouse extirpation has occurred mostly along the outer portions of pre-settlement range and contracted inward (Schroeder et al. 2004, Aldridge et al. 2008). Most areas along the outer portion of pre-settlement range are at lower elevations where land uses and habitat conversions have been concentrated, particularly on private lands. Moreover, this pattern is expected because populations on the periphery of their range immediately adjacent to areas where extirpation has occurred often are more vulnerable to

extirpation than populations closer to the center when anthropogenic factors disproportionately affect the periphery (Brown et al. 1996, Laliberte and Ripple 2004). This is the case for sage-grouse. By contrast, this may not be the case for declining populations of other species when peripheral areas provide refuge from habitat degradation occurring in core areas (Lomolino and Channell 1995, 2000).

Populations of many species at high risk along range peripheries may undergo extirpation during periods of high environmental variation, such as during a severe and prolonged drought. Extirpation also may occur in such areas when a combination of environmental, genetic, stochastic, and demographic sources of variation manifest over time in ways not easily predicted (Mills 2007). Populations in the periphery of a species range typically experience high temporal variation in abundance in contrast to core populations (Vucetich and Waite 2003); this variation may reflect the many sources of variation described above that contribute to extirpation in small populations of sage-grouse.

Second, populations in small, disjunct areas of occupied range may have a high risk of extirpation. This pattern also is expected, given principles of population viability, which have consistently shown that extinction probability increases for populations that become increasingly small and isolated (Purvis et al. 2000). Populations of Greater Sage-Grouse occupying small, disjunct areas in Washington, northeast California, southwest Oregon, north-central Idaho, eastern Idaho, northeast Utah, and southern Montana, which are separated from larger core populations, fit these conditions.

Third, populations in many areas of occupied range in the Great Plains may have a higher risk of extirpation. This result is not unexpected, given the relatively low sagebrush area in the Great Plains (Knick, *this volume*), which is dominated more by grasslands (Küchler 1964, 1970;

McArthur and Ott 1996). In addition, the southern part of the Great Plains has been altered by extensive energy development, resulting in extensive sagebrush loss and concomitant development of roads, power lines, and other infrastructure (Walker et al. 2007, Walker 2008; Naugle et al., *this volume*). Energy development in Wyoming has progressed, at varying rates in relation to varying energy prices, for many decades (Braun et al. 2002; Naugle et al., *this volume*). Consequently, long-term changes in sage-grouse environments based on energy development in the Wyoming portion of the Great Plains were reflected through the early 2000s in our estimates of sagebrush area and distance to transmission lines—two of the five discriminatory variables included in model 2 that we used to estimate environmental similarity with areas where extirpation has occurred.

Given that sagebrush is substantially less common in the Great Plains in contrast to other areas of sage-grouse range (Knick, *this volume*), our analyses suggest that sage-grouse in this zone may be vulnerable to further reductions in sagebrush area. Additional loss of sagebrush in the Great Plains would approach potential thresholds for sage-grouse extirpation faster than in other areas where sagebrush dominates a larger proportion of the landscape. Our results also indicate that other detrimental factors are at play in the Great Plains.

Finally, our mapped estimates of similarity could be used to identify strongholds for sage-grouse; that is, areas of occupied range where the risk of extirpation appears low, e.g., areas with similarity values $\leq 0.10$ (Fig. 5), and that compose the largest areas of contiguous range. Two large strongholds for Greater Sage-Grouse are evident. One, a western stronghold, is the extensive, contiguous area encompassing southeast Oregon, northwest Nevada, southwest Idaho, northeast Nevada, and east-central Nevada that includes most areas in the northern Great Basin, southern Great Basin, and Snake River Plain—the green areas within these zones in Fig. 5. The

other, an eastern stronghold, is the area encompassing south-central and southwest Wyoming in the Wyoming basins. This second stronghold is approximately one-half the size of the western stronghold. In addition, an area in east-central Idaho has low similarity to extirpated range (Fig. 5) but is smaller than either of the two primary strongholds.

No strongholds are evident for Gunnison Sage-Grouse that consist of expansive, contiguous areas where similarity with extirpated range is ≤0.10 (Fig. 5). Intensive management to conserve existing habitats and populations of the species, combined with efforts to restore habitats, are obvious needs for Gunnison Sage-Grouse (Oyler-McCance et al. 2001, 2005; Lupis et al. 2006).

Our documented spatial patterns of environmental similarity with extirpated range are similar to recent range-wide estimates of sage-grouse persistence (Aldridge et al. 2008). Similarities between these separate analyses are particularly compelling, given that different methods and variables were used. In that regard, our spatial estimates of environmental similarity with extirpated range, and those of persistence by Aldridge et al. (2008), are mutually reinforcing, thus providing a stronger basis for inferences made from each study (Johnson et al. 2002).

### Spatial Priorities for Management

Our mapped estimates of environmental similarity of areas currently occupied by sage-grouse with areas where extirpation has occurred could be used to help establish management priorities across existing sage-grouse range. Strongholds identified from our analysis are potential areas of focus for maintenance and improvement over time. Management emphasis on strongholds is more effective and efficient than devoting limited resources to restoration of areas where populations are at high risk of extirpation because of widespread habitat deficiencies

(Wisdom et al. 2005a, Meinke et al. 2008; Doherty et al., *this volume*). In the latter situation, it is highly uncertain as to whether populations can persist, or how effective it would be to use limited resources in an attempt to improve a myriad of challenging environmental conditions to assure population persistence. This uncertainty revolves around three related issues: (1) areas with high similarity to extirpated range could be population sinks, given that these areas are mostly along the boundary with extirpated range, and range contraction along this boundary appears to be an on-going process for sage-grouse; (2) areas with high similarity to extirpated range are associated with a variety of anthropogenic management challenges that may be difficult or impossible to mitigate, e.g., minimizing current infrastructure of roads, highways, transmission lines, cellular towers, and agricultural and urban areas that dominate these areas, thus negating benefits to restore sagebrush, which also is deficient in these areas; and (3) areas with high similarity to extirpated range are mostly at lower elevations characterized by warmer conditions that have low resistance to exotic plant invasions, and that have low resiliency for returning to native vegetation states following any natural or human-caused disturbances, including restoration treatments (Wisdom et al. 2005a, Meinke et al. 2008).

Despite these challenges, the presence of sage-grouse populations in areas with high similarity to extirpated range may help maintain a lower risk of extirpation for populations in strongholds, by maintaining a larger population size overall and thus helping buffer the negative effects of environmental stochasticity and loss of genetic variation. More isolated or disjunct populations, especially at the range periphery, may have different genetic, phenotypic, and behavioral characteristics important to the species. Understanding the role of these high-risk populations in relation to those in strongholds warrants immediate research attention (Nielson et al. 2001).

Regardless of the role of high-risk populations, effective management of strongholds is important because detrimental anthropogenic factors in strongholds are less common and extensive areas of sagebrush remain. Thus, the management challenge in strongholds is one of maintaining or improving current conditions, which largely translates to prevention of detrimental land uses and minimizing undesirable ecological processes (Wisdom et al. 2005a). In many cases, this combination of passive management and passive restoration involves modifications to existing land uses that maintain or improve conditions (McIver and Starr 2001). This contrasts with active restoration, requiring intensive management and large inputs to restore or rehabilitate conditions in areas where extensive degradation and loss of habitat has occurred, and which may be difficult or impossible to reverse for many sites formerly dominated by sagebrush (McIver and Starr 2001; Pyke, *this volume*).

If management emphasis is placed on strongholds, a comprehensive and detailed assessment of threats to habitats and populations within these areas is appropriate (Wisdom et al. 2005b). Most areas of sagebrush in the western stronghold are threatened by large-scale invasion of exotic plants, particularly cheatgrass (*Bromus tectorum*) (Suring et al. 2005; Miller et al., *this volume*). Minimizing this threat warrants comprehensive management of all human activities that act as vectors for spread and establishment of exotic plants, and that increase their competitive edge over native vegetation. Over 25 different human-associated disturbances would need to be effectively managed to reduce this threat (Wisdom et al. 2005a,b). Among these disturbances are obvious factors such as high densities of roads open to motorized travel and expansive areas of public land open to off-road motorized travel (Barton and Holmes 2007). A myriad of less obvious human-associated disturbances also are prevalent and warrant management attention (Wisdom et al. 2005a).

Another common threat in the western stronghold is displacement of sagebrush by highly invasive pinyon pine (*Pinus* spp.) and juniper (*Juniperus* spp.) woodlands (Suring et al. 2005; Miller et al., *this volume*). Woodland control can be achieved through aggressive mechanical or burning treatments; which treatments, if any, are appropriate and effective depends on local site conditions, the potential interaction with exotic plants, and the anticipated responses of affected sagebrush community types (Suring et al. 2005; Miller et al. 2007, *this volume*). Comprehensive assessment of risks posed by this threat, mapped across the western stronghold, would provide a basis for developing and implementing effective management controls (Suring et al. 2005).

The eastern stronghold continues to be a focal area of large-scale energy development, and attempts to mitigate the associated negative effects on sage-grouse populations have been ineffective (Holloran 2005, Walker et al. 2007, Walker 2008). If the eastern stronghold is to be maintained, a holistic re-design of mitigation practices for energy development is needed (Kiesecker et al. 2009). For mitigations to be effective, they must be implemented over substantially larger areas than current practices, which focus on small areas around leks at a scale too small to sustain year-round needs of sage-grouse populations (Walker et al. 2007; Walker 2008; Doherty et al., *this volume;* Naugle et al., *this volume*).

## RESEARCH AND INFORMATION NEEDS

Our analysis was one of the first to associate a diverse set of environmental factors with sage-grouse extirpation. As part of this process, we noted a number of deficiencies in spatial data. One was the lack of spatial data available for livestock grazing, which constitutes the most pervasive land use across the range of sage-grouse (Knick et al. 2003). Federal agencies are required to closely manage and monitor livestock grazing. However, associated data are not available in consistent, spatially explicit formats across the range of sage-grouse, or even for

smaller areas that span multiple administrative boundaries within or among federal agencies. This deficiency precluded our analysis of livestock grazing. Likewise, no other studies of potential effects of livestock grazing on sage-grouse have been conducted at regional or range-wide spatial extents because of this data deficiency (Crawford et al. 2004).

Primitive and secondary roads also may be under-estimated in current spatial layers. Our distance- and density-based road analyses might have changed with a more accurate inventory. In addition, exotic plant occurrence, another extensive landscape feature, has not been mapped accurately across the range of sage-grouse, and this factor may have substantial effects on habitat (Hemstrom et al. 2002, Rowland et al. 2005). Regional models of cheatgrass occurrence recently were developed and validated for western areas of sage-grouse range (Peterson 2005, Bradley and Mustard 2006, Meinke et al. 2008). Ultimately, such an approach is needed to estimate and map range-wide occurrence of the more common exotic plants, such that potential effects on sage-grouse extirpation can be evaluated range-wide. Similarly, more accurate, range-wide maps of the occurrence of pinyon pine and juniper woodlands would provide a basis for analyzing this variable in relation to range-wide patterns of sage-grouse extirpation.

Another data challenge for range-wide analyses is that some factors may be common or pervasive in specific parts of sage-grouse range, but uncommon or absent in most areas. Energy development is concentrated in Wyoming and adjacent areas but is spatially uncommon, concentrated in small areas, or absent elsewhere. Consequently, we could not evaluate energy development as a range-wide variable because we had insufficient sampling coverage, using historical sage-grouse locations in occupied and extirpated ranges, to evaluate different levels of energy development (but see earlier Discussion regarding variables evaluated that are associated with energy development).

Other factors that may affect sage-grouse populations are just emerging, such as West Nile virus (Naugle et al. 2005, Walker 2008; Walker et al., *this volume*). Such variables are not related to past extirpations, and the range-wide prevalence of West Nile virus within all populations is uncertain. Consequently, an evaluation was not possible.

Finally, identifying which environmental factors are operating in a cause-effect manner in relation to extirpation, and which may simply be correlative, is a challenge not easily addressed except through consideration of our results in relation to the larger body of sage-grouse literature. Our results confirm prior research documenting sage-grouse as a species whose persistence depends on adequate areas of sagebrush. This inference extends to other sagebrush variables--patch size, proximity among patches, and size of core areas—that also were associated with extirpation. These results illustrate the strong effect of sagebrush abundance and distribution on sage-grouse persistence; without large areas of contiguous sagebrush, sage-grouse cannot persist.

A cause-effect relationship of anthropogenic variables such as area in agriculture, human density, road density, and distance to highways is indicated by past research documenting the widespread conversion of sagebrush habitat to these land uses (Braun 1998, Vander Haegen et al. 2000; Knick et al., *this volume*); by the facilitation of exotic plant invasions into sagebrush habitats adjacent to these land uses (Hann et al. 1997), especially adjacent to roads (Gelbard and Belnap 2003); and by mortality of sage-grouse along roads and highways (Lyon and Anderson 2003, Aldridge and Boyce 2007).

The strong associations of elevation and land ownership with sage-grouse extirpation represent the widespread conversion of low-elevation, private lands to non-sagebrush land uses, such as agricultural and urban developments (Vander Haegen et al. 2000; Knick et al., *this*

*volume*), as well as the substantial loss of sagebrush from widespread exotic plant invasions at lower elevations (Hann et al. 1997, Meinke et al. 2008). In that context, elevation and land ownership are ideal indicators of underlying causes of extirpation.

Finally, two variables strongly associated with sage-grouse extirpation, distance to transmission lines and distance to cellular towers, have unknown relations with sage-grouse population dynamics at regional extents. New, mechanistic research is needed to understand the potential relation between these variables and sage-grouse extirpation. Until then, our results suggest that transmission lines and cellular towers warrant consideration as part of holistic conservation strategies for sage-grouse.

## CONSERVATION IMPLICATIONS

A variety of biotic, abiotic, and anthropogenic factors are associated with extirpation of sage-grouse. Consequently, holistic attention to a diverse set of environmental factors—beyond those considered for sage-grouse in current guidelines and management—appears necessary to help maintain population persistence.

Maintenance of desired conditions in areas identified as strongholds for Greater Sage-Grouse appears critical to the species' future persistence. Strongholds provide extensive areas of contiguous sagebrush that can be maintained and improved with less active management and fewer resource inputs. Restoration and rehabilitation of areas within and near the small, disjunct areas of Gunnison Sage-Grouse range likewise is important to recovery and viability of this species. The future of sage-grouse will depend on new, holistic management approaches that are strategically designed and effectively implemented range-wide, and that minimize all forms of detrimental factors and maximize best uses of limited resources.

## ACKNOWLEDGMENTS

K. Doherty and C. Aldridge provided valuable comments that substantially improved our paper. Comments from L. Bond and D. Marx improved our statistical methods and their description. J. Boyd assisted with data summaries, spatial analysis, and editing. Our work was supported by the Pacific Northwest Research Station, USDA Forest Service; the Forest and Rangeland Ecosystem Science Center, US Geological Survey; and the Washington Department of Fish and Wildlife. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

LITERATURE CITED

ALDRIDGE, C. L., AND M. S. BOYCE. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered Greater Sage-Grouse. Ecological Applications 17:508–526.

ALDRIDGE, C. L., S. E. NIELSEN, H. L. BEYER, M. S. BOYCE, J. W. CONNELLY, S. T. KNICK, AND M. A. SCHROEDER. 2008. Range-wide patterns of Greater Sage-Grouse persistence. Diversity and Distributions 14:983–994.

BAILLIE, J. E. M., C. HILTON-TAYLOR, AND S. N. STUART (EDITORS). 2004. 2004 IUCN red list of threatened species: a global species assessment. IUCN, Gland, Switzerland and Cambridge, UK.

BALMORI, A. 2005. Possible effects of electromagnetic fields from phone masts on a population of white stork (*Ciconia ciconia*). Electromagnetic Biology and Medicine 24:109–119.

BALMORI, A. 2006. The incidence of electromagnetic pollution on the amphibian decline: is this an important piece of the puzzle? Toxicological and Environmental Chemistry 88:287–299.

BALMORI, A., AND Ö. HALLBERG. 2007. The urban decline of the house sparrow (*Passer domesticus*): a possible link with electromagnetic radiation. Electromagnetic Biology and Medicine 26:141–151.

BARTON, D. C., AND A. L. HOLMES. 2007. Off-highway vehicle trail impacts on breeding songbirds in northeastern California. Journal of Wildlife Management 71:1617–1620.

BECK, J. L., K. P. REESE, J. W. CONNELLY, AND M. B. LUCIA. 2006. Movements and survival of juvenile Greater Sage-Grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070–1078.

BRADLEY, B. A., AND J. F. MUSTARD. 2006. Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. Ecological Applications 16:1132–1147.

BRAUN, C. E. 1998. Sage Grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139–156.

BRAUN, C. E., M. F. BAKER, R. L. ENG, J. S. GASHWILER, AND M. H. SCHROEDER. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin 88:165–171.

BRAUN, C. E., O. O. OEDEKOVEN, AND C. L. ALDRIDGE. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage-grouse. Transactions North American Wildlife and Natural Resources Conference 67:337–349.

BROWN, J. H., G. C. STEVENS, AND D. M. KAUFMAN. 1996. The geographic range: size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics 27:597–623.

COMER, P., J. KAGAN, M. HEINER, AND C. TOBALSKE. 2002. Current distribution of sagebrush and associated vegetation in the western United States (excluding NM and AZ). USGS Forest and Rangeland Ecosystems Science Center, Boise, ID. <http://sagemap.wr.usgs.gov/> (4 June 2009).

CONNELLY, J. W., AND C. E. BRAUN. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. Wildlife Biology 3:229–234.

CONNELLY, J. W., S. T. KNICK, M. A. SCHROEDER, AND S. J. STIVER. 2004. Range-wide conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, WY.

CONNELLY, J. W., M. A. SCHROEDER, A. R. SANDS, AND C. E. BRAUN. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

CRAWFORD, J. A., R. A. OLSON, N. E. WEST, J. C. MOSLEY, M. A. SCHROEDER, T. D. WHITSON, R. F. MILLER, M. A. GREGG, AND C. S. BOYD. 2004. Synthesis paper: ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2–19.

DOHERTY, K. E., D. E. NAUGLE, B. L. WALKER, AND J. M. GRAHAM. 2008. Greater Sage-Grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187–195.

EFRON, B. 1975. The efficiency of logistic regression compared to normal discriminant analysis. Journal of the American Statistical Association 70:892–898.

EVERAERT, J., AND D. BAUWENS. 2007. A possible effect of electromagnetic radiation from mobile phone base stations on the number of breeding house sparrows (*Passer domesticus*). Electromagnetic Biology and Medicine 26:63–72.

FERNIE, K. J., AND S. J. REYNOLDS. 2005. The effects of electromagnetic fields from power lines on avian reproductive biology and physiology: a review. Journal of Toxicology and Environmental Health, Part B 8:127–140.

GELBARD, J. L., AND J. BELNAP. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology 17:420-432.

GUSTAFSON, E. J., AND G. R. PARKER. 1994. Using an index of habitat patch proximity for landscape design. Landscape and Urban Planning 29:117–130.

HAIR, J. F., JR., R. E. ANDERSON, R. L. TATHAM, AND W. C. BLACK. 1992. Multivariate analysis with readings. Third edition, Macmillian Publishing Company, New York, NY.

HANN, W. J., J. L. JONES, M. G. KARL, P. F. HESSBURG, R. E. KEANE, D. G. LONG, J. P. MENAKIS, C. H. MCNICOLL, S. G. LEONARD, R. A. GRAVENMIER, AND B. G. SMITH. 1997. Landscape dynamics of the basin. Pp. 334–1056 *in* T. M. Quigley, and S. J. Arbelbide (technical editors). An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins. USDA Forest Service General Technical Report PNW-GTR-405, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

HEMSTROM, M. A., M. J. WISDOM, W. J. HANN, M. M. ROWLAND, B. C. WALES, AND R. A. GRAVENMIER. 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the interior Columbia Basin, U.S.A. Conservation Biology 16:1243–1255.

HOLLORAN, M. J. 2005. Greater Sage-Grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Ph.D. dissertation, University of Wyoming, Laramie, WY.

JOHNSON, D. H. 2002. The importance of replication in wildlife research. Journal of Wildlife Management 66:919–932.

KIESECKER, J. M., H. COPELAND, A. POCEWICZ, N. NIBBELINK, B. MCKENNEY, J. DAHLKE, M. HOLLORAN, AND D. STROUD. 2009. A framework for implementing biodiversity offsets: selecting sites and determining scale. BioScience 59:77–84.

KNICK, S. T., D. S. DOBKIN, J. T. ROTENBERRY, M. A. SCHROEDER, W. M. VANDER HAEGEN, AND C. VAN RIPER III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611–634.

KÜCHLER, A. W. 1964. Manual to accompany the map, potential natural vegetation of the conterminous United States. Special Publication number 36, American Geographic Society, New York, NY.

KÜCHLER, A. W. 1970. Potential natural vegetation. Pp. 89–92 *in* The national atlas of the United States of America, United States Department of the Interior, Geological Survey, U.S. Government Printing Office, Washington, DC.

LALIBERTE, A. S., AND W. J. RIPPLE. 2004. Range contractions of North American carnivores and ungulates. BioScience 54:123–138.

LOMOLINO, M. V., AND R. CHANNELL. 1995. Splendid isolation: patterns of geographic range collapse in endangered mammals. Journal of Mammalogy 76:335–347.

LOMOLINO, M. V., AND R. CHANNELL. 2000. Dynamic biogeography and conservation of endangered species. Nature 403:84–86.

LUPIS, S. G., T. A. MESSMER, AND T. BLACK. 2006. Gunnison Sage-Grouse use of Conservation Reserve Program fields in Utah and response to emergency grazing: a preliminary evaluation. Wildlife Society Bulletin 34:957–962.

LYON, A. G., AND S. H. ANDERSON. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486–491.

MCARTHUR, E. D., AND J. E. OTT. 1996. Potential natural vegetation in the 17 conterminous western United States. Pp. 16–28 *in* J. R. Barrow, E. D. McArthur, R. E. Sosebee, and R. J. Tausch (compilers). Proceedings: shrubland ecosystem dynamics in a changing environment. USDA Forest Service General Technical Report INT-GTR-338, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

MCGARIGAL, K., S. A. CUSHMAN, M. C. NEEL, AND E. ENE. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst, MA. <http://www.umass.edu/landeco/research/fragstats/fragstats.html> (4 June 2009).

MCIVER, J., AND L. STARR. 2001. Restoration of degraded lands in the interior Columbia River basin. Forest Ecology and Management 153:15–28.

MEINKE, C. W., S. T. KNICK, AND D. A. PYKE. 2008. A spatial model to prioritize sagebrush landscapes in the Intermountain West (U.S.A.) for restoration. Restoration Ecology <http://www3.interscience.wiley.com/cgi-bin/fulltext/120124299/PDFSTART> (15 June 2009)

MILLER, R. F., J. D. BATES, T. J. SVEJCAR, F. B. PIERSON, AND L. E. EDDLEMAN. 2007. Western juniper field guide: asking the right questions to select appropriate management actions. US Geological Survey Circular 1321, Washington, DC.

MILLS, L. S. 2007. Conservation of wildlife populations: demography, genetics, and management. Blackwell Publishing, Malden, MA.

MORRIS, W. F., AND D. F. DOAK. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Inc., Sunderland, MA.

NAUGLE, D. E., C. L. ALDRIDGE, B. L. WALKER, K. E. DOHERTY, M. R. MATCHETT, J. MCINTOSH, T. E. CORNISH, AND M. S. BOYCE. 2005. West Nile virus and sage-grouse: what more have we learned? Wildlife Society Bulletin 33:616–623.

NIELSON, J. L., J. M. SCOTT, AND J. L. AYCRIGG. 2001. Endangered species and peripheral populations: cause for conservation. Endangered Species Update 18:194–197.

OYLER-MCCANCE, S. J., K. P. BURNHAM, AND C. E. BRAUN. 2001. Influence of changes in sagebrush on Gunnison Sage Grouse in southwestern Colorado. Southwestern Naturalist 46:323–331.

OYLER-MCCANCE, S. J., J. ST. JOHN, S. E. TAYLOR, A. D. APA, AND T. W. QUINN. 2005. Population genetics of Gunnison Sage-Grouse: implications for management. Journal of Wildlife Management 69:630–637.

PETERSON, E. B. 2005. Estimating cover of an invasive grass (Bromus tectorum) using tobit regression and phenology derived from two dates of Landsat ETM+ data. International Journal of Remote Sensing 26:2491–2507.

PURVIS, A., J. L. GITTLEMAN, G. COWLISHAW, AND G. M. MACE. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society of London B 267:1947–1952.

RAPHAEL, M. G., M. J. WISDOM,, M. M. ROWLAND, R. S. HOLTHAUSEN, B. C. WALES, B. M. MARCOT, AND T. D. RICH. 2001. Status and trends of habitats of terrestrial vertebrates in relation to land management in the Interior Columbia River Basin. Forest Ecology and Management 153:63–88.

ROWLAND, M. M. 2004. Effects of management practices on grassland birds: Greater Sage-Grouse. US Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND.

ROWLAND, M. M., L. H. SURING, M. J. WISDOM, C. W. MEINKE, AND L. SCHUECK. 2005. Habitats for vertebrate species of conservation concern. Pp. 163–204 *in* M. J. Wisdom, M. M. Rowland, and L. H. Suring (editors). Habitat threats in the sagebrush ecosystem: methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, KS.

SAS, INC. 1990. SAS/STAT User's Guide, Version 6 fourth edition. SAS Institute, Inc., Cary, NC.

SCHROEDER, M. A., J. R. YOUNG, AND C. E. BRAUN. 1999. Sage grouse (*Centrocercus urophasianus*). Number 425 in A. Poole, and F. Gill (editors). The birds of North America. The Birds of North America, Inc., Philadelphia, PA.

SCHROEDER, M. A., C. L. ALDRIDGE, A. D. APA, J. R. BOHNE, C. E. BRAUN, S. D. BUNNELL, J. W. CONNELLY, P. A. DEIBERT, S. C. GARDNER, M. A. HILLIARD, G. D. KOBRIGER, S. M. MCADAM, C. W. MCCARTHY, J. J. MCCARTHY, D. L. MITCHELL, E.V. RICKERSON, AND S. J. STIVER. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

STIVER, S. J., A. D. APA, J. R. BOHNE, S. D. BUNNELL, P. A. DEIBERT, S. C. GARDNER, M. A. HILLIARD, C. W. MCCARTHY, AND M. A. SCHROEDER. 2006. Greater Sage-Grouse comprehensive conservation strategy. Western Association of Fish and Wildlife Agencies. Cheyenne, WY. <http://www.wafwa.org/pdf/GreaterSage-grouseConservationStrategy2006.pdf> (4 June 2009).

SURING, L. H., M. J. WISDOM, R. J. TAUSCH, R. F. MILLER, M. M. ROWLAND, L. SCHUECK, AND C. W. MEINKE. 2005. Modeling threats to sagebrush and other shrubland communities. Pp. 114–149 *in* M. J. Wisdom, M. M. Rowland, and L. H. Suring (editors). Habitat threats in

the sagebrush ecosystem: methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, KS.

UNITED STATES CENSUS BUREAU. 2001. U.S. Census 2000 block data. US Census Bureau Systems Support Division <http://www.census.gov/main/www/cen2000.html> (4 June 2009).

VANDER HAEGEN, W. M. 2007. Fragmentation by agriculture influences reproductive success of birds in a shrubsteppe landscape. Ecological Applications 17:934–947.

VANDER HAEGEN, W. M., F. C. DOBLER, AND D. J. PIERCE. 2000. Shrubsteppe bird response to habitat and landscape variables in eastern Washington, U.S.A. Conservation Biology 14:1145–1160.

VUCETICH, J. A., AND T. A. WAITE. 2003. Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape conservation genetics. Conservation Genetics 4:639–645.

WALKER, B. L. 2008. Greater Sage-Grouse response to coal-bed natural gas development and West Nile virus in the Powder River Basin, Montana and Wyoming, USA. Ph.D. dissertation, University of Montana, Missoula, MT.

WALKER, B. L., D. E. NAUGLE, AND K. E. DOUGHERTY. 2007. Greater Sage-Grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

WISDOM, M. J., R. S. HOLTHAUSEN, B. C. WALES, C. D. HARGIS, V. A. SAAB, D. C. LEE, W. J. HANN, T. D. RICH, M. M. ROWLAND, W. J. MURPHY, AND M. R. EAMES. 2000. Source habitats for terrestrial vertebrates of focus in the interior Columbia basin: broad-scale trends and management implications. USDA Forest Service General Technical Report

PNW-GTR-485, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

WISDOM, M. J., M. M. ROWLAND, B. C. WALES, M. A. HEMSTROM, W. J. HANN, M. G. RAPHAEL, R. S. HOLTHAUSEN, R. A. GRAVENMIER, AND T. D. RICH. 2002a. Modeled effects of sagebrush-steppe restoration on Greater Sage-Grouse in the interior Columbia Basin, U.S.A. Conservation Biology 16:1223–1231.

WISDOM, M. J., B. C. WALES, M. M. ROWLAND, M. G. RAPHAEL, R. S. HOLTHAUSEN, T. D. RICH, AND V. A. SAAB. 2002b. Performance of Greater Sage-Grouse models for conservation assessment in the interior Columbia Basin, U.S.A. Conservation Biology 16:1232–1242.

WISDOM, M. J., M. M. ROWLAND, AND R. J. TAUSCH. 2005a. Effective management strategies for sage-grouse and sagebrush: a question of triage? Transactions North American Wildlife and Natural Resources Conference 70:206–227.

WISDOM, M. J., M. M. ROWLAND, AND L. K. SURING (EDITORS). 2005b. Habitat threats in the sagebrush ecosystem: methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, KS.

TABLE 1. DESCRIPTIONS OF THE 22 ENVIRONMENTAL VARIABLES USED IN DISCRIMINANT FUNCTION ANALYSIS. ESTIMATES OF THE VARIABLES WERE MADE FOR THE TIME PERIOD 2000–2004, AND THUS ARE COMPATIBLE WITH THE TIME PERIOD IN WHICH SAGE-GROUSE RANGES WERE ESTIMATED (SCHROEDER ET AL. 2004). ESTIMATES OF THE 22 VARIABLES WERE BASED ON CONDITIONS WITHIN THE CIRCLES OF 18-KM RADIUS THAT ENCOMPASSED EACH OF THE 375 HISTORICAL LOCATIONS OF SAGE-GROUSE. RASTER-BASED VARIABLES WERE DERIVED OR ESTIMATED USING A 90 X 90-M CELL SIZE UNLESS STATED OTHERWISE.

| Variable | Type | Definition and estimation method |
|---|---|---|
| Sagebrush area (percent) | Raster | Percentage of 18-km radius composed of sagebrush cover types[a]. |
| Patch size | Raster | Mean size (hectares) of sagebrush patches, where a patch is defined as the cells of sagebrush cover types that are contiguous with one another (touching on at least one side)[b]. |
| Patch density | Raster | Number of sagebrush patches divided by the area[b]. |
| Edge density 1 | Raster | Number of edges between sagebrush patches and non-sagebrush cover types, weighted by sagebrush area. Weighting by sagebrush area differentiates between a low number of edges when little sagebrush is present versus a low number of edges when sagebrush occupies most or all of the area. Resulting values were transformed as 1/n, such that high edge density indicates a high amount of edge, and low edge density indicates low edge[b]. |
| Edge density 2 | Raster | Total length (meters) of all edges between sagebrush patches and non-sagebrush cover types divided by area[b]. |

| | | |
|---|---|---|
| Nearest neighbor | Raster | The mean distance (meters) between sagebrush patches, where distance between each patch is measured as the shortest distance (edge to edge) to another patch within the circle[b,c]. |
| Proximity index | Raster | The mean proximity (unitless scale) among sagebrush patches. Mean proximity is calculated as the area of each sagebrush patch divided by the squared mean distance of all distances between the patch and all other patches in the circle, with these values summed for all patches in the circle and divided by the total number of patches[b]. |
| Core area | Raster | The mean size (hectares) of core areas of sagebrush. A core area is defined as a sagebrush patch plus all additional cells of sagebrush within 100 m of the edge of each patch (i.e., all additional sagebrush within the distance of two cells from the edge of each sagebrush patch). |
| Distance to occupied-extirpated boundary | Vector | Distance (meters) from the sage-grouse historical location (the center of each circle) to the boundary between occupied and extirpated range[b]. |
| Precipitation | Raster | Mean annual precipitation (centemeters) within each 18-km circle for the period 1961–2004. Precipitation estimates were derived from parameter-elevation regression on independent slopes model (PRISM), which uses point data and a digital elevation model (DEM) to generate grid-based estimates of annual, monthly, and |

| | | |
|---|---|---|
| | | event-based climatic parameters[d]. |
| Elevation | Raster | Mean elevation (meters) among all cells, using a 1:24,000-scale digital elevation model downloaded from the United States Geological Survey National Elevation Dataset[d]. |
| Soil water capacity | Raster | The total amount of water available in all soil profiles (centimeter of water/centimeter of soil) for each cell, averaged over all cells. Estimates were derived from the USDA Natural Resources Conservation Service[d]. |
| Soil rock depth | Raster | The mean depth (centimeters) to bedrock, or soil depth, as averaged over all cells. Estimates were derived from the USDA Natural Resources Conservation Service[d]. |
| Soil salinity | Raster | The mean salinity (mmhos/ centimeter) of soil, as averaged over all cells. Estimates were derived from the USDA Natural Resources Conservation Service d. |
| Agriculture area | Raster | Percentage of cells of agricultural cover types[d]. |
| Human density | Raster | Number of humans/ha in 2000[e]. |
| Distance to roads | Vector | Distance (meters) to the nearest road. All roads identified in the 2000 United States Census Bureau 1:100,000 scale line files[d]. |
| Road density | Vector | Linear km of road per unit area. All roads identified in the 2000 United States Census Bureau 1:100,000 scale line files[d]. |
| Distance to highways | Vector | Distance (meters) to the nearest major highway[f]. |
| Distance to | Vector | Distance (meter) to the nearest electrical transmission lined. |

| | | |
|---|---|---|
| transmission lines | | |
| Distance to cellular towers | Vector | Distance (meter) to the nearest cellular tower, based on locations of towers registered with the Federal Communications Commission. |
| Land ownership | Raster | Dominant land ownership, either public or private, based on state and federal sources of ownership data[d]. These data were summarized as the percentage of circles dominated by public land. |

[a] Sagebrush cover types were defined and estimated by Comer et al. (2002) and further described by Wisdom et al. (2005b).

[b] Landscape statistics estimated using FRAGSTATS (McGarigal et al. 2002).

[c] Gustafson and Parker (1994).

[d] Data available at http://sagemap.wr.usgs.gov.

[e] US census block data (United States Census Bureau 2001).

[f] Major highways documented in the United States National Atlas (http://edcftp.cr.usgs.gov).

(Comer et al. 2002,Wisdom et al. 2005b).

TABLE 2. CLASSIFICATION ACCURACY AND RESULTING PERFORMANCE OF BIOTIC, ABIOTIC, AND ANTHROPOGENIC VARIABLES CONTAINED IN DISCRIMINANT FUNCTION MODELS THAT WERE USED TO DISCRIMINATE BETWEEN HISTORICAL LOCATIONS OF SAGE-GROUSE IN OCCUPIED VERSUS EXTIRPATED RANGES UNDER CROSS-VALIDATION. SEE METHODS FOR DETAILS REGARDING CROSS-VALIDATION.

| Discriminatory variables | Correctly classified to occupied range (percent)[a] | Correctly classified to extirpated range (percent)[a] | Total percent correctly classified[b] | Evenness of correctly classified[c] | Performance value (rank)[d] |
|---|---|---|---|---|---|
| Sagebrush area (percent)[e, f] | 76 | 65 | 141 | 11 | 130 (2) |
| Patch density | 100 | 0 | 100 | 100 | 0 |
| Patch size[f] | 41 | 96 | 137 | 55 | 82 (8) |
| Edge density 1 | 98 | 6 | 104 | 92 | 12 (17) |
| Edge density 2[e] | 96 | 4 | 100 | 92 | 8 (18) |
| Proximity index[f] | 35 | 86 | 121 | 51 | 70 (12) |
| Nearest neighbor | 99 | 0 | 99 | 99 | 0 |
| Mean core area[f] | 39 | 95 | 134 | 56 | 78 (11) |

| | | | | | |
|---|---|---|---|---|---|
| Distance to occupied-extirpated boundary[e, f] | 92 | 24 | 116 | 68 | 48 (16) |
| All biotic variables | 52 | 92 | 144 | 40 | 104 (6) |
| | | | | | |
| Precipitation | 98 | 0 | 98 | 98 | 0 |
| Elevation[e, f] | 85 | 50 | 135 | 35 | 100 (8) |
| Soil water capacity[f] | 90 | 29 | 119 | 61 | 58 (13) |
| Soil rock depth | 100 | 0 | 100 | 100 | 0 |
| Soil salinity[e, f] | 100 | 0 | 100 | 100 | 0 |
| All abiotic variables | 89 | 47 | 136 | 42 | 94 (9) |
| All biotic and abiotic variables | 54 | 92 | 146 | 38 | 108 (5) |
| | | | | | |
| Agriculture area (%)[f] | 92 | 40 | 132 | 52 | 80 (10) |
| Distance to roads | 100 | 0 | 100 | 0 | 0 |
| Human density[f] | 99 | 25 | 124 | 74 | 50 (15) |

| | | | | | |
|---|---|---|---|---|---|
| Road density[e, f] | 93 | 28 | 121 | 65 | 56 (14) |
| Distance to highways[f] | 100 | 0 | 100 | 0 | 0 |
| Distance to transmission lines[e, f] | 64 | 63 | 127 | 1 | 126 (4) |
| Distance to cellular towers[e, f] | 81 | 51 | 132 | 30 | 102 (7) |
| Land ownership[f] | 64 | 74 | 138 | 10 | 128 (3) |
| All anthropogenic variables | 96 | 42 | 138 | 54 | 84 (10) |
| All anthropogenic and abiotic variables | 94 | 52 | 146 | 42 | 104 (6) |
| All anthropogenic and biotic variables | 75 | 81 | 156 | 6 | 150 (1) |

[a] Percentage of historical locations in currently occupied or extirpated range correctly classified to that range based on the associated discriminatory variable or variables using cross-validation.

[b] Sum of correct classification percentages for occupied and extirpated ranges based on the associated discriminatory variable or variables.

[c] Absolute difference between percentages of locations correctly classified to occupied versus extirpated ranges.

[d] Performance value is the evenness subtracted from total percent correctly classified. A value of 200 represents highest performance, which is possible if all locations are correctly classified to occupied (100%) and to extirpated (100%) ranges, for a total percent of 200 and an evenness of 0 (100% minus 100%). Variables are ranked, shown in parentheses, according to their performance values with a rank of 1 representing the best performance considering all discriminant function models listed in Table 2. Each line of the table represents a discriminant function model that was evaluated.

[e] Variables with significant discriminatory value ($P < 0.05$) as estimated by forward stepwise discriminant analysis.

[f] Variables with non-overlapping 95% confidence intervals between mean values in occupied versus extirpated ranges (Figs. 2–4).

TABLE 3. CLASSIFICATION ACCURACY AND PERFORMANCE OF FOUR MODELS USED TO DISCRIMINATE BETWEEN HISTORICAL LOCATIONS OF SAGE-GROUSE IN OCCUPIED VERSUS EXTIRPATED RANGE USING CROSS-VALIDATION. DISCRIMINATORY VARIABLES IN EACH MODEL WERE SELECTED USING DIFFERENT CRITERIA. MODELS 1 AND 2 INCLUDED VARIABLES WITH INDIVIDUAL PERFORMANCE VALUES ≥75 AND ≥100 (TABLE 1). MODEL 3 CONTAINED VARIABLES SELECTED UNDER STEPWISE DISCRIMINANT ANALYSIS. MODEL 4 INCLUDED THE 15 VARIABLES WITH NON-OVERLAPPING 95% CONFIDENCE INTERVALS BETWEEN MEAN VALUES IN OCCUPIED VERSUS EXTIRPATED RANGES (FIGS. 2-4). VARIABLES USED IN ONE OR MORE OF THE MODELS INCLUDED SAGEBRUSH AREA (SB), PATCH SIZE (PS), EDGE DENSITY 2 (ED2), PROXIMITY INDEX (PI), MEAN CORE AREA (MCA), DISTANCE TO OCCUPIED-EXTIRPATED RANGE BOUNDARY (RB), ELEVATION (E), SOIL SALINITY (S), SOIL WATER CAPACITY (SWC), AGRICULTURE AREA (AA), ROAD DENSITY (RD), HUMAN DENSITY (HD), DISTANCE TO HIGHWAYS (DH), DISTANCE TO TRANSMISSION LINES (TL), DISTANCE TO CELLULAR TOWERS (CL), AND LAND OWNERSHIP (LO).

| Discriminatory models | Correctly classified to occupied range (percent) | Correctly classified to extirpated range (percent) | Total percent correctly classified | Evenness of correctly classified | Performance value[a] |
|---|---|---|---|---|---|
| Model 1 | | | | | |
| SB, PS, MCA, E, AA, DL, CT, LO | 54 | 93 | 147 | 39 | 106 |

| | | | | | |
|---|---|---|---|---|---|
| Model 2 | | | | | |
| SB, E, TL, CT, LO | 85 | 83 | 168 | 2 | 166 |
| Model 3 | | | | | |
| SB, ED, RB, E, S, RD, TL, CT | 90 | 70 | 160 | 20 | 140 |
| Model 4 | | | | | |
| SB, PS, PI, MCA, RB, E, SWC, S, AA, HD, RD, DH, TL, CL, LO | 77 | 88 | 165 | 11 | 154 |

[a] Evenness subtracted from total percent correctly classified.

TABLE 4. PERCENT AREA OF OCCUPIED RANGE BY CATEGORIES OF THE PROBABILITY OF SIMILARITY WITH EXTIRPATED RANGE, SUMMARIZED BY SAGE-GROUSE MANAGEMENT ZONE. PROBABILITIES OF SIMILARITY ARE SUMMARIZED IN 6 CATEGORIES: (1) 0.0–0.10; (2) >0.10–0.25; (3) >0.25–0.50; (4) >0.50–0.75; (5) >0.75–<0.90; AND (6) 0.90–1.0. PROBABILITIES WERE ESTIMATED FOR EACH OF 2,661 100,000-HA BLOCKS THAT ENCOMPASS THE OCCUPIED RANGE OF SAGE-GROUSE.

| | Categories of similarity to extirpated range | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 3 | | 4 | | 5 | | 6 | | |
| | 0.0–0.10 | | >0.10–0.25 | | >0.25–0.50 | | >0.50–0.75 | | >0.75–<0.90 | | 0.90–1.0 | | |
| Management zone | hectares | % area | hectares | % area | hectares | % area | hectares | % area | hectares | % area | hectares | % area | Total area |
| Great Plains | 9,783,456 | 49.9 | 876,405 | 4.5 | 962,934 | 4.7 | 778,925 | 4.0 | 1,068,834 | 5.4 | 6,176,855 | 31.5 | 19,611,209 |
| Wyoming Basins | 11,176,049 | 76.4 | 1,088,868 | 7.4 | 781,287 | 5.3 | 359,034 | 2.5 | 502,765 | 3.4 | 715,584 | 4.9 | 14,623,587 |
| Southern Great Basin | 8,426,483 | 82.2 | 756,360 | 7.4 | 336,628 | 3.3 | 454,331 | 4.4 | 108,158 | 1.1 | 175,149 | 1.7 | 10,257,109 |
| Snake River Plain | 11,531,252 | 79.7 | 451,982 | 3.1 | 555,622 | 3.8 | 434,949 | 3.0 | 443,068 | 3.1 | 1,044,541 | 7.2 | 14,461,414 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Northern Great Basin | 5,978,359 | 86.4 | 211,164 | 3.1 | 203,219 | 2.9 | 102,251 | 1.5 | 134,475 | 1.9 | 286,249 | 4.1 | 6,915,717 |
| Columbia Basin | 69,720 | 14.7 | 0 | 0.0 | 0 | 0.0 | 97,724 | 20.6 | 84,004 | 17.7 | 222,305 | 46.9 | 473,753 |
| Colorado Plateau | 507,907 | 56.2 | 174,546 | 19.3 | 36,991 | 4.1 | 94,962 | 10.5 | 52,531 | 5.8 | 36,666 | 4.1 | 903,603 |

FIGURE CAPTIONS

FIGURE 1. Distribution of 375 historical locations of sage-grouse (Schroeder et al. 2004). Locations are overlaid on occupied (grey) and extirpated (yellow) ranges of sage-grouse. Locations of different colors represent the classification accuracy of discriminant function analysis (model 2, Table 3). Red locations are those present in occupied range but incorrectly classified to extirpated range. Pink locations are those present in extirpated range but incorrectly classified to occupied range. Green locations were correctly classified to occupied and extirpated ranges.

FIGURE 2. Mean values and 95% confidence intervals for nine biotic variables associated with 239 historical locations in occupied range and 136 historical locations in extirpated range for sage-grouse.

FIGURE 3. Mean values and 95% confidence intervals for five abiotic variables associated with 239 historical locations in occupied range and 136 historical locations in extirpated range for sage-grouse.

FIGURE 4. Mean values and 95% confidence intervals for eight anthropogenic variables associated with 239 historical locations in occupied range and 136 historical locations in extirpated range for sage-grouse.

FIGURE 5. Probabilities of environmental similarity of areas currently occupied by sage-grouse with areas where extirpation has occurred, based on estimates from model 2 discriminant function analysis. Probabilities range from 0.0–1.0 and are mapped as a continuous variable. Areas in red show high similarity with extirpated range. areas in green show low similarity.

Figure 1.

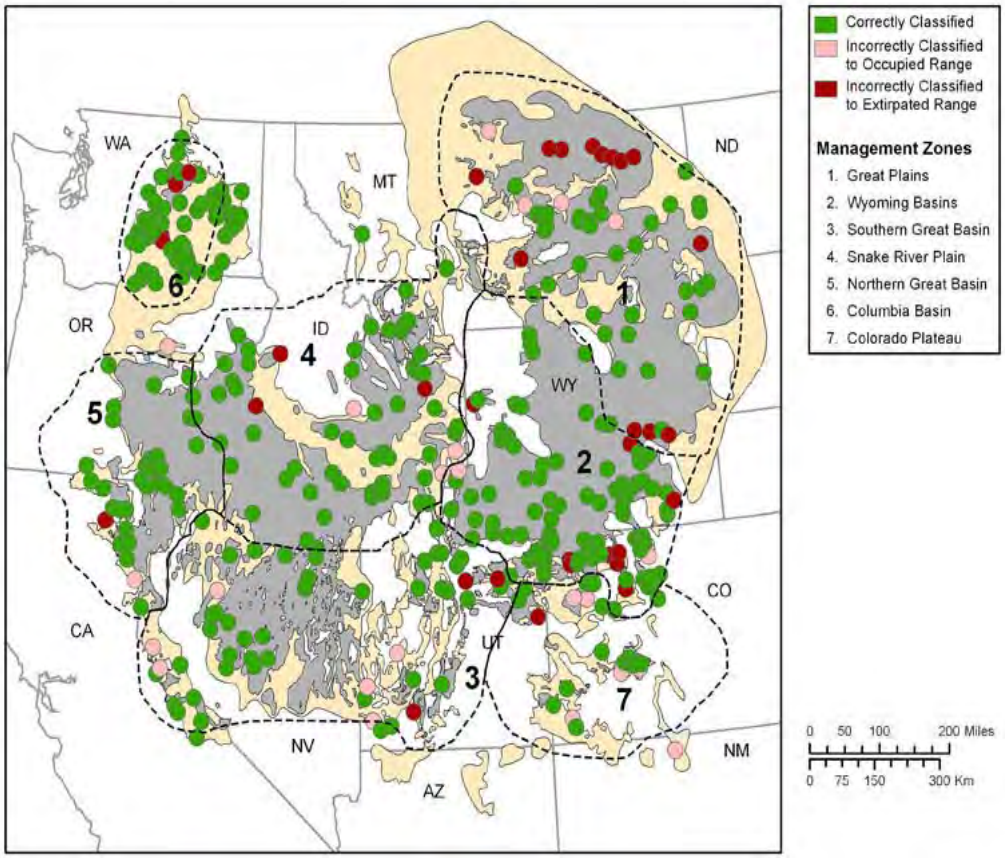

Correctly Classified
Incorrectly Classified to Occupied Range
Incorrectly Classified to Extirpated Range
Management Zones
1. Great Plains
2. Wyoming Basins
3. Southern Great Basin
4. Snake River Plain
5. Northern Great Basin
6. Columbia Basin
7. Colorado Plateau
WA
OR
CA
NV
ID
MT
WY
UT
AZ
CO
NM
ND
1
2
3
4
5
6
7
0 50 100 200 Miles
0 75 150 300 Km

Figure 2.

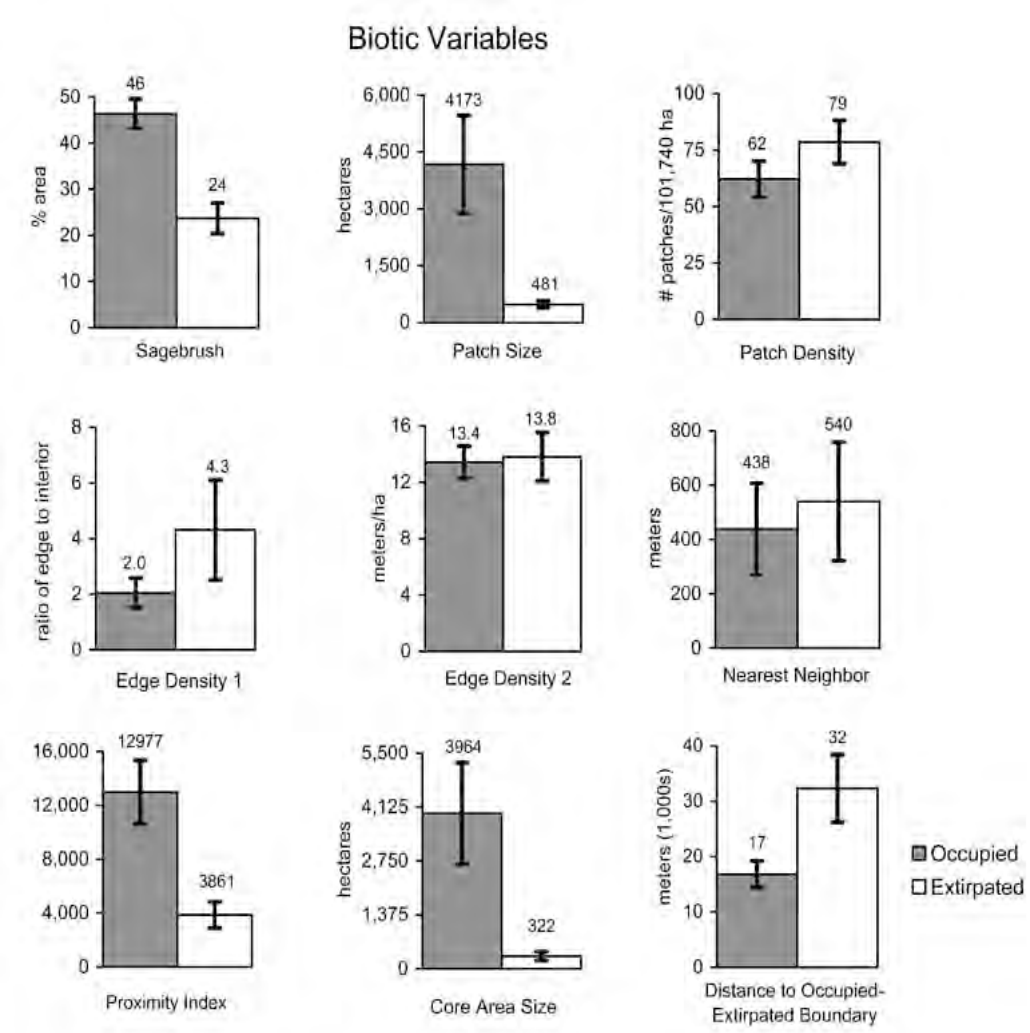

Biotic Variables
% area
46
24
Sagebrush
hectares
4173
481
Patch Size
# patches/101,740 ha
62
79
Patch Density
ratio of edge to interior
2.0
4.3
Edge Density 1
meters/ha
13.4
13.8
Edge Density 2
meters
438
540
Nearest Neighbor
12977
3861
Proximity Index
hectares
3964
322
Core Area Size
meters (1,000s)
17
32
Distance to Occupied-Extirpated Boundary
Occupied
Extirpated

Figure 3.

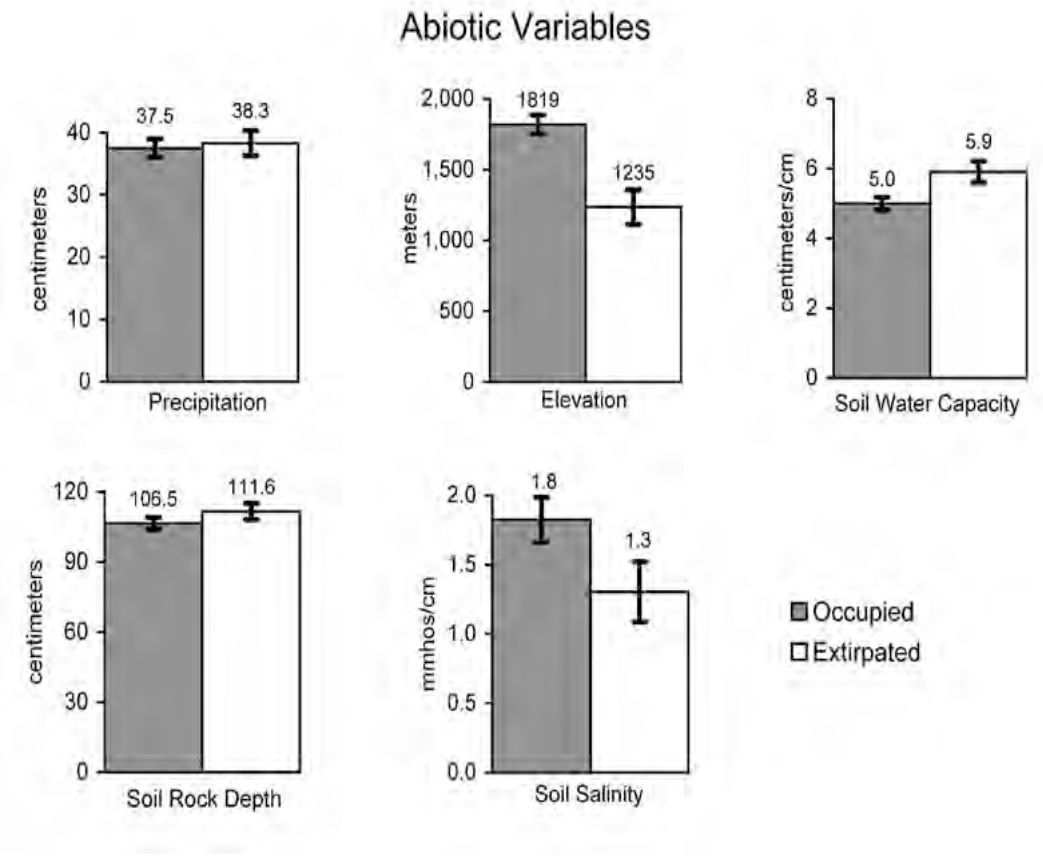

Abiotic Variables
centimeters
37.5
38.3
Precipitation
meters
1819
1235
Elevation
centimeters/cm
5.0
5.9
Soil Water Capacity
centimeters
106.5
111.6
Soil Rock Depth
mmhos/cm
1.8
1.3
Soil Salinity
Occupied
Extirpated

Figure 4.

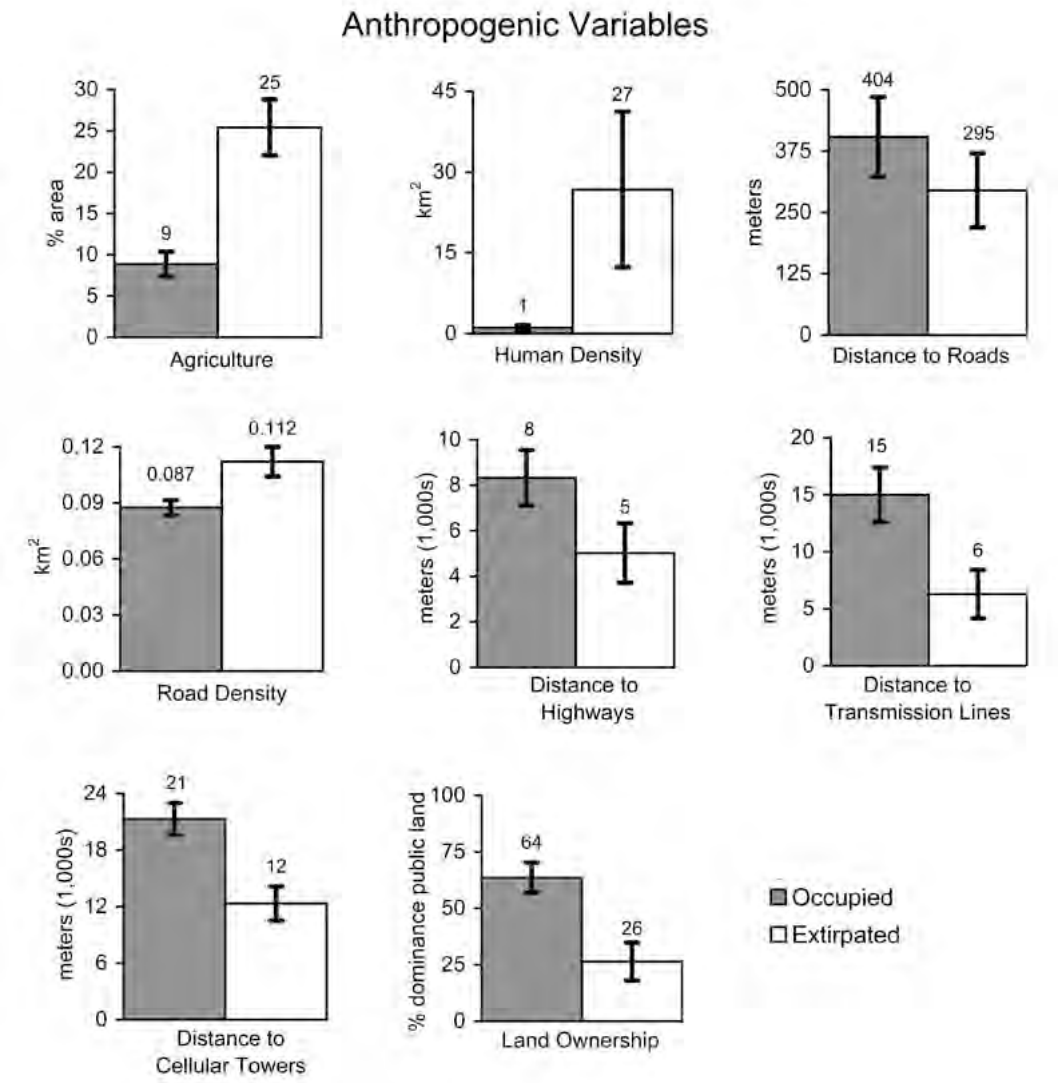
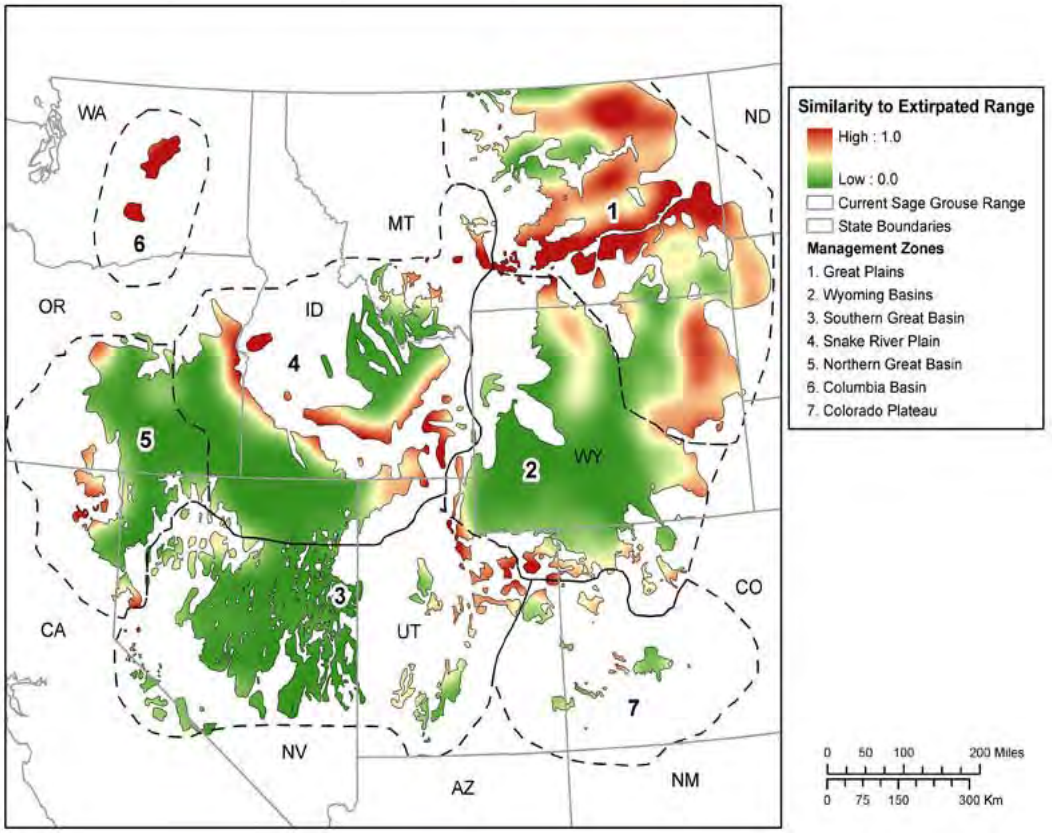

Anthropogenic Variables
% area
9
25
Agriculture
km2
1
27
Human Density
meters
404
295
Distance to Roads
km2
0.087
0.112
Road Density
meters (1,000s)
8
5
Distance to Highways
meters (1,000s)
15
6
Distance to Transmission Lines
meters (1,000s)
21
12
Distance to Cellular Towers
% dominance public land
64
26
Land Ownership
Occupied
Extirpated

Figure 5.


WA
ND
MT
OR
ID
WY
CO
CA
UT
NV
AZ
NM
1
2
3
4
5
6
7
Similarity to Extirpated Range
High : 1.0
Low : 0.0
Current Sage Grouse Range
State Boundaries
Management Zones
1. Great Plains
2. Wyoming Basins
3. Southern Great Basin
4. Snake River Plain
5. Northern Great Basin
6. Columbia Basin
7. Colorado Plateau
0 50 100 200 Miles
0 75 150 300 Km

University of Montana
ScholarWorks at University of Montana

Graduate Student Theses, Dissertations, & Professional Papers

Graduate School

2008

# Greater Sage-Grouse Response to Coal-Bed Natural Gas Development and West Nile Virus in the Powder River Basin, Montana and Wyoming, USA

Brett Lincoln Walker
*The University of Montana*

Follow this and additional works at: https://scholarworks.umt.edu/etd
Let us know how access to this document benefits you.

Recommended Citation
Walker, Brett Lincoln, "Greater Sage-Grouse Response to Coal-Bed Natural Gas Development and West Nile Virus in the Powder River Basin, Montana and Wyoming, USA" (2008). *Graduate Student Theses, Dissertations, & Professional Papers*. 499.
https://scholarworks.umt.edu/etd/499

This Dissertation is brought to you for free and open access by the Graduate School at ScholarWorks at University of Montana. It has been accepted for inclusion in Graduate Student Theses, Dissertations, & Professional Papers by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact scholarworks@mso.umt.edu.

# GREATER SAGE-GROUSE RESPONSE TO COAL-BED NATURAL GAS DEVELOPMENT AND WEST NILE VIRUS IN THE POWDER RIVER BASIN, MONTANA AND WYOMING, USA.

By

Brett Lincoln Walker

B.A., University of California at Berkeley, 1990
M.S., University of Montana, 2000

Dissertation

presented in partial fulfillment of the requirements
for the degree of

Doctor of Philosophy
in Wildlife Biology

The University of Montana
Missoula, MT

Spring 2008

Approved by:

Dr. David A. Strobel, Dean
Graduate School

Dr. David E. Naugle, Chair
Wildlife Biology Program

Dr. Thomas E. Martin
Wildlife Biology Program

Dr. Erick P. Greene
Division of Biological Sciences

Dr. Paul Krausman
Wildlife Biology Program

Dr. David A. Patterson
Dept. of Mathematical Sciences

© COPYRIGHT

by

Brett Lincoln Walker

2008

All Rights Reserved

Walker, Brett, Ph.D., Spring 2008 Fish and Wildlife Biology

Greater Sage-grouse Response to Coal-bed Natural Gas Development and West Nile Virus in the Powder River Basin, Montana and Wyoming, USA.

Chairperson: Dr. David E. Naugle

Understanding how population dynamics respond to landscape-scale disturbance and disease are crucial for effective wildlife management and conservation. Two new potential stressors on greater sage-grouse (*Centrocercus urophasianus*) populations in the Powder River Basin of Montana and Wyoming are coal-bed natural gas (CBNG) development and West Nile virus (WNv). I first examined how CBNG development, habitat, and other landscape features influenced trends in the abundance of displaying males and the status of sage-grouse leks. Second, I used rates of WNv-induced mortality and seroprevalence from radio-marked birds to estimate rates of WNv infection. Third, I studied the influence of female characteristics, season, and environmental variables on nest, brood, and female survival. I then used population models to estimate potential impacts of WNv on population growth. From 2001-2005, numbers of males on leks in CBNG fields declined more rapidly than leks outside CBNG. Of leks active in 1997 or later, only 38% within CBNG remained active by 2004-2005, compared to 84% of leks outside CBNG. By 2005, leks in CBNG had 46% fewer males per active lek than leks outside CBNG. Persistence of 110 leks was positively influenced by proportion sagebrush habitat within 6.4 km of the lek and negatively affected by CBNG development at multiple scales. Prohibiting CBNG development within 0.4 km of sage-grouse leks is inadequate to ensure lek persistence. From 2003-2005, minimum WNv-related mortality rates from 1 July-15 September ranged from 2.4-13.3% and maximum possible rates ranged from 8.2-28.9%. In spring 2005 and 2006, 10.3% and 1.8% respectively, of newly-captured females tested seropositive for neutralizing antibodies to WNv. Annual WNv infection rates were lower in habitats without CBNG development. Summer mortality from WNv occurred every year, decreased annual female survival rates by 0-27% per year, and reduced estimates of population growth by 7-10% per year. Changes in epizootiology of WNv and in distribution and management of surface water from CBNG development will play an important role in long-term impacts of WNv on greater sage-grouse populations in the Powder River Basin. Management should focus on eliminating man-made water sources that support breeding mosquitos known to vector the virus.

# DEDICATION

I dedicate this work to my parents, Ann Lincoln, Dan Shadoan, John Walker, and Linda Walker and to my wonderful family, near and far, both geographically and genetically, who offered support, unconditional love, patience, and understanding as I disappeared for years to study birds. Being surrounded by incredible people made me cherish my experience in Montana, especially Ty and Kristina Smucker, Dalit Ucitel and Greg Guscio, Alex Trillo, Jenny and Brian Woolf, Kathy Griffin, Cindy and Jeff Gilbert, Erick and Ann Greene, and Rob Domenech. Thank you for your friendship and many fine adventures. A dear friend, Jeanne Johnson, applied glue at regular intervals and taught me the skills to navigate in rough seas.

# ACKNOWLEDGMENTS

This research was supported by the Bureau of Land Management (BLM), Department of Energy, Montana Department of Fish, Wildlife, and Parks, National Fish and Wildlife Foundation, Wyoming Game and Fish Department, Wolf Creek Charitable Foundation, Anheuser-Busch Budweiser Conservation Scholarship, Petroleum Association of Wyoming, Western Gas Resources, Inc., the Northeast Wyoming Local Sage-grouse Working Group, Wyoming State Veterinary Laboratory, Montana Cooperative Wildlife Research Unit, and a Bertha Morton Fellowship from the University of Montana. I extend special thanks to the landowners and ranch managers in the Powder River Basin that opened their doors, generously allowed access to private lands, and assisted my field crew on many occasions: Charlie and Kathy Larsen, Jim Hamilton, Shawn and Kandra Ankney, Brian McCarty, John Heyneman, Tony and Vickie Line, Fra Porter, Dustin Shaw, Mary Jo Reavis, Shawn Gilbert, Bert and Susan Dow, Jeff and Tami Simmons, Micki Parker, Mark Moreland, David Kane, Hayden and Nancy Porter, Bruce Porter, Charlene Perry, Fred Trembath, Jim Hallworth, Phil and Kathy Ogle, Al and Dee Visborg, Phil and Denise Wood, Don and Kathy Spellman, Robert and Nancy Sorenson, Steve and Jalene Sorenson, Dale and Marie Smith, Robert Brug, Bob Johnson, Orville Carson, Leslie and Lester Drake, Bob Johnson, Mike Odegard, Consolidated Coal, Padlock Ranch, Decker Coal Co., Spring Creek Coal Co., and Fidelity Exploration and Production.

The Montana Department of Fish, Wildlife, and Parks and the Wyoming Game and Fish Department provided vehicles, logistical support, and lek-count data. Staff and interns at the Miles City, Billings, and Buffalo field offices of the BLM supported every phase of the project. We extend special thanks to Tom Rinkes, Roxanne Falise, Kent Undlin, Bobby Baker, Larry Rau, Tom Bills, Larry Gerard, Dan Thiele, Bert Jellison, John Ensign, and Rick Northrup. Tom Maechtle of Bighorn Environmental Consulting was a valued advisor and friend. Brendan Moynahan was instrumental in getting the project started. Dr. Blair Gustafson generously allowed use of facilities at the Country Hospital for Animals. The hard work, persistence, and quality of my field technicians made the project a success beyond everyone's expectations. I extend sincere thanks to Linette and Andy Sutphin, Pete Ryerson, Chad Wilsey, Erin Fairbank, Justin Streit, Larissa Yocom, Darren Wiens, Jeff Wright, Jesse Hankins, Chris Kirol, Vicki Patrek, Alison Mynsberge, Erik Blomberg, Jace Nelson, Kevin Keith, Greg Wann, Matthew Schnupp, Jon Fredlund, Jon Dinkins, Flavio Sutti, Matt Waterhouse, John Olszowy, and Jennifer Hess.

My advisor, Dr. David E. Naugle, patiently guided and supported every phase of the research, endured long hours of travel, discussion, and writing, and taught me valuable lessons about the role of science in policy, management, and politics. I thank him as a role model, colleague, and friend. I thank Scott Mills and Cynthia Hartway for assistance with population modeling and MATLAB programming, Jay Rotella for instruction and insight into demographic analyses, and Dan Pletscher for sharing wisdom and concern at critical times. I thank Tom Martin, Erick Greene, Dave Patterson, Elizabeth Crone, Doug Emlen, and Paul Krausman for serving on my committee. I offer special thanks to Tom Martin, Erick Greene, Dave Naugle, Scott Mills, and Dan Pletscher for their professional guidance and academic support at The University of Montana.

TABLE OF CONTENTS

Abstract…… iii

Dedication…… iv

Acknowledgements…….. v

Table of Contents……. vi

List of Tables……..……..... ix

List of Figures……..……..... xii

Chapter 1 – Introduction……... 1

Chapter 2 – Greater Sage-grouse Population Response to Coal-bed Natural Gas

Development……... 4

Study Area and Methods…… 9

Results…… 19

Discussion…….. 24

Management Implications…….. 28

Acknowledgements…… 31

Literature Cited……... 32

Figure Legends…… 39

Tables……. 43

Figures…… 48

Chapter 3 – West Nile Virus and Greater Sage-Grouse: Estimating Infection Rate

in a Wild Bird Population……... 55

Materials and Methods……... 58

Results…… 62

Discussion……... 63

References…….. 66

Tables……. 72

Figures…… 74

Figure Legends…… 75

Acknowledgements…… 76

Chapter 4 - Demographics of Greater Sage-Grouse in the Powder River Basin,

2003-2006…….. 77

Study Area……..... 80

Methods – Field Methods……... 81

Methods – Analyses……..... 85

Results…… 96

Discussion……...102

Management Implications.…… 108

Literature Cited……... 110

Tables……. 118

Figure Legends……147

Figures…… 150

Chapter 5 - Impacts of West Nile Virus on Population Growth of Greater

Sage-Grouse…….…..... 161

Methods…….. ……..... 166

Results…… 179

Discussion……... 181

Literature Cited……... 187

Tables……. 196

Figure Legends……197

Figures…… 200

Appendix A – Correlation structure……... 213

Appendix B – Vital rate summary……. 217

## List of Tables

Table 2-1. Status of greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, U.S.A as of 2004-2005, including only leks active in 1997 or later…….. 43

Table 2-2. Univariate model selection summary for different classes of landscape variables influencing greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005…..…….. 44

Table 2-3. Model selection summary for greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005.....…….. 45

Table 2-4. Model-averaged estimates of regression coefficients and standard errors, odds ratios, and lower and upper 95% confidence limits on odds ratios for effects of landscape variables on greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005……..….....…….. 47

Table 3-1. Mortality and West Nile virus (WNv) testing of radio-marked female sage-grouse during the peak WNv transmission period (1 July - 15 September) and seroprevalence the following spring in the Powder River Basin, 2003-2005, including birds from areas with extensive coal-bed natural gas development…..…….. 72

Table 3-2. Mortality and West Nile virus (WNv) testing of radio-marked female sage-grouse during the peak WNv transmission period (1 July - 15 September) and seroprevalence the following spring in the Powder River Basin, 2003-2005, excluding birds from areas with extensive coal-bed natural gas development.....……. 73

Table 4-1. Timing of clutch initiation and clutch completion for adult and yearling female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003…….....……... 118

Table 4-2a. Nest initiation rates ± SE, renesting rates ± SE, and second renesting rates ± SE for adult and yearling female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003. .....…….. 120

Table 4-2b. Renesting rates ± SE (proportion of females that had an unsuccessful first nest and survived detected on a second nest) for adult and yearling female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003, excluding birds that abandoned nests due to investigator disturbance…….....…….. 122

Table 4-3. Clutch size and hatching success for adult and yearling female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003. …….…….....…….. 123

Table 4-4. Apparent nest success and number and fate for nests of adult and yearling female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003….…….....…... 125

Table 4-5. Apparent proximate cause of failure for nests of adult and yearling female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003.…….…….....…….. 127

Table 4-6. Comparison of "quick" estimates of nest success and nest success estimated from maximum-likelihood estimates of daily survival rate based on a *Region*Year*Hen age + Nest attempt* model for adult and yearling female greater sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003. …….....…….. ……128

Table 4-7. Earliest and latest hatching dates, apparent brood survival, number and fate of broods, apparent chick survival, and minimum no. chicks surviving to 35d for adult and yearling female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003……..……... 130

Table 4-8. Suspected cause of death of radio-collared female sage-grouse near Decker, MT from 2003-2007, Buffalo, WY from 2004-2007, and Spotted Horse, WY in 2003-2004……...…….....……... 132

Table 4-9. Sample sizes for nest, brood, and female survival analyses and interval lengths for female survival analyses in 3 regions of the Powder River Basin, 2003-2006..…... 133

Table 4-10. *A priori* models of daily survival rate for greater sage-grouse nests in the Powder River Basin, 2003-2006……...…….....……... 134

Table 4-11. *A priori* models of daily survival rate for greater sage-grouse broods in the Powder River Basin, 2003-2006……...…….....……... 137

Table 4-12. *A priori* models of daily spring-summer female survival rate for greater sage-grouse in the Powder River Basin, spring 2003 - spring 2007….....……... 140

Table 4-13. *A priori* models of daily spring-summer female survival rate for greater sage-grouse in the Powder River Basin, spring 2003 - spring 2007, excluding mortalities confirmed positive for West Nile virus.……...…….....……... 143

Table 4-14. Spring-summer survival estimates ± SE for adult and yearling female greater sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003-2004, including and excluding mortalities confirmed positive for West Nile virus.……..……...…….....……... 145

Table 4-15. Annual survival estimates for adult and yearling female greater sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003-2004, including and excluding mortalities confirmed positive for West Nile virus.……..…….....…….... 146

Table 5-1. Estimated average reduction in annual population growth (i.e., finite rate of increase, λ) under various West Nile virus (WNv) impact scenarios relative to no WNv mortality based on life-stage simulation analysis using vital rates for female greater sage-grouse in the Powder River Basin, Montana and Wyoming, 2003-2006.....…….... 196

## List of Figures

Figure 2-1. Distribution and status of active, inactive, and destroyed greater sage-grouse leks, coal-bed natural gas wells, and major highways in the Powder River Basin, Montana and Wyoming, U.S.A.…….....…….. 48

Figure 2-2. Population indices based on male lek attendance for greater sage-grouse in the Powder River Basin, Montana and Wyoming, U.S.A., 2001-2005.....…….. 49

Figure 2-3. Number of male sage-grouse per active lek in coal-bed natural gas and outside coal-bed natural gas in the Powder River Basin, Montana and Wyoming, U.S.A., 2001-2005.…….....…….. 50

Figure 2-4. Timing of greater sage-grouse lek disappearance relative to coal-bed natural gas development in the Powder River Basin. …….…….....…….. 51

Figure 2-5. Estimated lek persistence as a function of proportion sagebrush habitat within 6.4 km and proportion coal-bed natural gas (CBNG) development within 0.8 km or

number of years within a CBNG field for greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005……..……. 52

Figure 2-6. Estimated lek persistence as a function of the size of a no-surface-infrastructure buffer around leks for greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005…..……... 53

Figure 2-7. Estimated lek persistence as a function of the size of a no-surface-infrastructure buffer around leks and the extent of coal-bed natural gas development outside that buffer for greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005…….……. 54

Figure 3-1. Predicted non-linear relationships between observed post-epizootic seroprevalence and actual infection rate over a range of mortality rates following infection for representative bird species……..…..……. 74

Figure 4-1. Expansion of coal-bed natural gas development in the Powder River Basin, 1997-2005……..……..…..……... 150

Figure 4-2. Daily survival rate of nests (with 95% CIs) in three regions of the Powder River Basin, 2003-2006……..……..…..……..... 151

Figure 4-3. Daily survival rate of nests (with 95% CIs) in relation to date and hen age based on nests in three regions of the Powder River Basin, 2003-2006...……..… 152

Figure 4-4. Estimated daily survival rate of nests during incubation (with 95% CIs) as nest age increases based on nesting data from three regions of the Powder River Basin, 2003-2006……..……..…..……... 153

Figure 4-5. Estimated nest success (with 95% CIs) in three regions of the Powder River Basin, 2003-2006 for first nests and renests of yearlings and adults based on a *Region*Year*Hen age+Attempt* model.…….…..…….... 154

Figure 4-6. Daily survival rate of broods (with 95% CIs) in three regions of the Powder River Basin, 2003-2006. ……..……..…..... 155

Figure 4-7. Estimated brood success (with 95% CIs) in three regions of the Powder River Basin, 2003-2006 based on a *Region*Year* model. ……..….....…….... 156

Figure 4-8. Estimated spring-summer survival (with 95% CIs) for greater sage-grouse females without broods and those that raised broods to 35 d in three regions of the Powder River Basin, 2003-2006, based on the best-approximating model (*Region*WNv+ Year+WBrood*).....……..……..….....…….... 157

Figure 4-9. Spring-summer survival (with 95% CIs) for yearling and adult females in three regions of the Powder River Basin from 2003-2007, based on a *Region*Year*Hen age* model.……..……..….....…….... 158

Figure 4-10. Fall-winter juvenile, yearling, and adult female survival (with 95% CIs) in three regions of the Powder River Basin from 2003 - 2006..……..... 159

Figure 4-11. Estimated annual survival of yearling and adult females in three regions of the Powder River Basin, 2003 - 2006 based on a *Region*Year*Hen age* model.…….. 160

Figure 5-1. Life-cycle and stage-based projection matrix for a 2-stage, pre-breeding, birth-pulse model for female greater sage-grouse in the Powder River Basin, Montana and Wyoming, USA.…….....……..…….....……... 200

Figure 5-2. Relationships between predicted no. days with West Nile virus transmission events based on a degree-day model (Zou et al. 2006*b*) and absolute decreases in spring-

summer survival and annual survival due to WNv-related mortality in three regions of the Powder River Basin, Montana and Wyoming, USA, 2003-2006. …..……..... 201

Figure 5-3. An example of the distribution of simulated WNv infection rates for female greater sage-grouse in the Powder River Basin, Montana and Wyoming, USA…..... 202

Figure 5-4. An example of the predicted distribution of the annual number of WNv transmission days based on temperature data from Sheridan Field Station, WY (station no. 488160) with degree-day criteria based on a 14.3º temperature threshold for virus amplification within *Culex tarsalis* and 109 degree-day extrinsic incubation period for median virus transmission and degree-day criteria modified to match observed WNv mortalities in sage-grouse near Decker, MT……..….....…….. 203

Figure 5-5. Variance in population growth (i.e., finite rate of increase, λ) based on mean elasticity values, coefficients of determination in life-stage simulation analysis for each vital rate, and for vital rates affected by different management strategies..... 204

Figure 5-6. Annual population growth (i.e., finite rate of increase, λ) regressed on yearling nest success (first nests), adult nest success (first nests), survival of chicks from yearling females, survival of chicks from adult females, survival of juveniles from first nests, survival of juveniles from second nests, annual yearling survival, and annual adult survival for female greater sage-grouse in the Powder River Basin, Montana and Wyoming, USA from 2003-2006 and for range-wide values. …..……..... 205

Figure 5-7. Distribution of simulated annual population growth rates (i.e., finite rate of increase, λ) for female greater sage-grouse based on life-stage simulation analysis using data on vital rates from the Powder River Basin, Montana and Wyoming, USA, 2003-2006, assuming no WNv impacts…….....…….. 209

Figure 5-8. Projected change in resistance to WNv disease of greater sage-grouse females over a 20-year period based on simulated vital rates from the Powder River Basin, 2003-2006 using life-stage simulation analysis.…..……. 210

Figure 5-9. Distribution of WNv-related mortality among female greater sage-grouse in the 1st year of the simulation and in the 20th year of the simulation with increasing resistance over time based on simulated infection rates from the Powder River Basin, 2003-2006, assuming no carryover effects of WNv infection.....…….. 211

Figure 5-10. Projected change in the proportion of WNv-infected resistant sage-grouse in the spring population over a 20-year period based on simulated vital rates from the Powder River Basin, 2003-2006 using life-stage simulation analysis. ….....….. 212

# CHAPTER 1. INTRODUCTION

Widespread concern over declines in greater sage-grouse (*Centrocercus urophasianus*) abundance and distribution have led to extensive research and management efforts to understand and reverse population declines. Recently, energy development and West Nile virus have emerged as two new potential stressors on sage-grouse populations. My dissertation research was originally designed to evaluate impacts of CBNG development on greater sage-grouse demography. However, the emergence of WNv as an additional stressor on sage-grouse populations in the PRB (Naugle et al. 2004, 2005; Walker et al. 2004) and the apparent causal link between CBNG and WNv mortality (Zou et al. 2006, Doherty 2007) has generated the need to investigate potential consequences of both coal-bed natural gas and WNv mortality on sage-grouse populations.

In Chapter 2, I examine how CBNG development, habitat, and other landscape features influenced trends in the abundance of displaying males in the PRB between 2001-2005 and the status of sage-grouse leks between 1997-2005. I then use these results to estimate approximate threshold densities of CBNG development and the size of lek buffers required to maintain various levels of population persistence. A condensed version of this chapter was published in the Journal of Wildlife Management in 2007 (Walker et al. 2007*a*). In Chapter 3, I use data on WNv-induced mortality and seroprevalence from the PRB to estimate rates of WNv infection from 2003-2006. A condensed version of this chapter was published in the journal Avian Diseases in 2007 (Walker et al. 2007*b*). In Chapter 4, I use data from radio-marked females in three

regions of the PRB from 2003-2006 to generate age-specific estimates of nest, brood, and adult female survival for use in population models in Chapter 5 and to study the influence of female characteristics, season, and environmental variables on nest, brood, and female survival. These analyses also form the foundation for future research on how local and landscape habitat and infrastructure variables influence key vital rates after controlling for other factors. In Chapter 5, I use age-specific demographic estimates from the PRB to parameterize a life-stage simulation analysis model to examine potential consequences of WNv mortality for population growth under different scenarios. Chapter 5 also forms the basis for a separate manuscript reviewing the ecology of WNv in sagebrush habitat, impacts on greater sage-grouse demography, and potential range-wide consequences of WNv for sage-grouse populations (Walker and Naugle 2008).

## Literature Cited

Doherty, M. K. 2007. Mosquito populations in the Powder River Basin, Wyoming: a comparison of natural, agricultural and effluent coal-bed natural gas aquatic habitats. Thesis. Montana State University, Bozeman, Montana, USA.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: pending crisis for Greater Sage-grouse. Ecology Letters: 7:704-713.

Naugle, D. E., C. L. Aldridge, B. L. Walker, K. E. Doherty, M. R. Matchett, J. McIntosh, T. E. Cornish, M. S. Boyce. 2005. West Nile virus and sage-grouse: what more have we learned? Wildlife Society Bulletin: 33:1-8.

Walker, B. L., D. E. Naugle, K. E. Doherty, T. E. Cornish. 2004. From the field: outbreak of West Nile virus in Greater Sage-grouse and guidelines for monitoring, handling, and submitting dead birds. Wildlife Society Bulletin 32:1000-1006.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007*a*. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644-2654.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2007*b*. West Nile virus and greater sage-grouse: estimating infection rate in a wild bird population. Avian Diseases 51:691-696.

Walker, B. L., and D. E. Naugle 2008. West Nile virus: ecology and impacts on greater sage-grouse populations. Studies in Avian Biology: in press.

Zou, L., S. N. Miller, E. T. Schmidtmann. 2006. Mosquito larval habitat mapping using remote sensing and GIS: implications of coalbed methane development and West Nile virus. Journal of Medical Entomology 43:1034-1041.

# CHAPTER 2. GREATER SAGE-GROUSE POPULATION RESPONSE TO ENERGY DEVELOPMENT AND HABITAT LOSS

*Abstract:* Modification of landscapes due to energy development may alter both habitat use and vital rates of sensitive wildlife species. Greater sage-grouse (*Centrocercus urophasianus*) in the Powder River Basin (PRB) of Wyoming and Montana have experienced widespread, rapid changes to habitat due to recent coal-bed natural gas (CBNG) development. We analyzed lek-count, habitat, and infrastructure data to assess how CBNG development and other landscape features influenced trends in the numbers of male sage-grouse observed and persistence of leks in the PRB. From 2001-2005, the numbers of males observed on leks in CBNG fields declined more rapidly than leks outside of CBNG. Of leks active in 1997 or later, only 38% within CBNG fields remained active by 2004-2005, compared to 84% of leks outside CBNG fields. By 2005, leks in CBNG fields had 46% fewer males per active lek than leks outside of CBNG. Persistence of 110 leks was positively influenced by the proportion of sagebrush habitat within 6.4 km of the lek. After controlling for habitat, we found support for negative effects of CBNG development within 0.8 km and 3.2 km of the lek and for a time lag between CBNG development and lek disappearance. Current stipulations that prohibit development within 0.4 km of sage-grouse leks on federal lands are inadequate to ensure lek persistence and may result in impacts to breeding populations over larger areas. Seasonal restrictions on drilling and construction do not address impacts caused by loss of sagebrush and incursion of infrastructure that can affect populations over longer periods of time. Development thresholds suggest that the current density of development

is several times greater than that which allows sage-grouse breeding populations to persist. Increased spatial restrictions on CBNG development, rapid implementation of more effective mitigation measures, or both may be required to reduce impacts of CBNG development on sage-grouse populations in the PRB.

*Keywords*: agriculture, *Centrocercus urophasianus*, coal-bed natural gas, coal-bed methane, energy development, greater sage-grouse, lek count, population, Powder River Basin, sagebrush

*The Journal of Wildlife Management 72: 2644-2654 2008*

Large-scale modification of habitat associated with energy development may alter habitat use or vital rates of sensitive wildlife species. Populations in developed areas may decline if animals avoid specific features of infrastructure such as roads or power lines (Trombulak and Frissell 2000, Nelleman et al. 2001, 2003) or if energy development negatively affects survival or reproduction (Holloran 2005, Aldridge and Boyce 2007). For example, mortality caused by collisions with vehicles and power lines reduces adult and juvenile survival in a variety of wildlife species (reviewed in Bevanger 1998 and Trombulak and Frissell 2000). Indirect effects of energy development on populations are also possible due to changes in predator or parasite communities (Knight and Kawashima 1993, Steenhof et al. 1993, Daszak et al. 2000) or changes in vegetation structure and composition associated with disturbance (Trombulak and Frissell 2000, Gelbard and Belnap 2003). Negative impacts may be exacerbated if features of

development that attract animals (e.g., ponds) simultaneously reduce survival and thereby function as ecological traps (Gates and Gysel 1978).

Rapidly expanding coal-bed natural gas (CBNG) development is a concern for conservation of greater sage-grouse (*Centrocercus urophasianus*) in the Powder River Basin (PRB) of northeastern Wyoming and southeastern Montana. The PRB supports an important regional population, with over 500 leks documented between 1967-2005 (Connelly et al. 2004). In the past decade, the PRB has also experienced rapidly increasing CBNG development, with impacts on wildlife habitat projected to occur over an area of approximately 24,000 $km^2$ (Bureau of Land Management 2003*a*, *b*). Coal-bed natural gas development typically requires construction of 2-7 km of roads and 7-22 km of power lines per $km^2$, depending on well density, as well as an extensive network of compressor stations, pipelines, and ponds (Bureau of Land Management 2003*b*). Approximately 10% of surface lands and 75% of mineral reserves in the PRB are federally owned and administered by the Bureau of Land Management (BLM) (Bureau of Land Management 2003*a*, *b*). Over 50,000 CBNG wells have been authorized for development on federal mineral reserves in northeastern Wyoming, at a density of 1 well per 16-32 ha, and as many as 18,000 wells are anticipated in southeastern Montana (Bureau of Land Management 2003*a, b*). According to data from the Wyoming Oil and Gas Conservation Commission and Montana Board of Oil and Gas Conservation, by the beginning of 2005, approximately 28,000 CBNG wells had been drilled on federal (~31%), state (~11%), and private (~58%) mineral holdings in the PRB. Mitigation for sage-grouse on BLM lands typically includes lease stipulations prohibiting surface infrastructure within 0.4 km of sage-grouse leks as well as restrictions on timing of

drilling and construction within 3.2 km of documented leks during the 15 March - 15 June breeding season and within crucial winter habitat from 1 December - 31 March (Montana only) (Bureau of Land Management 2003*a*, *b*). These restrictions can be modified or waived by BLM, or additional conditions of approval applied, on a case-by-case basis. In contrast, most state and private minerals have been developed with few or no requirements to mitigate impacts on wildlife.

Coal-bed natural gas development and its associated infrastructure may affect sage-grouse populations via several different mechanisms, and these mechanisms can operate at different scales. For example, males and females may abandon leks if repeatedly disturbed by raptors perching on power lines near leks (Ellis 1984), by vehicle traffic on nearby roads (Lyon and Anderson 2003), or by noise and human activity associated with energy development during the breeding season (Braun et al. 2002, Holloran 2005, Kaiser 2006). Collisions with nearby power lines and vehicles and increased predation by raptors may also increase mortality of birds at leks (Connelly et al. 2000*a*, 2000*b*). Alternatively, roads and power lines may indirectly affect lek persistence by altering productivity or survival of local populations at other times of the year. For example, mortality associated with power lines and roads occurs year-round (Patterson 1952, Beck et al. 2006, Aldridge and Boyce 2007). Ponds created during CBNG development may facilitate the spread of mosquitos that transmit West Nile virus (WNv), thereby increasing mortality in late summer (Walker et al. 2004, Zou et al. 2006, Walker et al. 2007). Loss and degradation of sagebrush habitat may also reduce carrying capacity of local breeding populations (Braun 1998, Connelly et al. 2000*b*, Crawford et al. 2004). Alternatively, birds may simply avoid otherwise suitable habitat if the density

of roads, power lines, or energy development increases above a certain threshold (Lyon and Anderson 2003, Holloran 2005, Kaiser 2006, Doherty et al. 2008).

Understanding how energy development affects sage-grouse populations also requires that we control for other landscape features that affect population size and persistence, including the extent of suitable habitat. Sage-grouse are closely tied to sagebrush habitats throughout their annual cycle, and variation in the amount of sagebrush habitat available for foraging and nesting is likely to influence the size of breeding populations and persistence of leks (Ellis et al. 1989, Schroeder et al. 1999, Leonard et al. 2000, Smith et al. 2005). For this reason, it is crucial to quantify and separate effects of habitat loss from those of energy development.

To assess how CBNG development and habitat loss influence sage-grouse populations in the PRB, we conducted 2 analyses based on region-wide lek-count data. First, we analyzed counts of the numbers of males displaying on leks (hereafter, "lek counts") to assess whether trends in the number of males counted and proportion of active and inactive leks differed between areas with and without CBNG development. Lek counts are widely used for monitoring sage-grouse populations, and at present, are the only data suitable for examining trends in population size and distribution at this scale (Connelly et al. 2003, 2004). Second, we used logistic regression to model lek status (i.e., active or inactive) in relation to landscape features hypothesized to influence sage-grouse demographics and habitat use at 3 spatial scales. The objectives of the lek-status analysis were first, to identify the scale at which habitat and non-CBNG landscape features influence lek persistence and second, to evaluate and compare effects of CBNG

development at different scales with those of non-CBNG landscape features after controlling for habitat.

## Study Area

We analyzed data from sage-grouse leks within an approximately 50,000-km$^2$ area of northeastern Wyoming and southeastern Montana (Figure 1). This area included all areas with existing or predicted CBNG development in the PRB (Bureau of Land Management 2003*a*, *b*) as well as surrounding areas without CBNG. Land use in this region was primarily cattle ranching with limited dry-land and irrigated tillage agriculture. Natural vegetation consisted of sagebrush-steppe and mixed-grass prairie interspersed with occasional stands of conifers. Sagebrush-steppe was dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) with an understory of native and non-native grasses and forbs. Plains silver sagebrush (*A. cana cana*) and black greasewood (*Sarcobatus vermiculatus*) co-occurred with Wyoming big sagebrush in drainage bottoms.

## Methods

### Lek-count trend analyses

*Lek-count data*. We used sage-grouse lek-count data in public databases maintained by Wyoming Game and Fish Department and Montana Department of Fish, Wildlife, and Parks as the foundation for analyses. We augmented databases with lek counts provided by consultants and by the BLM's Miles City field office for 37 leks (36 in Montana, 1 in Wyoming) known to have been counted but for which data were missing. We checked for and, when possible, corrected errors in the database after consultation with database managers and regional biologists for each state. We excluded

records with obvious errors, surveys in which lek status was not determined, leks without supporting count data, and duplicate leks prior to analysis.

*Coal-bed natural gas development*. We obtained data on the type, location, status, drilling date, completion date, and abandonment date of wells from public databases maintained by the Wyoming Oil and Gas Conservation Commission and Montana Board of Oil and Gas Conservation. Because wells are highly correlated with other features of development, such as roads, power lines, and ponds (D. E. Naugle, University of Montana, unpublished data), using locations of wells is a reliable way to measure the extent of CBNG development. We retained only those wells that were clearly in the ground, associated with energy development (gas, oil, stratification test, disposal, injection, monitoring, and water source wells), and likely to have infrastructure. We excluded wells that were plugged and abandoned, wells waiting on permit approval, wells drilled or completed in 2005 or later, and those with status reported as dry hole, expired permit, permit denied, unknown, or no report. We included wells in analyses starting in the year in which they were drilled or completed (i.e., started producing). For active wells without drilling or completion dates, we estimated start year based on approval and completion dates of wells in the immediate vicinity and in the same unit lease. Wells with current status reported as dormant, temporarily abandoned, or permanently abandoned were included until the year they were first reported abandoned. Because capped (i.e., "shut-in") wells may or may not have associated infrastructure, we included capped wells only in years in which they were surrounded by, or within 1 km of, a producing gas field.

We estimated the extent of CBNG development around each lek in each year. We first approximated the area affected by CBNG development by creating a 350-m buffer around all well locations using ArcInfo 8.2 (ESRI, Inc., Redlands, CA) and dissolving boundaries where buffers overlapped. We then estimated the proportion area within 3.2 km of the lek center covered by the buffer around wells. At current well density (1 well per 32-64 ha), a 350-m buffer around wells estimates the extent of CBNG development more accurately than larger or smaller buffer sizes. This metric is less sensitive to variation in spacing of wells than measures such as well density and therefore more accurate for estimating the total area affected by CBNG development.

*Trends in lek counts.* We examined lek-count data from 1988-2005. We categorized a lek as in CBNG if ≥40% of the area within 3.2 km was developed or if ≥25% was developed and ≥1 well was within 350 m of the lek center. We categorized a lek as outside CBNG if <40% of the area within 3.2 km was developed and no wells were within 350 m of the lek center. However, because few leks in CBNG were counted in consecutive years prior to 2001, we analyzed trends in lek-counts only from 2001-2005. We calculated the rate of increase in the number of males counted on leks for each year-to-year transition by summing count data across leks within each category according to their stage of development at the end of the first year of each year-to-year transition (Connelly et al. 2004). We summed data across leks to reduce the influence of geographic variation in detectability and used the maximum annual count for each lek to reduce the influence of within-year variation in detectability on the estimated rate of increase. Data for each transition were derived only from leks counted in both years and known to be active in at least 1 of the 2 years of the transition. We estimated mean rates

of increase in CBNG versus outside CBNG fields based on the slope of a linear regression of interval length versus rate of increase (Morris and Doak 2002). Wells completed between January and March (i.e., before lek counts were conducted) in the second year of each transition may have caused us to underestimate the amount of CBNG development around leks at the time counts were conducted. However, if CBNG development negatively affects populations, this would cause the difference between trends in lek-count data in CBNG and outside CBNG to be underestimated and produce a conservative estimate of impacts.

*Timing of lek disappearance*. If CBNG development negatively affects lek persistence, most leks in CBNG fields that became inactive should have done so following CBNG development. To explore this prediction, we examined the timing of lek disappearance in relation to when a lek was first considered in a CBNG field (i.e., ≥40% development within 3.2 km or ≥25% development and wells within 350 m of the lek center).

*Development threshold*. We estimated an approximate threshold density of CBNG development at which sage-grouse leks will remain active by calculating well densities around active leks affected by CBNG. This required assumptions about the scale and extent of CBNG around a lek at which development begins to affect lek persistence. Models with effects of CBNG within 3.2 km were strongly supported (see *Results*, below), whereas those with CBNG within 6.4 km received considerably less support. Thus, for this analysis, we conservatively assumed that only CBNG within 3.2 km would affect lek persistence. Impacts of 40% CBNG development at the 3.2-km scale were pronounced (see *Results*, below), so it is also reasonable to assume that CBNG

affects male lek attendance before development reached 40%. We used data on males per active lek to identify the approximate extent of development within 3.2 km at which male lek attendance begins to decline. We did this by comparing the number of males per lek at active leks with no CBNG versus those with CBNG over a range of increasing development. We varied the lower limit of development from 0.01% to 37.5% (in intervals of 2.5%) and the maximum was held constant at 92% (the highest observed value for any lek). We then calculated well densities around active leks that exceeded the identified cut-off values. Because wells are often drilled in groups into different coal seams from the same well pad, we then converted well densities into well-pad densities based on an average of 1.43 wells per pad (Bureau of Land Management 2003*b*).

**Lek-status analysis**

*Definition of leks*. We defined a lek as a site where multiple males were documented displaying on multiple visits within a single year or over multiple years. We defined a lek complex as multiple leks located <2.5 km from the largest and most regularly attended lek in the complex (Connelly et al. 2004). We defined an initial set of lek complexes based on those known prior to 1990. Leks discovered in 1990 or later were considered separate complexes, even if they occurred <2.5 km from leks discovered in previous years. This was done to avoid problems with the location of already-defined leks and lek complexes shifting as new leks were discovered or if new leks formed in response to nearby CBNG development. Leks newly discovered in the same year within 2.5 km of each other were grouped in the same lek complex. We used lek complexes as the sample unit for calculating proportion of active and inactive leks and in the lek-status

analysis, but because "lek complex" can refer either to multiple leks or to a single lek, hereafter we refer to both simply as a "lek".

*Lek status*. We determined the final status of leks by examining count data from 2004-2005. We considered a lek active if ≥ 1 male was counted in 2004 or 2005, whichever was the last year surveyed. To minimize problems with non-detection of males, we considered a lek inactive only if: 1) at least 3 consecutive ground or air visits in the last year surveyed failed to detect males, or 2) if surveys in the last 3 consecutive years the lek was checked (2002-2004 or 2003-2005) failed to detect males. We classified the status of leks that were not surveyed or were inadequately surveyed in 2004 or 2005 as unknown. Survey effort in the PRB increased 5-fold from 1997-2005, and included systematic aerial searches for new leks and repeated air and ground counts of known leks within and adjacent to CBNG fields. Therefore, it is unlikely that leks shifted to nearby sites without being detected. Many leks in the PRB disappeared during a region-wide population decline in 1991-1995 (Connelly et al. 2004), well before most CBNG development in the PRB began. To eliminate leks that became inactive for reasons other than CBNG, we calculated proportions of active and inactive leks in CBNG and outside CBNG based only on leks active in 1997 or later.

*Scale*. We calculated landscape metrics at 3 distances around each lek: 0.8 km (201 ha), 3.2 km (3,217 ha), and 6.4 km (12,868 ha). The 0.8-km scale was selected to represent processes that impact breeding birds at or near leks, while avoiding problems with spatial error in lek locations. The 6.4-km scale reflects processes that occur at larger scales around the lek, such as loss of nesting habitat, demographic impacts on local breeding populations, or landscape-scale avoidance of CBNG fields. The 3.2-km scale is

that at which state and federal agencies apply mitigation for CBNG impacts (e.g., timing restrictions), and it is important to determine the appropriateness of managing at a 3.2-km scale versus at smaller or larger scales.

*Habitat variables*. Each model in our analysis represented a distinct hypothesis, or combination of hypotheses, regarding how landscape features influence lek persistence. We included 2 types of habitat variables in the analysis, the proportion of sagebrush habitat and the proportion of tillage agriculture in the landscape around each lek. Because the scale at which habitat most strongly influenced lek persistence was unknown, we considered habitat variables at all 3 scales. We calculated the amount of sagebrush habitat and tillage agriculture around each lek at each scale using ArcInfo 8.2 based on classified SPOT-5 satellite imagery taken in August 2003 over an approximately 15,700 $km^2$ area of the PRB. We restricted the lek-status analysis to leks within the SPOT-5 satellite imagery because the only other type of classified imagery available for this region (Thematic Mapper at 30-m resolution) is unreliable for measuring the extent of sagebrush habitat (Moynahan 2004). Areas with tillage agriculture were visually identified from the imagery and manually digitized. Classification accuracy was 83% for sagebrush habitat (i.e., sagebrush-steppe and sagebrush-dominated grassland). We excluded 20 leks for which >10% of classified habitat data were unavailable due to cloud cover or proximity to the edge of the imagery.

*Road, power line, and CBNG variables.* We hypothesized that infrastructure can affect lek persistence in 3 ways and included different variables to examine each hypothesis. Roads, power lines, and CBNG development may affect lek persistence in proportion to their extent on the landscape. Alternatively, the effects of roads and power

lines may depend their distance from the lek, in which case they are expected to drop off rapidly as distance increases. Coal-bed natural gas development may also influence lek status depending on how long the lek has been in a CBNG field. If CBNG increases mortality, it may be several years before local breeding populations are reduced to the point that males no longer attend the lek (Holloran 2005). Avoidance of leks in CBNG fields by young birds (Kaiser 2006) combined with high site fidelity of adults to breeding areas (Schroeder et al. 1999) would also result in a time lag between full CBNG development and lek disappearance.

We used TIGER/Line® 1995 public-domain road layers for Wyoming and Montana (U.S. Census Bureau 1995) to estimate the proportion of each buffer around each lek within 350 m of a road at each of the 3 scales. We used 1995 data, rather than a more recent version, to represent roads that existed on the landscape prior to CBNG development. We obtained autumn 2005 GIS coverages of power lines directly from utility companies and used this layer to estimate the proportion of each buffer around each lek within 350 m of a power line at each scale. Year-specific power line coverages were not available, so this variable includes both CBNG and non-CNBG power lines. We estimated the extent of CBNG development around each lek at each scale by calculating the proportion of the total buffer area around the lek center covered by a dissolved 350-m buffer around well locations. If a lek was a complex, we first placed a buffer around all lek centers in the complex then dissolved the intersections to create a single buffer. We selected a 350-m buffer around roads, power lines, and CBNG wells for 2 reasons. First, quantitative estimates of the distance at which infrastructure affects habitat use or vital rates of sage-grouse were not available, and 350 m is a reasonable

distance over which to expect impacts to occur, such as increased risk of predation near power lines or increased risk of vehicle collisions near roads. Second, we also wished to maintain a consistent relationship between well, road, and power line variables and the amount of area affected by each feature. We measured how long a lek was in a CBNG field as the number of years prior to 2005 during which the lek had ≥40% CBNG development within 3.2 km or ≥25% CBNG within 3.2 km and ≥ 1 well within 350 m of the lek center.

*Analyses.* We used a hierarchical analysis framework to evaluate how landscape features influenced lek status (i.e., active or inactive). Our first goal was to identify the scale at which habitat, roads, and power lines affected lek persistence. Our second goal was to evaluate and compare effects of CBNG development at different scales with those of roads and power lines after controlling for habitat. In both cases, we used an information-theoretic approach (Burnham and Anderson 2002) to select the most parsimonious model from a set of plausible candidate models. All analyses were conducted using logistic regression in R (version 2.3.1, R Development Core Team 2006). We used a logit-link function to bound persistence estimates within a (0,1) interval. Almost all CBNG development within the extent of the SPOT-5 imagery occurred after 1997, so we restricted our analysis to leks known to have been active in 1997 or later to eliminate those that disappeared for reasons other than CBNG development. We also excluded 4 leks known to have been destroyed by coal mining.

To identify the most relevant scale(s) for each landscape variable, we first allowed univariate models at different scales to compete. Variables assessed for scale effects included: (1) proportion sagebrush habitat, (2) proportion tillage agriculture, (3)

proportion area affected by power lines, and (4) proportion area affected by non-CBNG roads. We then used the scale for each variable that best predicted lek status to construct the final set of candidate models. We also included models with squared distance to nearest road and squared distance to nearest power line in the final model set. To assess different possible mechanisms of CBNG impacts, we evaluated models with the extent of CBNG development or the number of years since the lek was classified as in a CBNG field. To assess the scale at which CBNG impacts occur, we included models with the extent of CBNG effects at all 3 scales. We also included models with interactions between habitat and CBNG metrics to evaluate whether effects of CBNG development are amelioriated by the amount of sagebrush habitat around the lek. To avoid problems with multicollinearity, we did not allow models with correlated variables (i.e., $r > |0.7|$) in the final model set.

We judged models based on Akaike's Information Criterion adjusted for small sample size ($AIC_c$), and examined beta coefficients and associated standard errors in all models to determine the direction and magnitude of effects. We estimated overdispersion by dividing the residual deviance of the global model by the deviance degrees of freedom. Goodness-of-fit testing was conducted in R following methods described in Hosmer et al. (1997). We used parametric bootstrapping (Efron and Tibshirani 1993) to obtain means, standard errors, and 95% confidence limits for persistence estimates because coefficients of variation for most beta estimates were large (Zhou 2002). Due to model uncertainty, we used model averaging to obtain unconditional parameter estimates and variances (Burnham and Anderson 2002). We compared the relative importance of habitat, CBNG, and infrastructure in determining lek persistence by summing Akaike

weights across all models containing each class of variable (Burnham and Anderson 2002). We also calculated evidence ratios to compare the likelihood of the best approximating habitat-plus-CBNG, habitat-plus-infrastructure, and habitat-only models.

To assess whether a known West Nile virus outbreak or habitat loss associated with tillage agriculture disproportionately influenced model selection and interpretation, we also reanalyzed the dataset after removing specific leks. The first analysis excluded 4 leks near Spotted Horse, Wyoming known to have disappeared after 2003 likely due to WNv-related mortality (Walker et al. 2004). The second analysis excluded 20 leks that had ≥5% agriculture at 1 or more of the 3 scales examined.

To evaluate the effectiveness of the stipulation for no surface infrastructure within 0.4 km of a lek, we examined the estimated probability of lek persistence without development versus that under full CBNG development with a 0.4-km buffer. We also used models with effects of CBNG within 3.2 km and CBNG within 6.4 km to estimate the probability of lek persistence over a range of lek buffer sizes from 0.4 to 6.4 km. This second analysis assumes that effects of CBNG only occur within the maximum distance specified under each model. We excluded data based on model with effects of CBNG within 0.8 km because effects of CBNG were apparent at both larger scales.

## Results

*Trends in lek counts.* From 2001-2005, lek-count indices in CBNG fields declined by 82%, at a rate of 35% per year (mean rate of increase in CBNG = 0.65, 95% CI: 0.34-1.25) whereas indices outside CBNG declined by only 12%, at a rate of 3% per year (mean rate of increase outside CBNG = 0.97, 95% CI: 0.50-1.87) (Figure 2). The

mean number of males per active lek was similar between leks in CBNG and outside CBNG in 2001, but averaged 46% ± 8% (mean ± SE; range 33-55%) lower for leks in CBNG from 2002-2005 (Figure 3).

*Lek status.* Among leks active in 1997 or later, fewer leks remained active by 2004-2005 in CBNG fields (38%) than outside CBNG fields (84%) (Table 1). Of the 10 remaining active leks in CBNG fields, all were classified as being in CBNG in 2000 or later.

*Timing of lek disappearance*. Of 12 leks in CBNG fields monitored intensively enough to determine the year when they disappeared, 12 became inactive after or in the same year that development occurred (Figure 4). The average time between full CBNG development and lek disappearance was 4.1 ± 0.9 years (mean ± SE).

*Development thresholds*. Values for males per active lek and well-pad density were positively skewed, so we examined both median and mean values. Median values for males per active lek began to diverge once CBNG development exceeded 2.5% within 3.2 km. In contrast, mean values for leks with CBNG were approximately 2 males per lek lower even at the minimum level of development. After accounting for this initial difference, mean values for males per active lek began to diverge once CBNG development exceeded 7.5%. We approximated development thresholds using both values. A total of 67 active leks had >2.5% CBNG development within 3.2 km. Median density around these leks was 1 well pad per 305 ha (mean ± SE; 171 ± 31 ha). A total of 55 active leks had >7.5% CBNG development within 3.2 km. Median density around these leks was 1 well pad per 229 ha (mean ± SE; 146 ± 26 ha).

*Lek-status analysis.* We analyzed data from 110 leks of known status within the SPOT-5 imagery that were confirmed active in 1997 or later. Proportion sagebrush habitat and proportion tillage agriculture best explained lek persistence at the 6.4-km scale (Table 2). Proportion power lines also best explained lek persistence at the 6.4-km scale (although power line effects at the 3.2-km scale were also supported), whereas proportion roads best explained lek persistence at the 3.2-km scale.

The final model set consisted of 19 models: 2 models based on habitat only (i.e., sagebrush, sagebrush plus tillage agriculture), 4 models with habitat plus power line variables, 4 models with habitat plus road variables, and 9 models with habitat plus CBNG variables (Table 3). Goodness-of-fit testing using the global model revealed no evidence of lack of fit ($P = 0.49$). Our estimate of the variance inflation factor based on the global model ($\hat{c} = 0.96$) indicated no evidence of overdispersion.

Despite substantial model uncertainty, the top 8 of 19 models all included a moderate to strong positive effect of sagebrush habitat on lek persistence and a strong negative effect of CBNG development, measured either as proportion CBNG development within 0.8 km, proportion CBNG development within 3.2 km, or number of years in a CBNG field. These 8 models were well supported, with a combined Akaike weight of 0.96. Five of the 8 models were within 2 $\Delta AIC_c$ units of the best approximating model, whereas all habitat-plus-infrastructure and habitat-only models showed considerably less support (> 6 $\Delta AIC_c$ units lower). Evidence ratios indicate that the best habitat-plus-CBNG model was 28 times more likely to explain patterns of lek persistence than the best habitat-plus-infrastructure model and 50 times more likely than the best habitat-only model. Models 1 and 2 both included a negative effect of proportion

CBNG development within 0.8 km. Models with negative effects of number of years in CBNG (model 3) and proportion CBNG development within 3.2 km (model 4) also had considerable support. Although regression coefficients suggested that CBNG within 6.4 km also had a negative impact on lek persistence (Table 4), models with CBNG at 6.4 km showed considerably less support (~5-7 $\Delta AIC_c$ units lower). Tillage agriculture appeared in 1 well-supported model (model 2), and the coefficient suggested that tillage agriculture had a strong negative effect on lek persistence. However, this effect was poorly estimated, and the same model without tillage agriculture (model 1) was more parsimonious. Models containing effects of roads unrelated to CBNG development received little or no support in our analysis. Regression coefficients suggested negative effects of proximity to power lines and of proportion power line development within 6.4 km, but models with power line effects were only weakly supported (~6-8 $\Delta AIC_c$ units lower). Coefficients for interaction terms did not support an interaction between habitat and CBNG variables. The best approximating model accurately predicted the status of 79% of 79 active leks and 47% of 31 inactive leks. The summed Akaike weight for CBNG variables (0.97) was nearly identical to that of sagebrush habitat (1.00) and greater than that for the effects of tillage agriculture (0.26), power lines (0.02) or non-CBNG roads (0.01). Unconditional, model-averaged estimates and 95% confidence limits for beta estimates and odds ratios show that loss of sagebrush habitat and addition of CBNG development had effects of similar magnitude (Table 4).

The model-averaged estimate for the effect of CBNG within 0.8 km was close to those of the best approximating model (model 1, $\beta_{CBNG\ 0.8\ km} = -3.91 \pm 1.11$ SE) (Table 4). Thus, we illustrate the effects CBNG within 0.8 km on lek persistence using estimates

from that model (Figure 5a). We also illustrate results from model 3, which indicated that leks disappeared, on average, within 3-4 years of full CBNG development (Figure 5b). The current 0.4-km stipulation for no surface infrastructure leaves 75% of the landscape within 0.8 km and 98% of the landscape within 3.2 km open to CBNG development. In an average landscape around a lek in our analysis (i.e., 74% sagebrush habitat, 26% other land cover types), 75% CBNG development within 0.8 km would drop the probability of lek persistence from 86% to 24% (Figure 5a). Similarly, 98% CBNG development within 3.2 km would drop the average probability of lek persistence from 87% to 5%. Lek persistence was projected to increase with larger no-surface-infrastructure buffers around leks. Background rates of lek persistence in areas without CBNG development were ~85%. The estimated minimum buffer size required to maintain average lek persistence at >50% (i.e., to allow a 35% drop in average lek persistence) ranged from 2.6-5.2 km (Figure 6 *a, b*). In contrast, maintaining average lek persistence at >75% is estimated to require a 3.0-6.0 km lek buffer (Figure 6 *a, b*). Similar results are illustrated by models with varying levels of CBNG development and different sizes of NSO buffers around leks (Figure 7 *a*, *b*).

*Secondary analyses*. Analysis of reduced datasets did not meaningfully change model fit, model selection, or interpretation, nor did it alter the magnitude or direction of estimated CBNG effects. After excluding leks affected by WNv, the top 8 of 19 models and all 3 models within 2 $\Delta AIC_c$ units included a positive effect of sagebrush within 6.4 km and a negative effect of CBNG development. Model-averaged estimates of CBNG effects were similar to those from the original analysis ($\beta_{\text{Sagebrush 6.4 km}} = 3.96 \pm 1.97$ SE; $\beta_{\text{CBNG 0.8 km}} = -3.48 \pm 1.15$ SE; $\beta_{\text{CBNG 3.2 km}} = -4.39 \pm 1.52$ SE; $\beta_{\text{CBNG 6.4 km}} = -4.57 \pm 2.06$

SE; $\beta_{\text{Years in CBNG}}$ = -1.30 ± 0.61 SE). After excluding leks with ≥5% tillage agriculture, the top 4 of 11 models and 4 of 5 models within 2 $\Delta AIC_c$ units included a positive effect of sagebrush within 6.4 km and a negative effect of CBNG development. Estimates of CBNG effects were again similar to the original model-averaged values ($\beta_{\text{Sagebrush 6.4 km}}$ = 4.03 ± 2.29 SE; $\beta_{\text{CBNG 0.8 km}}$ = -3.34 ± 1.41 SE; $\beta_{\text{CBNG 3.2 km}}$ = -4.83 ± 2.06 SE; $\beta_{\text{CBNG 6.4 km}}$ = -4.76 ± 3.21 SE; $\beta_{\text{Years in CBNG}}$ = -2.44 ± 1.25 SE).

## Discussion

Coal-bed natural gas development appeared to have severe negative effects on sage-grouse breeding populations as indexed by male lek attendance and lek persistence. Although the small number of transitions (n = 4) in the trend analysis limited our ability to detect differences between trends, effect sizes were nonetheless large and suggest more rapidly declining breeding populations in CBNG fields. Effects of CBNG development explained lek persistence better than effects of power lines, pre-existing roads, WNv mortality, or tillage agriculture, even after controlling for availability of sagebrush habitat. Approximate development thresholds suggest that the current density of development may be several times greater than that which allows sage-grouse leks and their associated breeding populations, to persist. Strong support for models with negative effects of CBNG at both the 0.8-km and 3.2-km scales indicate that the current restriction on surface infrastructure within 0.4 km is insufficient to protect breeding populations. Support for a lag time between full CBNG development and lek disappearance indicates that monitoring effects of a landscape-level change like CBNG may require several years before changes in lek status are detected.

In our study, non-CBNG roads did not appear to influence lek persistence, even though vehicle collisions and disturbance of leks near roads can have negative impacts on sage-grouse (Lyon and Anderson 2003, Holloran 2005). This may be because most roads in the PRB prior to CBNG development were rarely-traveled dirt tracks rather than the shaled, all-weather roads associated with CBNG development. Alternatively, negative impacts of roads may have been masked by the tendency for male sage-grouse to be attracted to roadways as display sites, for leks near roads to have higher detectability, or because areas in which males display (e.g., broad ridgetops, valley bottoms) are also good for building roads (Schroeder et al. 1999, Rowland 2004). Although models with power line effects were only weakly supported, coefficients nonetheless suggested that power lines (including those associated with CBNG) had a negative effect on lek persistence. Because CBNG development requires construction of both roads and power lines, impacts of CBNG could involve impacts from both features. West Nile virus also has contributed to local lek extirpations in the PRB (Walker et al. 2004). However, unless CBNG development facilitates the spread of WNv into sage-grouse habitat, impacts of the virus should be similar in areas with and without CBNG. Thus, the impact of WNv by itself cannot explain declining breeding populations in CBNG. Rather, increased WNv-related mortality may be an indirect effect of CBNG development (Zou et al. 2006). Other indirect effects, such as increased livestock grazing due to newly-available CBNG water, or changes in predator abundance caused by addition of ponds or power lines, may also indirectly influence sage-grouse populations.

Although CBNG development and loss of sagebrush habitat both contributed to declines in lek persistence, much more of the landscape in the PRB has potential for

CBNG than for tillage agriculture, suggesting that CBNG will have a greater impact on populations at the regional scale. In our analyses, we were unable to distinguish between conversion of sagebrush to cropland that would have occurred in the absence of CBNG development and that which occurred because CBNG water became available for irrigation following development. Although sage-grouse sometimes use agricultural fields during brood-rearing (Schroeder et al. 1999, Connelly et al. 2000*b*), large-scale conversion of sagebrush habitat to irrigated cropland in conjunction with CBNG development would clearly be detrimental to populations (Leonard et al. 2000, Smith et al. 2005), particularly because birds in agricultural areas likely experience elevated mortality due to pesticides and WNv (Connelly et al. 2000*b*, Doherty 2007).

Accumulated evidence across studies suggests that sage-grouse populations typically decline following energy development (Braun 1986, Remington and Braun 1991, Braun et al. 2002, Holloran 2005), but our study is the first to quantify and separate effects of energy development from those of habitat loss. Our results are similar to those of Holloran (2005), who found that "natural gas field development within 3-5 km of an active greater sage-grouse lek will lead to dramatic declines in breeding populations," that leks heavily impacted by development typically became inactive within 3-4 years, and that energy development within 6.2 km of leks can decrease male attendance. As in other parts of their range, sage-grouse populations in the PRB likely have declined due to cumulative impacts of habitat loss caused by anthropogenic change and other unknown population stressors (Crawford et al. 2004, Connelly et al. 2004). New threats, such as WNv, have also emerged (Naugle et al. 2004, Walker et al. 2007). Nonetheless, our analysis indicates that energy development has contributed to recent population declines

in the PRB. More importantly, the scale of future development in the PRB suggests that, without more effective mitigation, CBNG will continue to impact populations over an even larger area.

It is unclear whether declines in lek attendance within CBNG fields were caused by impacts to breeding birds at the lek, reduced survival or productivity of birds in the surrounding area, avoidance of developed areas, or some combination thereof. We simultaneously observed greater support for CBNG models but decreasing magnitude of CBNG coefficients at smaller scales around leks, and model uncertainty precluded us from identifying the specific mechanism by which development causes impacts. Although sage-grouse appear to avoid areas with CBNG development in the PRB in winter (Doherty et al. 2008), birds may also avoid CBNG development in the spring and summer. Kaiser (2006) and Holloran et al. (2007) found that yearling females avoided nesting in portions of their natal areas with natural gas development, and yearling males were recruited to leks inside developed fields at lower rates, suggesting displacement to leks on the periphery. Birds breeding within gas fields may also show lower productivity (Lyon and Anderson 2003) or reduced survival compared to birds in natural habitats (Holloran 2005), either of which could result in reduced population growth (see Chapter 5). Experimental research using a before-after, control-impact design with radio-marked birds would be required to identify the relative importance of each mechanism in driving population declines within CBNG. Although this would allow us to identify mechanisms underlying declines, based on our findings and those of others (e.g., Holloran 2005, Aldridge and Boyce 2007, Doherty et al. 2008), such an experiment would likely be detrimental to the affected populations. Nonetheless, ongoing development provides an

opportunity to test mitigation measures in an adaptive management framework, with the ultimate goal of determining how to maintain robust sage-grouse populations in areas with CBNG development. The current pace and scale of CBNG development suggest that effective mitigation measures should be implemented quickly to prevent impacts from becoming more widespread.

## Management implications

Our analysis indicates that maintaining extensive stands of sagebrush habitat over large areas (6.4 km or more) around leks is required for sage-grouse breeding populations to persist. This recommendation matches those of all major reviews on sage-grouse habitat requirements (Schroeder et al. 1999, Connelly et al. 2000*b*, Connelly et al. 2004, Crawford et al. 2004, Rowland 2004).

Our findings also refute the idea that prohibiting surface infrastructure within 0.4 km of the lek is sufficient to protect breeding populations, and indicate that increasing the size of no-development zones around leks would increase the probability of lek persistence. The buffer size required depends on the amount of suitable habitat around the lek and the level of impact deemed acceptable. For example, to maintain lek persistence at 50% would require a buffer size of at least 1.6-2.5 km (based on models with CBNG within 3.2 km and 6.4 km), an area 16-39 times larger than that provided by the current 0.4-km buffer. The need for larger buffer sizes is supported by several lines of reasoning. First, impacts from CBNG infrastructure (e.g., avoidance, collisions, increased raptor predation) can affect all seasonal habitats year-round (e.g., nesting, brood-rearing, summer, fall, and winter), not just birds attending leks during the breeding

season. Second, although timing restrictions likely reduce disturbance during the breeding season in the year the field is developed, they do not prevent impacts of infrastructure at other times of the year (e.g., winter; Doherty et al. 2008) or during the production phase, which may last several decades. Morevoer, based on lek-to-nest distances, a 0.4-km buffer is likely to protect <2% of all nesting females (Figure 1 *in* Holloran and Anderson 2005). Because leks in CBNG also have fewer males per lek, buffer sizes estimated solely from data on lek persistence may be too conservative. In practice, estimates of required buffer sizes may be less if buffers from adjacent leks overlap.

A new strategy may be necessary to maintain sage-grouse populations in regions with extensive CBNG development. I suggest a three-tier strategy of establishing core areas with little or no development, implementing more stringent on-site mitigation, and requiring off-site mitigation when on-site mitigation efforts fail. Protecting areas of undeveloped, high-quality sage-grouse habitat in the project area should be top priority. At present, there is little evidence that restrictions other than no surface occupancy allow sage-grouse to persist in CBNG landscapes, that former CBNG fields can or will be restored to a condition that meet year-round sage-grouse habitat requirements, or that populations can be easly reestablished in areas where they have been extirpated. Protected areas need only be maintained until gas production has ceased, until populations in former CBNG fields are reestablished, or until mitigation measures are identified that avoid major impacts to populations. Population goals in conservation plans for four of the five states (Wyoming, Colorado, North Dakota, and Montana) and two Canadian provinces (Alberta and Saskatchewan) experiencing oil and gas

development in the eastern half of the species' range all focus on maintaining the current distiribution of greater sage-grouse and maintaining or increasing abundance (WGFD 2003, MFWP 2005, NDGFD 2005, CDOW 2007). Currently, 83% of federal minerals within the eastern range of greater sage-grouse in the U.S. have already been leased with current 0.4-km lek buffer and timing stipulations (Naugle et al. 2008). The severity of impacts observed under current stipulations (Holloran 2005, Doherty et al. 2008, this study) and the current pace and extent of leasing suggests that the potential for impacts from oil and gas impacts throughout this species' eastern distribution is rapidly increasing. Establishment of large core areas without energy development may be required to maintain greater sage-grouse populations large and robust enough to meet state and provincial population targets and that will continue to sustain historical land uses, such as livestock grazing, hunting, and agriculture.

Improved mitigation within sage-grouse seasonal habitats may also allow improved persistence of breeding populations. Previous research suggests that a more effective mitigation strategy would include, at minimum, burying power lines (Connelly et al. 2000*b*), minimizing road and well pad construction, vehicle traffic, and industrial noise (Lyon and Anderson 2003, Holloran 2005), and managing CBNG-produced water to prevent the spread of mosquitos that vector WNv (Zou et al. 2006, Doherty 2007, Walker et al. 2007). Habitat improvement projects within CBNG fields may not improve population persistence if such areas act as population sinks. Because sage-grouse use large areas of mixed land ownership, a lack of regulation of CBNG in some areas may undermine mitigation efforts on adjacent federal, state, or private lands. For that reason, implementation of enhanced mitigation measures by operators regardless of mineral

ownership would be valuable, but will require broad-based support among stakeholders. Regardless, adaptive management will be required to to determine if and how robust sage-grouse populations can be maintained in CBNG fields. Off-site mitigation may be necessary if enhanced mitigation measures within CBNG fields cannot be implemented fast enough or broadly enough to meet overall population targets.

Successful conservation of sage-grouse populations in the PRB depends on the strategy adopted. Stakeholders must also establish acceptable population targets for areas with coal-bed natural gas development. The success or failure of conservation strategies for sage-grouse in the PRB may set a precedent for how impacts of are mitigated as energy development increases throughout the west.

## Acknowledgments

We thank D. J. Thiele, T. P. Thomas, J. Binfet, J. M. Sandrini, and B. A. Jellison of the Wyoming Game and Fish Department, B. J. Baker of Montana BLM, and R. D. Northrup of Montana Fish, Wildlife, and Parks for providing lek-count data and checking lek databases. J. D. Berry of Western Water Consultants Engineering and K. M. Clayton of Thunderbird Wildlife Consulting provided supplemental lek-count data. The University of Montana Wildlife Spatial Analysis Laboratory processed and analyzed GIS data. J. J. Rotella of Montana State University provided R code, and J. M. Graham of the University of Montana provided advice on statistical analyses. Funding was provided by the BLM, United States Department of Energy, Montana Department of Fish, Wildlife and Parks, Wyoming Game and Fish Department, Wolf Creek Charitable Foundation, National Fish and Wildlife Foundation, Petroleum Association of Wyoming, Western

Gas Resources, Inc., Anheuser-Busch Companies, Incorporated, and the University of Montana. We also wish to thank numerous private landowners in the PRB for providing access to leks. J. W. Hupp, J. L. Beck, and M. A. Gregg provided valuable feedback on the original manuscript.

## Literature Cited

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: a habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508-526.

Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070-1078.

Bevanger, K. 1998. Biological and conservation aspects of bird mortality caused by electricity power lines: a review. Biological Conservation 86:67 -76.

Braun, C. E. 1986. Changes in sage-grouse lek counts with advent of surface coal mining. Proceedings: Issues and Technology in the Management of Impacted Western Wildlife, Thorne Ecological Institute 2:227-231.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139-156.

Braun, C. E., O. O. Oedekoven, and C. L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular

emphasis on sage grouse. Transactions of the North American Wildlife and Natural Resources Conference 67:337-349.

Bureau of Land Management [BLM]. 2003*a*. Final Environmental Impact Statement and Proposed Plan Amendment for the Powder River Basin Oil and Gas Project. <http://www.blm.gov/wy/st/en/info/NEPA/bfodocs/prb-feis.html> Accessed 18 March 2007.

Bureau of Land Management [BLM]. 2003*b*. Montana Statewide Final Oil and Gas EIS and Amendment of the Powder River and Billings Resource Management Plans. <http://www.mt.blm.gov/mcfo/cbm/eis/index.html> Accessed 18 March 2007.

Burnham, K. P, and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Colorado Division of Wildlife. 2007. Colorado Greater Sage-grouse Conservation Plan, Public Review Draft. Denver, CO.

Connelly, J. W., A. D. Apa, R. B. Smith and K. P. Reese. 2000*a*. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. Wildlife Biology 6:227-232.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000*b*. Guidelines to manage sage-grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. Station Bulletin 80. University of Idaho College of Natural Resources Experiment Station, Moscow, Idaho, USA.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Moseley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2-19.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife–threats to biodiversity and human health. Science 287:443-449.

Doherty, K. E., D. E. Naugle, and B. L. Walker. 2008. Sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187-195.

Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York, New York, USA.

Ellis, K. L. 1984. Behavior of lekking sage grouse in response to a perched golden eagle. Western Birds 15:37-38.

Ellis, K. L., J. R. Parish, J. R. Murphy, and G. H. Richins. 1989. Habitat use by breeding male sage grouse: a management approach. Great Basin Naturalist 49:404-407.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field–forest ecotones. Ecology 59: 871–883.

Gelbard, J. L., and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology 17:420-432.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation. University of Wyoming, Laramie, Wyoming. 223 pp.

Hosmer, D. W., T. Hosmer, S. le Cessie, and S. Lemeshow. 1997. A comparison of goodness-of-fit tests for the logistic regression model. Statistics in Medicine 16:965-980.

Kaiser, R. C. 2006. Recruitment by greater sage-grouse in association with natural gas development in western Wyoming. Thesis, University of Wyoming, Laramie, Wyoming. 91 pp.

Knight, R. L., and J. Y. Kawashima. 1993. Responses of raven and red-tailed hawk populations to linear right-of-ways. Journal of Wildlife Management 57:266-71.

Leonard, K. M., K. P. Reese, and J. W. Connelly. 2000. Distribution, movements and habitats of sage grouse, *Centrocercus urophasianus,* on the Upper Snake River Plain of Idaho: changes from the 1950's to the 1990's. Wildlife Biology 6:265-270.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage-grouse nest initiation and movement. Wildlife Society Bulletin 31:486-491.

Montana Fish, Wildlife, and Parks. 2005. Management plan and conservation strategies for sage-grouse in Montana – final. Unpublished report. Helena, Montana, USA. 200 pages.

Morris, W., and D. F. Doak. 2002. Quantitative Conservation Biology. Sinauer Associates, Sunderland, Massachusetts, USA.

Moynahan, B. J. 2004. Landscape-scale factors affecting population dynamics of greater sage-grouse (*Centrocercus urophasianus*) in north-central Montana, 2001-2004. Dissertation. University of Montana, Missoula, MT. 141 pp.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: pending crisis for greater sage-grouse. Ecology Letters 7:704-713.

Naugle, D. E., C. A. Aldridge, B. L. Walker, K. E. Doherty, M. R. Matchett, J. McIntosh, T. E. Cornish, and M. S. Boyce. 2005. West Nile virus and sage-grouse: What more have we learned? Wildlife Society Bulletin 33:616-623.

Naugle, D. E., K. E. Doherty, B. L. Walker, M. H. Holloran, J. M. Kiesecker, H. Copeland, B. A. Rutledge, E. T. Rinkes, and T. J. Christiansen. 2008. Cumulative impacts of energy development on greater sage-grouse in North America. Studies in Avian Biology: In press.

Nelleman, C., I. Vistnes, P. Jordhøy, and O. Strand. 2001. Winter distribution of wild reindeer in relation to power lines, roads, and resorts. Biological Conservation 101:351-360.

Nelleman, C. I., I. Vistnes, P. Jordhøy, O. Strand, and A. Newton. 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. Biological Conservation 113:307-317.

North Dakota Game and Fish Department (NDGFD). 2005. Management plan and conservation strategies for greater sage-grouse in North Dakota. J. J. McCarthy and J. D. Kobriger, authors. Unpublished report. Bismarck, North Dakota, USA. 96 pages.

Patterson, R. L. 1952. The Sage Grouse in Wyoming. Wyoming Game and Fish Commission and Sage Books, Inc., Denver, Colorado.

R Development Core Team. 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Remington, T. E. and C. E. Braun. 1991. How surface coal mining affects sage grouse, North Park, Colorado. Proceedings: Issues and Technology in the Management of Impacted Western Wildlife. Thorne Ecological Institute 5:128-132.

Rowland, M. M. 2004. Effects of management practices on grassland birds: greater sage-grouse. Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA. Northern Prairie Wildlife Research Center Online. http://www.npwrc.usgs.gov/resource/ literatr/grasbird/grsg/grsg.htm (Version 12AUG2004). Accessed 14 February 2007.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage-grouse (*Centrocercus urophasianus*). Account 425 *in* A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

Smith, J. T., L. D. Flake, K. F. Higgins, G. D. Kobriger, and C. G. Homer. 2005. Evaluating lek occupancy of greater sage-grouse in relation to landscape cultivation in the Dakotas. Western North American Naturalist 65:310-320.

Steenhof, K., M. N. Kochert, and J. A. Roppe. 1993. Nesting by raptors and common ravens on electrical transmission line towers. Journal of Wildlife Management 57:272-281.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18-30.

U. S. Census Bureau. 1995. TIGER/Line® 1995 data. Available from the Wyoming Natural Resources Data Clearinghouse. http://www.sdvc.uwyo.edu/24k/road.html. Accessed 3 August 2006.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2004. Outbreak of West Nile virus in greater sage-grouse and guidelines for monitoring, handling, and submitting dead birds. Wildlife Society Bulletin 32:1000-1006.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2007. West Nile virus and greater sage-grouse: estimating infection rate in a wild population. Avian Diseases 51:691-696.

Walker, B. L. 2008. Greater sage-grouse response to coal-bed natural gas development and West Nile virus in the Powder River Basin, Montana and Wyoming, USA. Dissertation. University of Montana, Missoula, Montana, USA.

Wyoming Game and Fish Department (WGFD). 2003. Wyoming greater sage-grouse conservation plan. Unpublished report. Cheyenne, Wyoming, USA. 97 pages.

Zhou, S. 2002. Estimating parameters of derived random variables: comparison of the Delta and parametric bootstrap methods. Transactions of the American Fisheries Society 131:667-675.

Zou, L., S. Miller, and E. Schmidtmann. 2006. Mosquito larval habitat mapping using remote sensing and GIS: implications of coal-bed methane development and West Nile virus. Journal of Medical Entomology 43:1034-1041.

Figure 1. Distribution and status of active, inactive, and destroyed greater sage-grouse leks, coal-bed natural gas wells, and major highways in the Powder River Basin, Montana and Wyoming, U.S.A. The dashed line shows the extent of SPOT-5 satellite imagery. This map excludes leks that went inactive prior to 1997 and leks whose status in 2004-2005 was unknown. The status of leks within a lek complex are depicted separately. Dot sizes of active leks represent the final count of displaying males in 2004 or 2005, whichever was the last year surveyed: small = 1-25 males, medium = 26-50 males, large = 51-75 males.

Figure 2. Population indices based on male lek attendance for greater sage-grouse in the Powder River Basin, Montana and Wyoming, U.S.A., 2001-2005 for: (a) all leks combined, and (b) leks categorized as in coal-bed natural gas fields or outside coal-bed natural gas fields on a year-by-year basis. Sample sizes in parentheses above each year-to-year transition indicate the number of leks available for calculating rates of increase for that transition.

Figure 3. Number of male sage-grouse per active lek in coal-bed natural gas (gray) and outside (black) coal-bed natural gas in the Powder River Basin, Montana and Wyoming, U.S.A., 2001-2005. Error bars represent 95% confidence intervals (error bars for leks outside CBNG are too small to be visible). Sample sizes in parentheses above each index indicate the number of active leks available for calculating males per active lek in each year.

Figure 4. Timing of greater sage-grouse lek disappearance relative to coal-bed natural gas development in the Powder River Basin. Small dot = 1 lek, medium dot = 2 leks, large dot = 3 leks. Twelve of 13 inactive leks in coal-bed natural gas fields for which the year when the lek disappeared could be accurately determined became inactive after or in the same year as development reached ≥40% within 3.2 km (or >25% development within 3.2 km with ≥1 well within 350 m of the lek center).

Figure 5. Estimated lek persistence as a function of proportion sagebrush habitat within 6.4 km and either (a) proportion coal-bed natural gas (CBNG) development within 0.8 km or (b) number of years within a CBNG field for greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005. Means and 95% confidence intervals (dashed lines) are based on parametric bootstrapping. In (a), black lines are estimated lek persistence with no CBNG development, and gray lines are estimated lek persistence with 75% CBNG development within 0.8 km. Seventy-five percent CBNG development within 0.8 km is equivalent to full development under the Bureau of Land Management's current restriction on surface infrastructure within 0.4 km of active sage-grouse leks. In (b), black lines are estimated lek persistence prior to CBNG development, and gray lines are estimated lek persistence after 3 years in a developed CBNG field (i.e., ≥40% CBNG within 3.2 km or ≥25% CBNG and ≥1 well within 350 m of the lek center).

Figure 6. Estimated lek persistence as a function of the size of a no-surface-infrastructure buffer around leks for greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005. Means and 95% confidence intervals (dashed lines) are based on model-averaged coefficients and standard errors presented in Table 4. All results are for leks in an average landscape (74% sagebrush habitat, 26% other cover types within 4 miles of the lek) and assume full coal-bed natural gas (CBNG) development outside the lek buffer (i.e., all areas outside the buffer are within 350 m of a CBNG well). Results in (a) assume that lek persistence is only affected by CBNG development within 3.2 km of the lek. Results in (b) assume that lek persistence is affected by CBNG development within 6.4 km of the lek. The minimum buffer size considered (0.4 km) is the Bureau of Land Management's current standard lease stipulation.

Figure 7. Estimated lek persistence as a function of the size of a no-surface-infrastructure buffer around leks and the extent of coal-bed natural gas development outside that buffer for greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005. Means and 95% confidence intervals (dashed lines) are based on model-averaged coefficients and standard errors presented in Table 4. All results are for leks in an average landscape (74% sagebrush habitat, 26% other cover types within 4 miles of the lek). Results in (a) assume that lek persistence is only affected by CBNG development within 3.2 km (2.0 mi.) of the lek. In (a), buffer sizes are 0.4 km (0.25 mi.; pale gray), 1.0 km (0.6 mi.; medium gray), and 1.6 km (1.0 mi.; dark gray). Results in (b) assume that lek persistence is affected by CBNG development within 6.4 km (4.0 mi.)

of the lek. In (b), buffer sizes are 1.0 km (0.6 mi.; pale gray), 1.6 km (1.0 mi.; medium gray), and 3.2 km (2.0 mi.; dark gray). The minimum buffer size considered in (a) was 0.4 km, which is the Bureau of Land Management's current standard lease stipulation.

Table 1. Status of greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, U.S.A as of 2004-2005 including only leks active in 1997 or later. See text for definitions of active and inactive leks and for how leks were categorized as in coal-bed natural gas development (In CBNG) vs. outside coal-bed natural gas (Outside CBNG). Lek complexes were considered as a single lek.

| | In CBNG | | Outside CBNG | |
|---|---|---|---|---|
| Lek status | No. | %[a] | No. | %[a] |
| Active | 10 | 38 | 211 | 84 |
| Inactive | 16 | 62 | 39 | 16 |
| Unknown | 1 | | 43 | |
| Total active + inactive | 26 | | 250 | |

[a] Percentages are based on the total number of active + inactive leks only.

Table 2. Univariate model selection summary for different classes of landscape variables influencing greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005. Models within each class are listed in order of decreasing maximum log-likelihood (LL).

| Model[a] | LL | *K* | *n* | $\Delta AIC_c$ | $w_i$ | Estimate | SE |
|---|---|---|---|---|---|---|---|
| *Sagebrush* | | | | | | | |
| 6.4 km | -60.05 | 2 | 110 | 0.00 | 0.70 | 5.20 | 1.68 |
| 3.2 km | -60.95 | 2 | 110 | 1.81 | 0.28 | 4.38 | 1.53 |
| 0.8 km | -63.43 | 2 | 110 | 6.77 | 0.02 | 2.26 | 1.15 |
| *Tillage Agriculture* | | | | | | | |
| 6.4 km | -55.52 | 2 | 110 | 0.00 | 0.79 | -20.98 | 6.02 |
| 3.2 km | -56.83 | 2 | 110 | 2.63 | 0.21 | -19.31 | 6.30 |
| 0.8 km | -60.92 | 2 | 110 | 10.81 | 0.00 | -10.44 | 4.59 |
| *Power Lines* | | | | | | | |
| 6.4 km | -58.69 | 2 | 110 | 0.00 | 0.52 | -6.06 | 1.76 |
| 3.2 km | -58.81 | 2 | 110 | 0.24 | 0.46 | -4.92 | 1.43 |
| 0.8 km | -62.12 | 2 | 110 | 6.84 | 0.02 | -2.51 | 0.99 |
| *Roads* | | | | | | | |
| 3.2 km | -64.59 | 2 | 110 | 0.00 | 0.50 | -2.50 | 1.99 |
| 6.4 km | -65.20 | 2 | 110 | 1.21 | 0.27 | -1.52 | 2.35 |
| 0.8 km | -65.41 | 2 | 110 | 1.63 | 0.22 | -0.08 | 0.87 |

Table 3. Model selection summary for greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005. Maximum log-likelihood (LL), number of parameters ($K$), $\Delta AIC_c$ values, and $AIC_c$ weights ($w_i$) listed for each model in order of increasing $\Delta AIC_c$ units, starting with the best approximating model. All models shown. The $AIC_c$ value of the best approximating model in the analysis was 108.54.

| No. | Model[a] | LL | $K$ | $n$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|---|---|
| 1 | Sagebrush 6.4 + CBNG 0.8 | -51.16 | 3 | 110 | 0.00 | 0.24 |
| 2 | Sagebrush 6.4 + Agriculture 6.4 + CBNG 0.8 | -50.48 | 4 | 110 | 0.80 | 0.16 |
| 3 | Sagebrush 6.4 + Years in CBNG | -51.56 | 3 | 110 | 0.80 | 0.16 |
| 4 | Sagebrush 6.4 + CBNG 3.2 | -51.70 | 3 | 110 | 1.09 | 0.14 |
| 5 | Sagebrush 6.4 * CBNG 0.8 | -50.98 | 4 | 110 | 1.81 | 0.10 |
| 6 | Sagebrush 6.4 * Years in CBNG | -51.32 | 4 | 110 | 2.48 | 0.07 |
| 7 | Sagebrush 6.4 + Agriculture 6.4 + CBNG 3.2 | -51.52 | 4 | 110 | 2.88 | 0.06 |
| 8 | Sagebrush 6.4 + CBNG 6.4 | -53.69 | 3 | 110 | 5.07 | 0.02 |
| 9 | Sagebrush 6.4 + Agriculture 6.4 + Dist. Power Line[2] | -53.39 | 4 | 110 | 6.63 | 0.01 |
| 10 | Sagebrush 6.4 + Agriculture 6.4 + CBNG 6.4 | -53.48 | 4 | 110 | 6.81 | 0.01 |
| 11 | Sagebrush 6.4 + Agriculture 6.4 | -55.08 | 3 | 110 | 7.84 | 0.00 |
| 12 | Sagebrush 6.4 + Power Lines 6.4 | -55.08 | 3 | 110 | 7.84 | 0.00 |
| 13 | Sagebrush 6.4 + Agriculture 6.4 + Power Lines 6.4 | -54.07 | 4 | 110 | 7.99 | 0.00 |
| 14 | Sagebrush 6.4 + Agriculture 6.4 + Dist. Road[2] | -54.47 | 4 | 110 | 8.78 | 0.00 |
| 15 | Sagebrush 6.4 + Agriculture 6.4 + Roads 3.2 | -54.49 | 4 | 110 | 8.83 | 0.00 |
| 16 | Sagebrush 6.4 + Dist. Power Line[2] | -57.36 | 3 | 110 | 12.41 | 0.00 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 17 | Sagebrush 6.4 | -60.05 | 2 | 110 | 15.67 | 0.00 |
| 18 | Sagebrush 6.4 + Roads 3.2 | -59.39 | 3 | 110 | 16.46 | 0.00 |
| 19 | Sagebrush 6.4 + Dist. Road$^2$ | -59.46 | 3 | 110 | 16.62 | 0.00 |

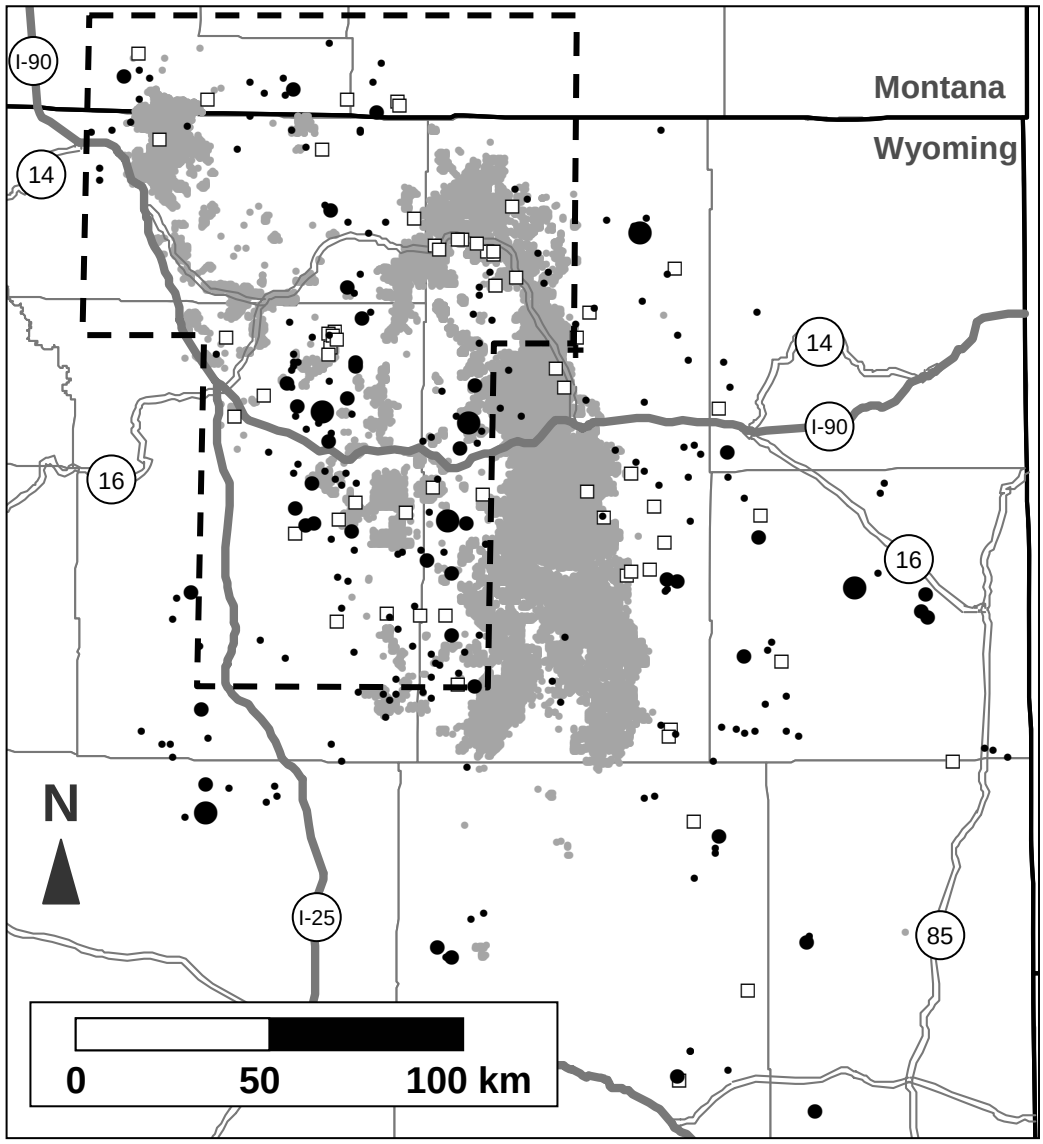
[a] CBNG = coal-bed natural gas development. Numbers refer to the radius (km) around the lek at which the variable was measured.

Table 4. Model-averaged estimates of regression coefficients (β) and standard errors (SE), odds ratios, and lower (LCL) and upper (UCL) 95% confidence limits on odds ratios for effects of landscape variables on greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005.

| Variable[a] | β | SE | Odds Ratio | Odds Ratio LCL | Odds Ratio UCL |
|---|---|---|---|---|---|
| Intercept | -1.25 | 1.40 | - | - | - |
| Sagebrush | 4.06 | 2.03 | 58.241 | 1.083 | 3131.682 |
| Agriculture | -8.76 | 8.73 | $1.57 \times 10^{-4}$ | $5.81 \times 10^{-12}$ | $4.22 \times 10^{3}$ |
| CBNG 0.8 km | -3.67 | 1. 18 | 0.026 | 0.003 | 0.257 |
| CBNG 3.2 km | -4.72 | 1.50 | 0.009 | 0.001 | 0.169 |
| CBNG 6.4 km | -5.11 | 2.04 | 0.006 | 0.0001 | 0.328 |
| Years in CBNG[b] | -1.41 | 0.58 | 0.244 | 0.078 | 0.761 |

[a] CBNG = coal-bed natural gas development.

[b] The estimated regression coefficient for Years in CBNG could only be derived from one model.







Boundary of SPOT-5 satellite imagery
Coal-bed natural gas wells
Inactive lek
Destroyed lek
Active lek:
- Small (1-25 males)
- Medium (26-50 males)
- Large (51-75 males)

Figure 2

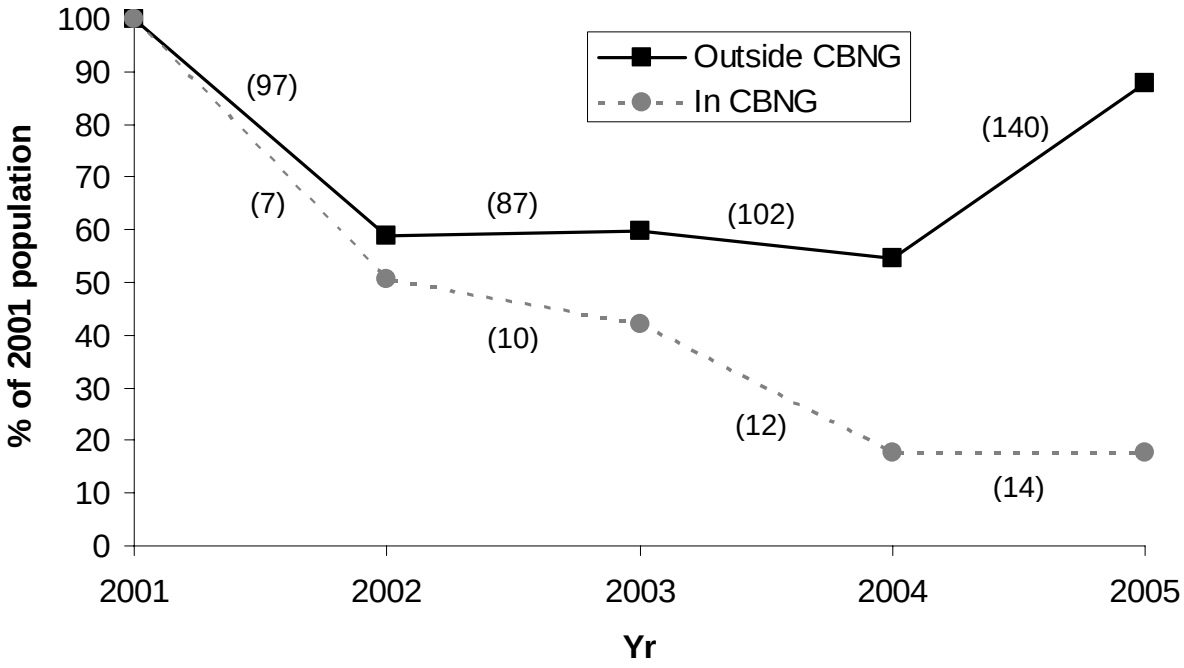

100
90
80
70
60
50
40
30
20
10
0
% of 2001 population
2001
2002
2003
2004
2005
Yr
Outside CBNG
In CBNG
(97)
(7)
(87)
(10)
(102)
(12)
(140)
(14)

Figure 3

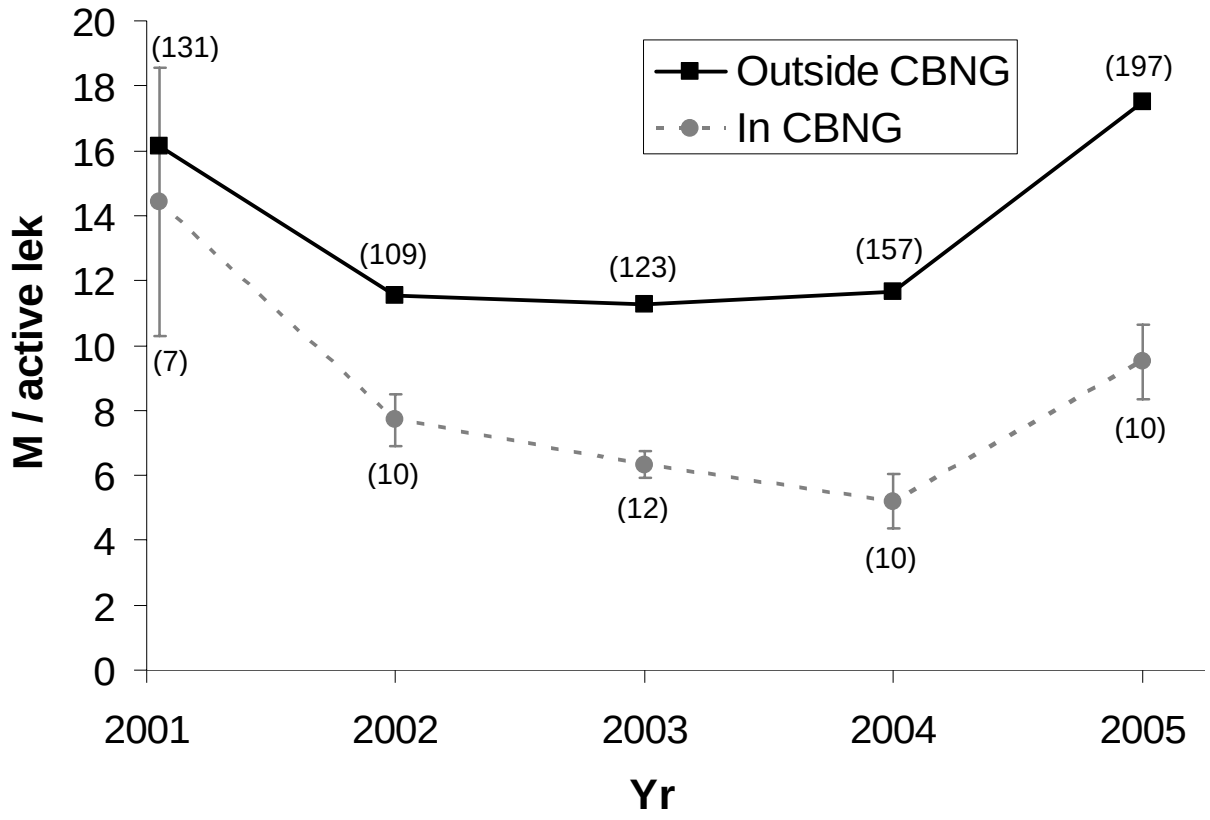

20
18
16
14
12
10
8
6
4
2
0
M / active lek
(131)
(109)
(123)
(157)
(197)
(7)
(10)
(12)
(10)
(10)
Outside CBNG
In CBNG
2001
2002
2003
2004
2005
Yr

Figure 4

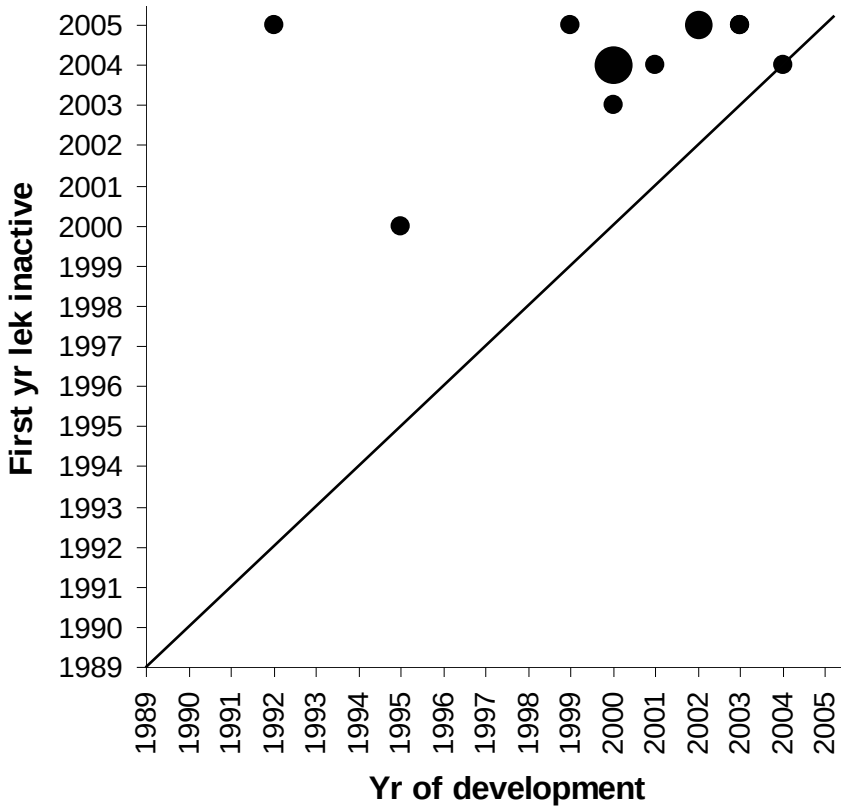
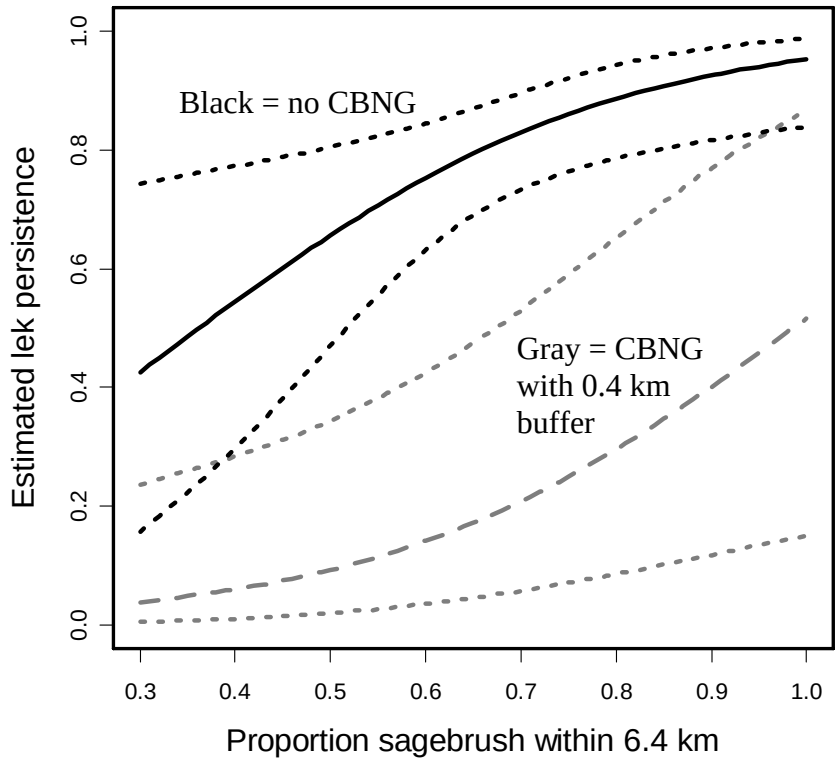

First yr lek inactive
2005
2004
2003
2002
2001
2000
1999
1998
1997
1996
1995
1994
1993
1992
1991
1990
1989
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
Yr of development

Figure 5

a


Black = no CBNG
Gray = CBNG with 0.4 km buffer
Estimated lek persistence
0.0
0.2
0.4
0.6
0.8
1.0
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Proportion sagebrush within 6.4 km

b

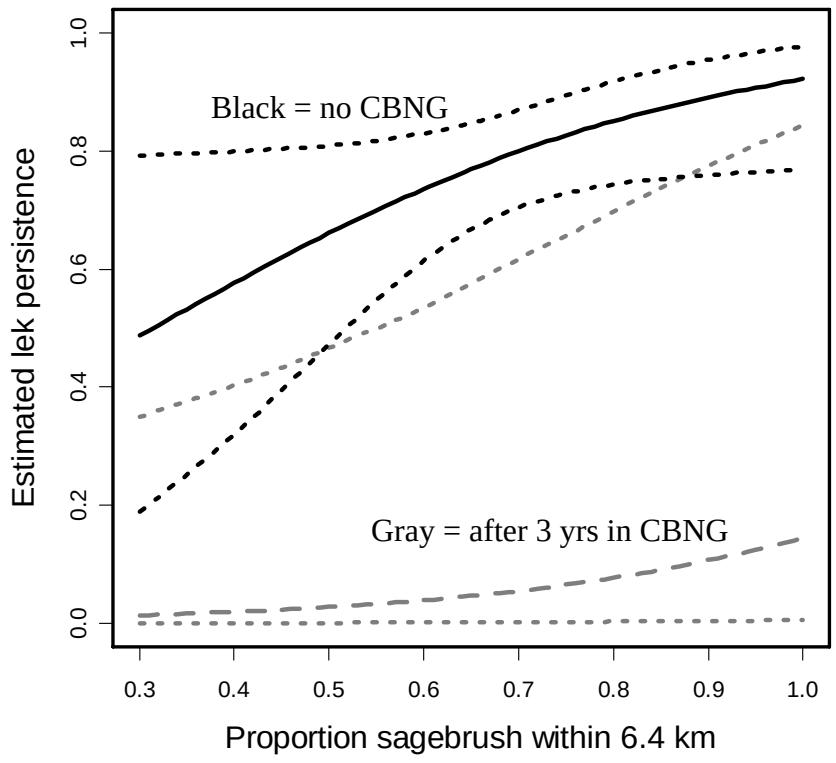
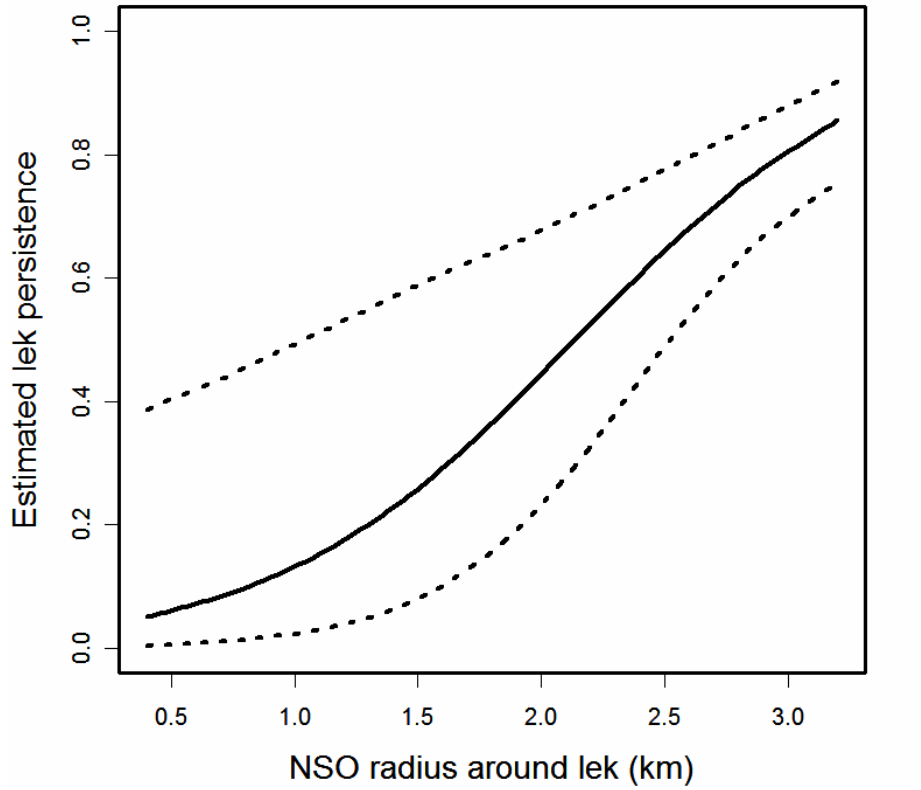

Black = no CBNG
Gray = after 3 yrs in CBNG
Estimated lek persistence
0.0
0.2
0.4
0.6
0.8
1.0
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Proportion sagebrush within 6.4 km

Figure 6.

a


Estimated lek persistence
0.0
0.2
0.4
0.6
0.8
1.0
0.5
1.0
1.5
2.0
2.5
3.0
NSO radius around lek (km)

b

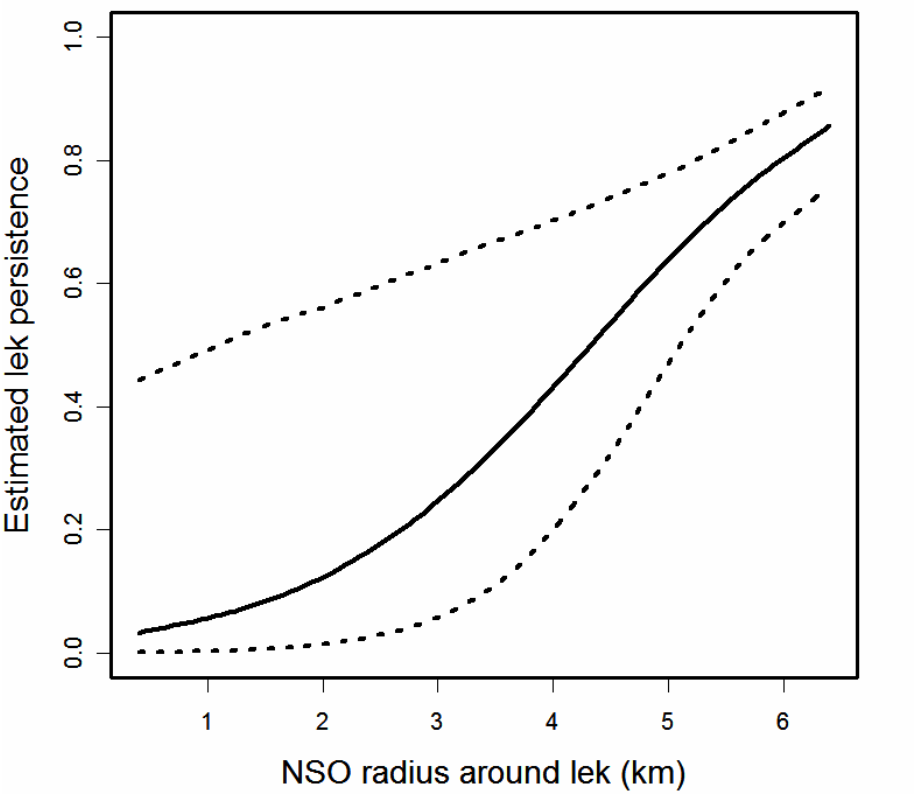
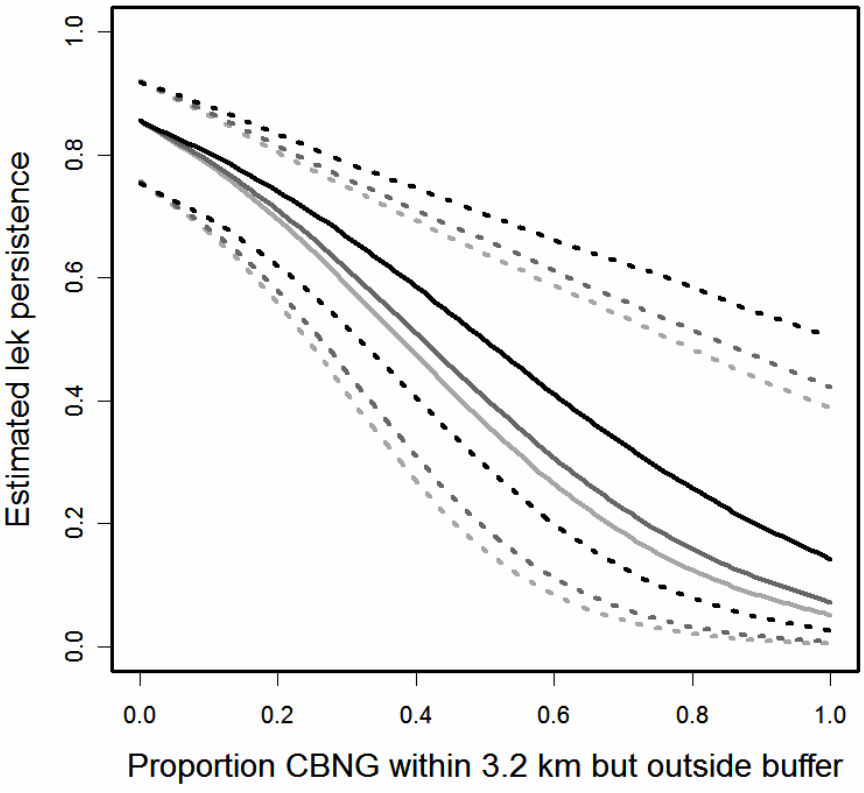
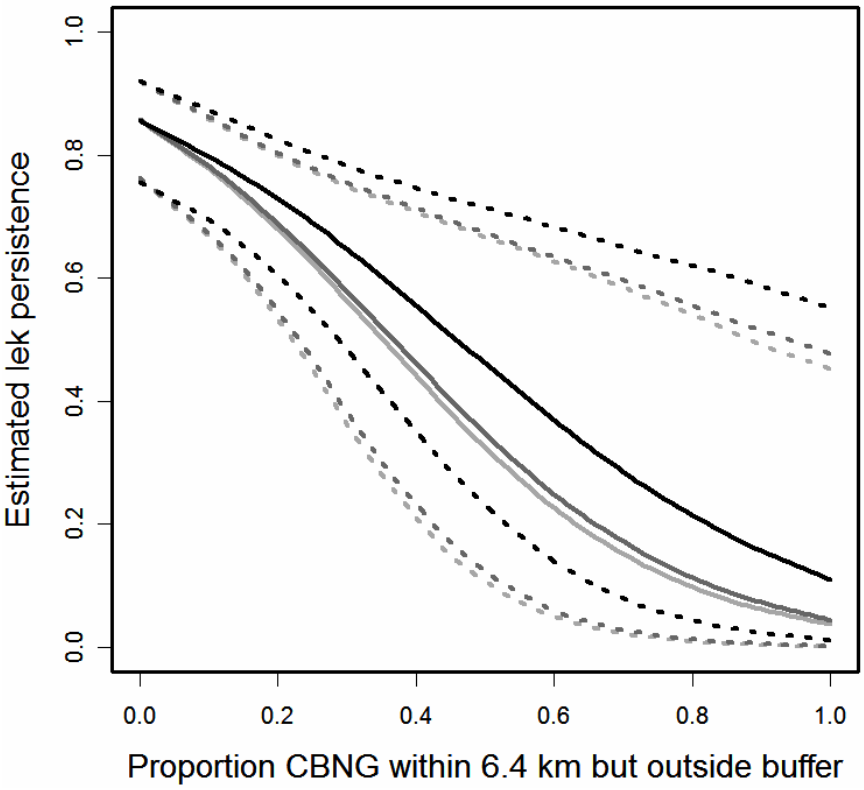

Estimated lek persistence
0.0
0.2
0.4
0.6
0.8
1.0
1
2
3
4
5
6
NSO radius around lek (km)

Figure 7.

a


Estimated lek persistence
0.0
0.2
0.4
0.6
0.8
1.0
Proportion CBNG within 3.2 km but outside buffer

b


Estimated lek persistence
0.0
0.2
0.4
0.6
0.8
1.0
Proportion CBNG within 6.4 km but outside buffer

# CHAPTER 3. WEST NILE VIRUS AND GREATER SAGE-GROUSE: ESTIMATING INFECTION RATE IN A WILD BIRD POPULATION

*Abstract*. Understanding impacts of disease on wild bird populations requires knowing not only mortality rate following infection, but also the proportion of the population that is infected. Greater sage-grouse (*Centrocercus urophasianus*) in western North America are known to have a high mortality rate following infection with West Nile virus (WNv), but actual infection rates in wild populations remain unknown. We used rates of WNv-related mortality and seroprevalence from radio-marked females to estimate infection rates in a wild greater sage-grouse population in the Powder River Basin (PRB) of Montana and Wyoming from 2003-2005. Minimum WNv-related mortality rates ranged from 2.4-13.3% among years and maximum possible rates ranged from 8.2-28.9%. All live-captured birds in 2003 and 2004 tested seronegative. In spring 2005 and spring 2006, 10.3% and 1.8% respectively, of newly-captured females tested seropositive for neutralizing antibodies to WNv. These are the first documented cases of sage-grouse surviving infection with WNv. Low to moderate WNv-related mortality in summer followed by low seroprevalence the following spring in all years indicates that annual infection rates were between 4-29%. This suggests that most sage-grouse in the PRB have not yet been exposed and remain susceptible. Impacts of WNv in the PRB in the near future will likely depend more on annual variation in temperature and changes in vector distribution than on the spread of resistance. Until the epizootiology of WNv in sagebrush-steppe ecosystems is better understood, we suggest that management to reduce impacts of WNv focus on eliminating man-made water sources that support breeding

mosquitos known to vector the virus. Our findings also underscore problems with using seroprevalence as a surrogate for infection rate and for identifying competent hosts in highly susceptible species.

Keywords: *Centrocercus urophasianus*, coal-bed natural gas, energy development, flavivirus, greater sage-grouse, infection rate, sagebrush-steppe, West Nile virus.

Assessing risks posed by emerging infectious disease is an important part of conservation planning and management for avian species of concern (6, 9, 20). Human modifications to wildlife habitat often facilitate the spread of infectious diseases (6, 8, 20), and disease outbreaks may undermine efforts to maintain viable or harvestable populations (21, 26, 35, 39).

Predicting impacts of emerging infectious disease and identifying suitable strategies to control its spread requires knowing both the prevalence of disease and the mortality rate of infected individuals (16, 17). Mortality rate is typically estimated by experimentally infecting wild-caught animals in the laboratory (e.g., 4, 16). Ideally, prevalence (i.e., exposure) would be measured by infection rate, defined as the proportion of the population that is exposed to the pathogen during an outbreak and becomes infected. Unfortunately, infection rates in wild populations are difficult to estimate (17, 18, 21). For that reason, most studies instead report seroprevalence as a surrogate for infection rate (e.g., 1, 2, 9, 11, 19, 28, 33). Drawing inferences regarding exposure based solely on seroprevalence assumes a linear relationship between the two. However, because seroprevalence estimates exclude infected individuals that die prior to sampling,

seroprevalence may underestimate infection rate in susceptible species with high disease-related mortality (13, 17). Estimates of host competence that rely on seroprevalence suffer from the same problem. If infected hosts die soon after transmitting the virus, measures of seroprevalence after the outbreak will underestimate true disease prevalence and the importance of that host in the transmission cycle. Thus, to fully understand the prevalence, impacts, and epizootiology of disease in wild bird populations requires that we estimate not only mortality rate and seroprevalence, but also actual disease-related mortality, which in turn allows estimation of infection rates.

Knowing infection rate is also crucial for identifying potential strategies for mitigating disease impacts to susceptible species. If infection rates are low, it suggests that exposure is uncommon, and that it may be possible to further reduce exposure by managing vectors, alternative hosts, or both. In contrast, if infection rates are uniformly high, then focusing on other management strategies, such as vaccination, may be more effective.

The recent spread of West Nile virus (WNv) in North America represents an important potential stressor on native bird populations, including greater sage-grouse (*Centrocercus urophasianus*) (hereafter "sage-grouse"). Sage-grouse are gallinaceous birds native to western semi-arid sagebrush (*Artemisia* spp.) habitats (30). Previously widespread, the species has been extirpated over almost half of its original range due to loss, fragmentation, and degradation of sagebrush habitat (5, 15, 29). The species' conservation status has precipitated a coordinated effort to assess risks to populations and implement conservation and management actions to mitigate those risks (5). West Nile virus was first detected in dead sage-grouse in 2002. By 2003, WNv-related mortality

had reduced late-summer survival of adult females by 25% (22) and resulted in near-extirpation of a local breeding population in northeastern Wyoming (36). In summer 2004, survival was 10% lower (86%) at sites across the species' range with confirmed WNv mortalities than at sites without (96%) (23). The extreme susceptibility of sage-grouse was confirmed in 2004 when, in separate laboratory trials, all non-vaccinated birds (n=44) experimentally infected with WNv died within 6-8 days, regardless of dosage (4, T. Cornish, unpublished data). As of fall 2006, sage-grouse mortalities positive for WNv have been confirmed in 11 of 13 states and provinces where the species still occurs (23, 34). Despite concern over impacts of WNv on sage-grouse, actual prevalence of the virus in wild populations remains unknown.

Recent reviews of West Nile virus (WNv) have identified a lack of data on infection rates from wild populations as a major hindrance to understanding impacts of this recently-arrived pathogen on North American birds (21, 26). To better understand the prevalence and potential impacts of WNv on sage-grouse, we used rates of WNv-related mortality and seroprevalence from radio-marked females to retrospectively estimate annual WNv infection rates in a wild population from 2003-2005. We also examine implications of low infection rates for managing WNv risk in sage-grouse conservation and management strategies.

## Materials and Methods

Female sage-grouse were captured and radio-marked from 2003-2006 as part of a study assessing impacts of coal-bed natural gas development on sage-grouse populations in the Powder River Basin (PRB) of southeastern Montana and northeastern Wyoming,

USA (elevation 1000-1400m). Study sites primarily consisted of semi-arid sagebrush-steppe and shortgrass prairie interspersed with mesic shrubland, greasewood (*Sarcobatus vermiculatus*) bottomlands, irrigated and dry-land crops, riparian woodland, and conifer forest. Dominant plant species in sagebrush-steppe included Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and Plains silver sagebrush (*A. cana cana*) with an understory of native and exotic grasses and forbs.

We monitored radio-marked females every 2-4 days during the peak WNv transmission period (1 July - 15 September) in each year (36). Dead birds that yielded testable carcasses (i.e., carcasses with brain, wing or leg bones, internal organs, or spinal column present) underwent complete necropsies and microscopic examination of tissues by histopathology at the Wyoming State Veterinary Laboratory (Laramie, WY). Each carcass was tested for WNv using real-time polymerase chain reaction (31) and immunohistochemistry (14). Select cases positive for WNv were confirmed by isolation of the virus from one or more tissues (brain, heart, kidney, or bone marrow) in Vero cell cultures (32).

We used a Kaplan-Meier product limit estimator with staggered-entry design to estimate mortality in each year from 2003-2005 (38). Because 40% of 50 mortalities over the three years did not yield testable carcasses, mortality estimates based only on carcasses that tested positive for WNv infection may have underestimated actual WNv-related mortality. For that reason, we calculated both minimum WNv-related mortality based on mortalities confirmed positive for WNv and maximum possible WNv-related mortality based on total mortalities minus those confirmed negative for WNv. The maximum possible estimate included mortalities for which no carcass (e.g., only a radio-

transmitter) was recovered, the carcass was not testable (e.g., too decomposed), or if tests were inconclusive. Individuals captured after 1 July were left-censored on the date of capture, and individuals that disappeared prior to 15 September (i.e., fate unknown) were right-censored on the last date they were located (38). We estimated dates of mortality as the mid-point between last date observed alive and the first date observed dead. In some cases, we estimated timing of mortality more accurately from the condition of the carcass.

To determine whether sage-grouse survived infection with the virus, we collected blood samples from live-captured birds in August-September 2003 (n = 55), March-April 2004 (n = 66), August-October 2004 (n = 46), March-April 2005 (n = 58), and March-April 2006 (n = 109). Blood samples were refrigerated, centrifuged, and serum decanted within 12 hours of capture, then frozen until testing. Serum samples were tested for neutralizing antibodies to WNv using a micro plaque reduction neutralization test (PRNT) (37). All samples positive for WNv were also tested for St. Louis encephalitis virus, the only other flavivirus in this region known to cross-react serologically with WNv (3). We report seroprevalence as the proportion of females that tested positive (PRNT titer 1:100) for antibodies to WNv and calculated 95% confidence intervals using logistic regression.

We used rates of WNv-related mortality during the WNv season and observed seroprevalence the following spring to calculate infection rates in each year from 2003-2005. We based our calculations on the mathematical model of Komar et al. (17), who showed that infection rate, I, can be expressed in terms of post-epizootic seroprevalence, S, and mortality rate following WNv infection, M, as follows:

$$I = S / [1 - M + (S * M)] \quad (1)$$

Because mortality rate, M, can be expressed as WNv-related mortality, $\Delta P$, divided by infection rate (i.e., $M = \Delta P / I$), substituting for M and rearranging the equation allowed us to calculate infection rate from WNv-related mortality rate and post-epizootic seroprevalence:

$$I = \Delta P + S - (S * \Delta P) \quad (2)$$

Because WNv-related mortality reduces post-epizootic population size and inflates the seroprevalence estimate, the $S*\Delta P$ term in Equation 2 is used to adjust the post-epizootic seroprevalence estimate to reflect seroprevalence based on population size prior to, rather than following, the outbreak. Our method assumes: (1) that additional WNv-related mortality did not occur between the end of the WNv transmission period and when serum samples were collected the following spring, and (2) that birds seropositive in spring were infected the previous summer. Coal-bed natural gas development may facilitate the spread of WNv by increasing the amount of surface water available to support breeding mosquitos (40). To better understand background rates of WNv mortality and infection in the absence of coal-bed natural gas development, we estimated rates with and without data from birds in or near areas with extensive coal-bed natural gas development.

To assess the accuracy of seroprevalence as a measure of actual infection rates, we also examined the relationship between infection rate and post-epizootic seroprevalence over a range of observed susceptibilities across species (4, 16).

## Results

Estimated minimum WNv-related mortality was low in all years, ranging from 2.4% in 2005 to 13.3% in 2003 (Table 1). Maximum possible WNv-related mortality was low to moderate, ranging from 8.2% to 28.9% (Table 1). WNv-related mortality was higher in 2003, the 6$^{th}$ warmest summer on record in the PRB, than in 2004 and 2005, the 86$^{th}$ and 41$^{st}$ warmest, respectively (24). Rates of WNv mortality and infection were substantially lower for 2003 and slightly lower for 2004 when data from birds in areas with extensive coal-bed natural gas development were removed (Table 2).

All serum samples through fall 2004 (n = 167) tested negative for WNv. In spring 2005, six of 58 (10.3%) females captured tested seropositive. In spring 2006, two of 109 (1.8%) females tested seropositive. All females seropositive for WNv tested negative for St. Louis encephalitis virus (PRNT titers <1:10). Of the six seropositive females in 2005, four were yearlings (i.e., hatched in 2004) and two were adults (i.e., hatched in 2003 or earlier). Of the two seropositive females in 2006, one was a yearling (i.e., hatched in 2005), and one was an adult (i.e., hatched in 2004 or earlier). All birds were of normal mass for their age (mean ± SE; adult: 1.64 ± 0.05 kg, n =3; yearling: 1.44 ± 0.04 kg, n = 5) and exhibited no overt signs of WNv-related disease at capture (e.g., morbidity, ataxia, tilted head, drooping wings, or impaired flight) (4, 18, 36). Seropositive females also initiated nests at the same time as other hens and had normal clutch sizes. The presence of neutralizing antibodies to WNv in yearlings captured in spring indicates that antibodies were detectable for at least 5 months following exposure. Seropositive females were distributed across six leks at four different study sites. Microsatellite analyses demonstrated that none of the eight females were related and thus can be considered

independent replicates for seroprevalence calculations (K. L. Bush, University of Alberta, unpublished data).

Estimates of both minimum and maximum possible infection rates in the PRB were low to moderate in all three years (Table 1). Estimates of minimum infection rate ranged from 4.2-13.6% and maximum possible infection rate from 9.9%-28.9%. Infection rates were higher in 2003 than in 2004 or 2005. Sample sizes were insufficient to provide precise estimates of mortality, seroprevalence, or infection rate on a site-by-site basis.

In this study, seroprevalence estimates underestimated infection rate by a small amount in all three years of the study (Table 1). However, the relationship between infection rate and post-epizootic seroprevalence was increasingly non-linear with increasing susceptibility, and the difference between the two metrics for susceptible species was largest at intermediate infection rates (Figure 1).

## Discussion

This study presents the first empirically-derived estimate of actual WNv infection rate reported for any wild bird population. In this study, estimates of seroprevalence and infection rate were similar. However, this is to be expected when infection rates and seroprevalence are both low (Figure 1). Because of the extreme susceptibility of sage-grouse, had actual infection rates been higher, the difference between observed seroprevalence and estimated infection rates would likely have been much greater. For susceptible species, seroprevalence may substantially underestimate both the prevalence and impacts of disease and confound inferences regarding exposure (e.g., habitat- or species-specific exposure rates). For example, in Rock Pigeons (*Columba livia*), which

are largely resistant to WNv (16), seroprevalence likely provides a reliable measure of exposure (e.g., 1; Figure 1). In contrast, for susceptible species (e.g., corvids, sage-grouse, American White Pelican [*Pelecanus erythrorhyncos*], and Ring-billed Gull [*Larus delawarensis*]; [4, 16, 18]), the value of seroprevalence data for making inferences about infection rates in the absence of information on mortality is suspect (Figure 1). Inferences regarding exposure in species with unknown susceptibility – including the vast majority of Nearctic and Neotropical species – may also be called into question. Despite low observed seroprevalence, sage-grouse are also considered competent amplifying hosts for WNv (4). The duration of infectious viremia in captive sage-grouse (3-5 days) was comparable to other avian species considered competent reservoirs, such as corvids, blackbirds, and raptors (16). Together, these findings underscore problems inherent with using seroprevalence as a surrogate for infection rate and for identifying competent hosts in the absence of data on disease-related mortality.

The discovery of WNv-specific antibodies in live sage-grouse also represents the first documented evidence that individuals of this species can survive WNv infection. Seropositive birds in our study likely survived because they successfully mounted an immune response to infection. However, it is also possible that seropositive birds acquired antibodies via passive vertical transmission from their mothers (12, 33). Although we observed no overt evidence of sub-lethal effects, if overwinter survival of infected birds was reduced compared to their uninfected counterparts, we may have underestimated infection rates.

How WNv will affect sage-grouse populations in the PRB in the future is unclear. Over the next decade, we suspect that impacts will depend less on resistance to disease

than on variation in temperature (23, 27, 41) and changes in vector distribution (40). First, resistance appears to be neither widespread nor common. Low infection rates indicate that most sage-grouse in the PRB probably have not been exposed to WNv and remain susceptible. Second, temperature strongly affects physiological and ecological processes that influence WNv transmission (7, 27, 41), and outbreaks are typically associated with prolonged periods of above-average temperature and drought (10). In our study, timing and extent of mortality across years were consistent with this hypothesis, with lower mortality rates and later peaks of mortality in years with lower June-August temperatures (2004-2005) (23). Third, construction of ponds associated with coal-bed natural gas development increased larval mosquito habitat by 75% from 1999-2004 over a 21,000-$km^2$ area of the PRB (40). Coal-bed natural gas development is anticipated to continue in the PRB for the next 10-15 years in occupied sage-grouse habitats.

Estimates of both seroprevalence and infection rate in our study were generally lower than seroprevalence estimates for many species in suburban, forested, farmland, urban, or wetland sites in other parts of the U.S. (e.g., 1, 2, 11, 17, 28, 33) but similar to those in desert regions of California (27). Due to seasonal drought in summer, sagebrush-steppe may support fewer avian or mammalian hosts or fewer mosquito vectors than other, more mesic habitats. Reservoir and amplifying hosts for WNv in this ecosystem remain unknown and likely cannot be managed over large geographic scales. For this reason, we suggest that management to reduce impacts of WNv in sage-grouse habitat focus on eliminating mosquito breeding habitat in anthropogenic water sources, particularly coal-bed natural gas ponds.

## References


1. Allison, A. B., D. G. Mead, S. E. J. Gibbs, D. M. Hoffman, and D. E. Stallknecht. West Nile Virus viremia in wild rock pigeons. Emer. Infect. Dis. 10:2252-2255. 2004.
2. Beveroth, T. A., M. P. Ward, R. L. Lampman, A. M. Ringia, and R. J. Novak. Changes in seroprevalence of West Nile virus across Illinois in free-ranging birds from 2001 through 2004. Am. J. Trop. Med. Hyg. 74:174-179. 2006.
3. Calisher, C. H. Antigenic classification and taxonomy of flaviviruses (family Flaviviridae) emphasizing a universal system for the taxonomy of viruses causing tick-borne encephalitis Acta Virologica 32:469-78. 1988.
4. Clark, L., J. Hall, R. McLean, M. Dunbar, K. Klenk, R. Bowen, and C. A. Smeraski. Susceptibility of greater sage-grouse to experimental infection with West Nile virus. Journal of Wildlife Diseases 42:14-22. 2006.
5. Connelly, J. W, S. T. Knick, M. A. Schroeder, and S. J. Stiver. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Cheyenne, Wyoming. 610 pages. 2004.
6. Daszak P., A. A. Cunningham, and A. D. Hyatt. Emerging infectious diseases of wildlife – threats to biodiversity and human health. Science 287:443-449. 2000.
7. Dohm, D. J., M. L. O'Guinn, and M. J. Turell. Effect of environmental temperature on the availability of *Culex pipiens* (Diptera: Culicidae) to transmit West Nile virus. Journal of Medical Entomology 39:221-225. 2002.
8. Dobson A., and J. Foufopoulos. Emerging infectious pathogens of wildlife. Phil. Trans. Roy. Soc. Series B Biological Sciences 356:1001-1012. 2001.

9. Dusek, R. J., D. Richardson, K. F. Egstad, and D. M. Heisey. Evaluating red-cockaded woodpeckers for exposure to West Nile virus and blood parasites. Southeastern Naturalist 5:561-565. 2006.
10. Epstein, P. R., and C. Defilippo. West Nile virus and drought. Global Change and Human Health 2:2-4. 2001.
11. Godsey, Jr., M. S., M. S. Blackmore, N. A. Panella, K. Burkhalter, K. Gottfried, L. A. Halsey, R. Rutledge, S. A. Langevin, R. Gates, K. M. Lamonte, A. Lambert, R. S. Lanciotti, C. G. M. Blackmore, T. Loyless, L. Stark, R. Oliveri, L. Conti, and N. Komar. West Nile virus epizootiology in the southeastern United States, 2001. Vector-Borne and Zoonotic Diseases 5:82-89. 2005.
12. Hahn, D. C., N. M. Nemeth, E. Edwards, P. R. Bright, and N. Komar. Passive West Nile Virus antibody transfer from maternal eastern screech-owls (*Megascops asio*) to progeny. Avian Diseases 50:454-455. 2006.
13. Heisey, D. M., D. O. Joly, and F. Messier. The fitting of general force-of-infection models to wildlife disease prevalence data. Ecol. 87:2356-2365. 2006.
14. Kiupel, M. H., H. A. Simmons, S. D. Fitzgerald, A. Wise, J. G. Sikarskie, T. M. Cooley, S. R. Hollamby, and R. Maes. West Nile virus infection in eastern fox squirrels (*Sciurus niger*). Vet. Pathol. 40:703-707. 2003.
15. Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634. 2003.

16. Komar, N., N. Panella, S. Langevin, A. Brault, M. Amador, E. Edwards, and J. Owen. Avian hosts for West Nile virus in St. Tammany Parish, Louisiana. Am. J. Trop. Med. Hyg. 73:1031-1037. 2005.
17. Komar, N., S. Langevin, S. Hinten, N. Nemeth, E. Edwards, D. Hettler, B. Davis, R. Bowen, and M. Bunning. Experimental infection of North American birds with the New York 1999 strain of West Nile virus. Emer. Infect. Dis. 9:311-22. 2003.
18. Marra, P. P., S. Griffing, C. Caffrey, A. M. Kilpatrick, R. Mclean, C. Brand, E. Saito, A. P. Dupuis, L. Kramer, and R. Novak. West Nile virus and wildlife. Bioscience 54:393-402. 2004.
19. Marshall, J. S., D. A. Zuwerink, R. A. Restifo, and T. C. Grubb, Jr. West Nile virus in the permanent-resident bird community of a fragmented Ohio landscape. Ornith. Monogr. 60:79-85. 2006.
20. McCallum, H. and A. Dobson. Detecting disease and parasite threats to endangered species and ecosystems. Trends Ecol. and Evol. 10:190-193. 2005.
21. McLean, R. G. West Nile virus in North American birds. Ornithol. Monogr. 60:44-64. 2006.
22. Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. West Nile virus: pending crisis for greater sage-grouse. Ecol. Lett. 7:704-13. 2004.

23. Naugle, D. E., C. L. Aldridge, B. L. Walker, K. E. Doherty, M. R. Matchett, J. McIntosh, T. E. Cornish, and M. S. Boyce. West Nile virus and sage-grouse: what more have we learned? Wildl. Soc. Bull. 33:616-23. 2005.

24. National Oceanic and Atmospheric Administration. National Climatic Data Center. Asheville, North Carolina. Accessed 17 Jan 2007. Available at: http://www.ncdc.noaa.gov/oa/climate/research/cag3/cag3.html.

25. Oyler-McCance, S. J., S. E. Taylor, and T. W. Quinn. A multilocus population genetic survey of the greater sage-grouse across their range. Molec. Ecol. 14:1293-1310. 2005.

26. Peterson, A., N. Komar, O. Komar, A. Navarro-Siguenza, M. Robbins, and E Martinez-Meyer. West Nile virus in the New World. Bird Cons. Internat. 14:215-232. 2004.

27. Reisen, W. K., Y. Fang, and V. M. Martinez. Effects of temperature on the transmission of West Nile virus by *Culex tarsalis* (Diptera: Culicidae). J. Med. Entomol. 43:309-317. 2006.

28. Ringia, A. M., B. J. Blitvitch, H.-Y. Koo, M. Van de Wyngaerde, J. D. Brawn, and R. J. Novak. Antibody prevalence of West Nile virus in birds, Illinois, 2002. Emerging Infectious Diseases 10:1120–1124. 2004.

29. Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. Distribution of sage-grouse in North America. Condor 106:363-76. 2004.

30. Schroeder, M. A., J. R. Young, and C. E. Braun. Sage grouse (*Centrocercus urophasianus*) in A. Poole and F. Gill, editors. Birds of North America, No. 425. The Birds of North America, Inc., Philadelphia, Pennsylvania USA. 28 pages. 1999.

31. Shi, P. High-throughput detection of West Nile virus RNA. J. Clin. Microbiol. 39:1264-1271. 2001.

32. Steele, K. E., M. J. Linn, R. J. Schoepp, N. Komar, T. W. Geisbert, R. M. Manduca, P. P. Calle, B. L. Raphael, T. L. Clippinger, T. Larsen, J. Smith, R. S. Lanciotti, N. A. Panella, and T. S. McNamara. Pathology of fatal West Nile virus infections in native and exotic birds during the 1999 outbreak in New York City, New York. Veterinary Pathology 37:208-224. 2000.

33. Stout, W. E., A. G. Cassini, J. K. Meece, J. M. Papp, R. N. Rosenfield, and K. D. Reed. Serologic evidence of West Nile virus infection in three wild raptor populations. Avian Diseases 49:371-375. 2005.

34. U.S. Geological Survey. Wildlife Health Bulletin 06-08. West Nile virus in greater sage-grouse [Internet]. [Modified 2006 Nov 7; cited 2006 Nov 14]. Available from: http://www.nwhc.usgs.gov/publications/wildlife_health_bulletins/WHB_06_08.jsp.

35. Van Riper III, C., S. G. Van Riper, M. L. Goff, and M. Laird. The epizootiology and ecological significance of malaria in Hawaiian land birds. Ecol. Monogr. 56:327-44. 1986.

36. Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. Outbreak of West Nile virus in greater sage-grouse and guidelines for monitoring handling and submitting dead birds. Wildl. Soc. Bull. 32:1000-1006. 2004.

37. Weingartl, H. M., M. A. Drebot, Z. Hubálek, J. Halouzka, M. Andonova, A. Dibernardo, C. Cottam-Birt, J. Larence, and P. Marszal. Comparison of assays for the detection of West Nile virus antibodies in chicken serum. Can. J. Vet. Res. 67:128-32. 2003.

38. Winterstein, S. R., K. H. Pollock, and C. M. Bunck. Analysis of survival data from radio-telemetry studies. In: Radio Tracking and Animal Populations (Millspaugh, J. J., and J. M. Marzluff, eds.), Academic Press, San Diego, CA, pp. 351-380. 2001.

39. Wünschmann, A., and A. Ziegler. West Nile virus-associated mortality events in domestic chukar partridges (*Alectoris chukar*) and domestic Impeyan pheasants (*Lophophorus impeyanus*). Avian Diseases 50:456-459. 2006.

40. Zou, L., S. N. Miller, and E. T. Schmidtmann. Mosquito larval habitat mapping using remote sensing and GIS: implications of coalbed methane development and West Nile virus. J. Med. Entomol. 43:1034-1041. 2006.

41. Zou, L., S. N. Miller, and E. T. Schmidtmann. A GIS tool to estimate West Nile virus risk based on a degree-day model. [Cited 2006 Feb 27]. Environmental Monitoring and Assessment, DOI 10.1007/s10661-006-9373-8. Available from: http://www.springerlink.com/content/q448082p32456846. 2006.

Table 1. Mortality and West Nile virus (WNv) testing of radio-marked female sage-grouse during the peak WNv transmission period (1 July - 15 September) and seroprevalence the following spring in the Powder River Basin, 2003-2005, including birds from areas with extensive coal-bed natural gas development. Estimated minimum and maximum possible mortality (ΔP), seroprevalence (S), and minimum and maximum possible infection rates (I) given as mean (95% CI). Two typographical errors were discovered after publication of Walker et al. (2007). The lower confidence limit in 2004 was 0.110, not 0.011, and the number of females monitored in 2003 was 59, not 46.

| Yr | No. sites | No. females | No. deaths | No. tested | + /- tests | Median date WNV deaths | ΔP (min) | ΔP (max) | S | I (min) | I (max) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2003 | 3 | 59 | 15 | 10 | 6/4 | 8/03 (7/24-8/05) | 0.133 (0.048-0.219) | 0.289 (0.178-0.399) | 0.000 (-) | 0.133[A] (0.048-0.219) | 0.289[A] (0.178-0.399) |
| 2004 | 6 | 118 | 17 | 9 | 4/5 | 8/23 (8/03-9/04) | 0.037 (0.003-0.071) | 0.094 (0.042-0.147) | 0.103 (0.047-0.212) | 0.136 (0.070-0.202) | 0.187 (0.110-0.265) |
| 2005 | 6 | 123 | 18 | 11 | 3/8 | 8/6 (7/28-8/07) | 0.024 (0.000-0.053) | 0.082 (0.033-0.132) | 0.018 (0.005 – 0.070) | 0.042 (0.011-0.074) | 0.099 (0.047-0.150) |

[A] Seroprevalence was 0.0 in fall 2003 and spring 2004, so the estimated infection rate in 2003 equaled estimated mortality.

Table 2. Mortality and West Nile virus (WNv) testing of radio-marked female sage-grouse during the peak WNv transmission period (1 July - 15 September) and seroprevalence the following spring in the Powder River Basin, 2003-2005, excluding birds from areas with extensive coal-bed natural gas development. This allows estimation of background infection rates in the absence of coal-bed natural gas development. Estimated minimum and maximum possible mortality (ΔP), seroprevalence (S), and minimum and maximum possible infection rates (I) given as mean (95% CI).

| Yr | No. sites | No. females | No. deaths | No. tested | + /- tests | ΔP (min) | ΔP (max) | S | I (min) | I (max) |
|---|---|---|---|---|---|---|---|---|---|---|
| 2003 | 2 | 49 | 7 | 4 | 0/4 | 0.000 (-) | 0.143 (0.047-0.239) | 0.000 (-) | 0.000[A] (-) | 0.143 [A] (0.047-0.239) |
| 2004 | 4 | 110 | 14 | 7 | 2/5 | 0.020 (0.000-0.046) | 0.081 (0.030-0.131) | 0.103 (0.047-0.212) | 0.121 (0.060-0.182) | 0.175 (0.104-0.246) |
| 2005 | 6 | 123 | 18 | 11 | 3/8 | 0.024 (0.000-0.053) | 0.082 (0.033-0.132) | 0.018 (0.005 – 0.070) | 0.042 (0.011-0.074) | 0.099 (0.047-0.150) |

[A] Seroprevalence was 0.0 in fall 2003 and spring 2004, so the estimated infection rate in 2003 equaled estimated mortality.

Figure 1.

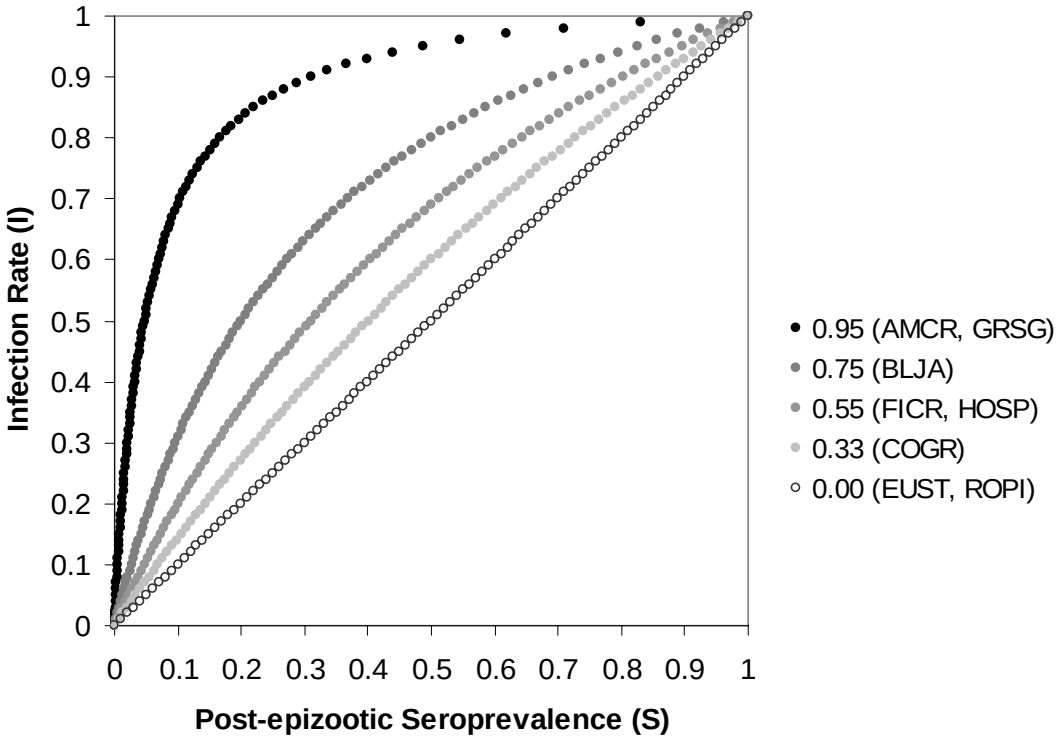

Infection Rate (I)
Post-epizootic Seroprevalence (S)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0.95 (AMCR, GRSG)
0.75 (BLJA)
0.55 (FICR, HOSP)
0.33 (COGR)
0.00 (EUST, ROPI)

Figure 1. Predicted non-linear relationships between observed post-epizootic seroprevalence (S) and actual infection rate (I) over a range of mortality rates following infection (M) for representative species (4, 17). Abbreviations: AMCR = American Crow (*Corvus brachyrhyncos*), GSGR = Greater Sage-grouse (*Centrocercus urophasianus*), BLJA = Blue Jay (*Cyanocitta cristata*), FICR = Fish Crow (*Corvus ossifragus*), HOSP = House Sparrow (*Passer domesticus*), COGR = Common Grackle (*Quiscalus quiscula*), EUST = European Starling (*Sturnus vulgaris*), ROPI = Rock Pigeon (*Columba livia*). Divergence between post-epizootic seroprevalence and infection rate increases with susceptibility and is highest at intermediate infection rates.

**Acknowledgements**

This work was supported by funding from the Bureau of Land Management, Department of Energy, and the Wyoming State Veterinary Laboratory. Additional project support came from Montana Department of Fish, Wildlife and Parks, Wyoming Game and Fish Department, National Fish and Wildlife Foundation, Montana Cooperative Wildlife Research Unit, Wolf Creek Charitable Foundation, Petroleum Association of Wyoming, Western Gas Resources, Inc., Anheuser-Busch Companies, Inc., the University of Wyoming, and the University of Montana. We thank V. Ezenwa and M. Poss for helpful comments on the manuscript.

# CHAPTER 4. DEMOGRAPHICS OF GREATER SAGE-GROUSE IN THE POWDER RIVER BASIN, 2003-2006.

*Abstract*: Obtaining reliable estimates of demographic rates and their variability over time and space is crucial for assessing and modeling the effects of potential stressors on long-term population growth for sensitive or declining wildlife species. We used maximum-likelihood methods to generate year and age-specific estimates of greater sage-grouse (*Centrocercus urophasianus*) nest, brood, and female survival rates in three regions of the Powder River Basin (Decker, MT; Buffalo, WY; Spotted Horse, WY)from 2003-2006. To assess the effect of West Nile virus (WNv) on female survival, we ran female survival analyses with and without WNv-related mortalities. We also compared maximum-likelihood estimates of nest success against values of apparent nest success and "quick" estimates of nest success derived from apparent nest success. We observed consistently high rates of nest initiation and hatching success. We also documented higher renesting rates and clutch sizes among adult females than among yearlings. Daily survival rates for nests were high during laying (0.993 ± 0.007) and higher for adult females than for yearlings. We also documented a pattern of higher daily nest survival rates earlier and later in the incubation period than in the middle. Spring precipitation the previous year had a positive effect on daily nest survival. Nest success and brood success showed parallel patterns within each region. Nest and brood success near Buffalo were lower in 2004 and high in 2005 and 2006; nest and brood success near Decker were higher in 2003 and 2004 than in 2005 and 2006. We observed the highest estimates of nest success ever reported for this species (95%) near Buffalo in 2006. Nest success

estimates obtained using the "quick" method were generally comparable with estimates derived from maximum-likelihood estimators, suggesting that the "quick" method is useful for correcting previously published estimates of apparent nest success. Parallel patterns of nest and brood survival suggest that these vital rates are influenced by similar suites of predators, or in similar ways by annual environmental (e.g., precipitation), habitat (e.g., grass height), or ecological conditions (e.g., predator abundance). Female survival was lowest in the Spotted Horse region in 2003 due to an outbreak of WNv and consistently lower in the Buffalo region than near Decker. We observed the lowest estimate of annual adult female survival (35%) ever reported for this species near Buffalo in 2005. Unexplained variation in nest, brood, and female survival across regions suggest that further investigation of local- or landscape-level habitat and anthropogenic features influencing sage-grouse and their major predators is warranted. On average, WNv-related mortality during the summer reduced annual female survival by 5% (range = 0-27%). Mortality due to WNv was an important new source of mortality in the Powder River Basin. The potential for detrimental effects of WNv on sage-grouse populations caused by landscape-level increases in anthropogenic water sources (e.g., coal-bed natural gas ponds) needs to be considered in resource management plans.

***Keywords***: *Centrocercus urophasianus*, coal-bed natural gas, demographics, greater sage-grouse, mortality, Powder River Basin, sagebrush, vital rates, West Nile virus.

Obtaining reliable estimates of demographic rates and their variability over time and space is important for assessing and modeling the effects of potential stressors on

long-term population growth. All studies of greater sage-grouse published prior to 2003 reported demographic rates based on capture-recapture data (Zablan et al. 2003) or using traditional metrics such as apparent nest success and apparent survival. A "quick" method of estimating daily nest survival (Johnson and Klett 1985) has also been used to study regional patterns of nest success in sage-grouse (Holloran et al. 2005). However, numerous advances have been made in analysis techniques for demographic rates, particularly in the application of group- and time-specific covariates to survival data (Dinsmore et al. 2002, Rotella et al. 2004, Shaffer 2004), and these techniques have provided new insights into sage-grouse ecology and management (Hausleitner 2003, Moynahan 2004, Aldridge 2005, Holloran 2005, Sika 2006). Due to potential discrepancies between nest success estimates obtained from different estimation methods (Moynahan et al. 2006*a*), it is also important to test whether estimates of apparent nest success can even be used in population modeling. Assessing the role of potential stressors such as West Nile virus (WNv) on long-term population growth also requires estimating the effect of that stressor on vital rates, after controlling for the effects of other important factors.

The objectives of this study were to: (1) generate robust year and age-specific estimates of greater sage-grouse nest, brood, and annual female survival based on maximum-likelihood methods in three regions of the Powder River Basin from 2003-2006; (2) compare estimates of nest success obtained from maximum-likelihood methods versus traditional metrics such as apparent nest success and those calculated using Johnson and Klett's (1985) "quick" method; (3) assess the influence of WNv-related mortality on annual female survival; and (4) assess how variation in nest and brood age,

female reproductive status, and precipitation influence vital rate estimates. Our estimates rates also provide baseline data for future comparisons of how vital rates change as coal-bed natural gas development expands into previously undeveloped landscapes in the Powder River Basin.

## Study Area

We conducted research in three regions of the Powder River Basin in southeastern Montana and northeastern Wyoming: (1) three sites near Decker, Montana (Bighorn Co.) from 2003-2006, (2) six sites near Buffalo, Wyoming (Johnson Co.) from 2004-2006, and (3) one site near Spotted Horse, Wyoming (Campbell Co.) in 2003-2004 (Figure 1). We studied the Spotted Horse site only in 2003-2004 because sage-grouse populations in the area were largely extirpated by an outbreak of WNv in summer 2003 (Walker et al. 2004).

These three regions vary in elevation from 1100-1600 m. They experience cold, dry winters, cool, wet springs, and hot, dry conditions in summer and fall. Average annual precipitation varies from 11-15 in with most precipitation coming in the form of winter snow (19-57 in annually) and rain in April - June (Western Regional Climate Center, Reno, Nevada, USA). Natural landscapes consisted of rolling uplands with sagebrush-steppe, mixed-grass prairie, and badlands, occasional stands of conifers, and valleys with alkali bottoms, riparian shrubs, and woodland. Sagebrush-steppe was dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) with an understory of native and non-native grasses and forbs. Plains silver sagebrush (*A. cana cana*) and black greasewood (*Sarcobatus vermiculatus*) co-occurred with Wyoming big

sagebrush in alkali bottoms. Land use was primarily cattle ranching with limited dry-land and irrigated tillage agriculture. The Spotted Horse region had widespread coal-bed natural gas development and large blocks of non-native pasture and tillage agriculture during 2003-2004. In the other two regions, the extent of coal-bed natural gas development expanded during the course of the study (Figure 1).

Sage-grouse inhabited areas of sagebrush-steppe from October-June. From July-September, birds used sagebrush-steppe, mixed-grass prairie, and areas with irrigated and dryland agriculture. Sage-grouse in the Decker region were largely non-migratory, showing average movements between breeding, summering, and wintering areas of <5 km. Many females in the Buffalo region were migratory, moving up to 30 km between nesting, summer, and winter areas (Doherty et al. 2008). Too few birds remained alive in the Spotted Horse region to draw conclusions about migratory status.

## Methods

### Field Methods

We captured and radio-marked females by rocket-netting (Giesen et al. 1982), spotlighting and hoop-netting (Wakkinen et al. 1992), and running modified walk-in traps (Schroeder and Braun 1991) on or near leks from mid-March through early April in each year. In the Decker and Spotted Horse regions, we also captured females by spotlighting and hoop-netting in brood-rearing areas in July-August and in sagebrush habitats in September and October. Upon capture, females were fitted with 21.6-g necklace-style radio collars with a 4-hour mortality switch (Model A4060, Advanced Telemetry Systems, Inc., Isanti, Minnesota) and address label. They were then banded with a size

20, individually-numbered, inscribed aluminum band (National Band and Tag Co., Newport, KY), aged by primary feather color, shape, and wear as juvenile, yearling, or adult (Eng 1995, Crunden 1963) and sexed by plumage, size, and tarsus length.

*Nest monitoring.* We used radio-telemetry to track marked females to nests during the nesting period (i.e., early April through the end of June). When we found a nest, we recorded its location using a hand-held global positioning system unit (eTrex Legend model, Garmin International, New York, New York) and monitored its status every 2-6 d until the eggs hatched or failed. The incubation period (i.e., the time between when the last egg is laid until hatch) for greater sage-grouse is 25-29 d (Schroeder et al. 1999). To eliminate the possibility of predators using markers to locate nests, we left no markers of any type. In 2003, we initially flushed females from the nest on the first visit to determine clutch size, but found that it increased the probability of nest abandonment. Thus, for the remainder of 2003, and in 2004-2006, we eliminated this problem by locating nesting females visually without flushing them. In many cases, mimicking the mooing sounds and slow, loud movement of cows while tracking females allowed close approach to nests and prevented females from flushing. Following the initial visit, we monitored the status of nests from a distance of 10-30 m using binoculars or by triangulating females to known nest locations using radio telemetry from 20-50 m away. If a hen was off the nest at the time of the visit, we checked the nest contents to determine nest status. Estimating clutch size is required to measure hatching success and apparent chick survival. In 2003-2005, we obtained a minimum estimate of clutch size based on the number of eggs counted following depredation or hatch. However, the number of eggs counted after hatch was sometimes less than that number counted and confirmed

prior to hatch. Therefore, in 2006, we conducted clutch counts by flushing the hen from the nest 21-24 d after the estimated incubation start date. Flushing females late in incubation caused no nest abandonment.

We considered a nest successful if ≥1 egg hatched; hatched eggs were identified by detached egg membranes (Klebenow 1969). One nest with an infertile clutch incubated for 54 d was considered successful. Nests were classified as unsuccessful if they were depredated, naturally abandoned, if the hen died during incubation. Because nest contents are not always reliable indicators of nest fate in sage-grouse (Coates 2007), if the nest appeared to have been depredated close to the predicted hatching date or if nest fate was unknown, we searched for evidence of chicks with radio-collared females for at least 3 visits following nest termination.

Although sage-grouse females generally do not begin incubation until the clutch is complete (Schroeder et al. 1999), they sometimes are found on nests during laying (Moynahan et al. 2006*a*). For nests that hatched, we estimated incubation start date by backdating 28 d from the estimated (or known) hatch date. Unless the hatch date was known more accurately, we estimated actual hatch date as the midpoint of the interval between visits before and after the nest hatched. For nests that did not hatch, we assumed that incubation started at the midpoint of the interval immediately preceding the first of two consecutive nest visits in which the hen was on the nest. We tested the validity of this assumption by comparing predicted hatch dates using the midpoint method against actual hatch dates of successful nests. Because the difference between predicted and actual hatch dates for successful nests averaged only 0.21 ± 0.15 d (mean ± SE; n = 219), estimates of incubation start date, and therefore nest age, were minimally biased. For

unsuccessful nests in which the female was already on the nest the first time she was located, we approximated incubation start date based on when the nest was depredated if it had been active for >21 d. Incubation start dates for some unsuccessful nests were classified as unknown. We estimated clutch initiation dates by subtracting the estimated number of days laying from the estimated incubation start date. Number of days laying was calculated as clutch size multiplied by a laying rate of 1.5 d per egg (Schroeder et al. 1999). When clutch size was unknown, we calculated initiation dates using the median clutch size for known-aged birds for each attempt (i.e., 8 for first nests of adults, 7 for renests of adults, 7 for first nests of yearlings, and 6 for renests of yearlings).

*Brood monitoring and survival.* We monitored females with broods every 3-5 d until 35 d post-hatch. On each visit, we attempted to determine whether or not she had a brood by approaching the hen, searching for chicks, and observing hen behavior. We classified a hen as having a brood if chicks were observed or heard near the hen, if the hen gave a wing-dragging or flutter-hopping display, walked or ran away from the observer while vocalizing rather than flying, or aggressively approached the observer. At approximately 35 d post-hatch, we conducted both a night-time spotlight count and a day-time flush count to determine whether the brood survived and how many chicks survived to 35 d. Chicks typically roost in the immediate vicinity of the hen at night, which increases detectability by 40% over day-time flush counts (B. Walker, unpublished data). We chose 35 d post-hatch as a cut-off because most chick mortality has already occurred by this age (Burkepile et al. 2002, Huwer 2004, Aldridge 2005, Gregg et al. 2007), chicks younger than 25 d old are difficult to detect roosting underneath the hen, and most females with broods have not yet congregated in flocks. We classified broods as having

survived to 35 d if ≥1 chick was found with the hen on either the spotlight count or flush count and the hen had not been seen with other adults prior to 35 d. Brood survival was classified as unknown if the brood hen could not be followed for the full 35-d period or if the brood hen was found in a flock with other adults and juveniles prior to 35 d post-hatch. We considered a brood to have failed if the female flew long distance before chicks were 10 d old or if she was located in an adult-only flock prior to 35 d post-hatch.

*Female survival.* We attempted to monitor female survival every 2-5 d from April through mid-September in each year from 2003-2006, every 45 d during fall-winter 2003-2004, 2004-2005, and 2005-2006, and approximately every 90 d during fall-winter 2006-2007. From April-September, most checks were visits by ground crews, whereas most checks during fall and winter were from the air. We attempted to locate and confirm mortality of radio-marked females as soon as practicable following detection of a mortality signal. Because aging radio-transmitters began to malfunction after reaching 2-3 times their guaranteed battery life (i.e., they produced weak, irregular signals or unpredictably switched back and forth between mortality and live mode), we right censored these individuals the last time their status as alive or dead was visually confirmed after unusual signals were first noted. To eliminate potential bias due to capture-related stress or injury, we censored the first interval following capture.

**Analyses**

*Nest initiation, renesting rate, clutch size, and hatching success.* We estimated age-specific nest initiation rates as the proportion of females found on a nest divided by the number of females alive and adequately monitored during the nesting period (i.e.,

early April through the last known clutch completion date for first nests) in that year for each age class (yearling vs. adult). We considered females to have been adequately monitored if they were visually located at least once every 7 d during the nesting period. We estimated renesting rate as the proportion of females found on a second nest divided by the number of females alive and adequately monitored from the failure of their first nest through the end of the renesting period in any given year for each age class. We estimated clutch size only from clutches in which clutch size was confirmed. Because of our nest-monitoring protocol, we were not always able to obtain accurate clutch count data for nests depredated prior to the clutch count or hatching date. We measured age-specific hatching success as the total number of successfully hatched eggs in all nests divided by the total number of eggs laid in nests with known clutch size for each age class. We calculated standard errors for nest initiation, renesting rate, and hatching success as the square root of the theoretical variance of a proportion ($\sigma^2 = pq/n$), where $p$ = proportion that nested, renested, or hatched, $q = 1 - p$, and $n$ = number of sample units included in the analysis.

*Apparent nest, brood, and female survival.* We calculated apparent nest success as the number of successful nests divided by the total number of nests of known fate. Similarly, we calculated apparent brood success as the number of successful broods divided by the total number of broods of known fate and apparent chick survival as the total maximum number of chicks counted on the 35-d spotlight or flush count divided by the total number of chicks that hatched among broods of known fate. Brood fate was considered unknown if females with chicks flocked with other females prior to 35-day chick counts or if hens died when chicks were 15-35 d of age. Many brood females in

the Buffalo region were not monitored throughout the 35-d brood-rearing period because they crossed onto inaccessible property or could not be relocated. Therefore, estimates of apparent brood success and apparent chick survival are based on only a subset of broods in the brood-survival analysis. Broods were assumed to have failed if hens died when chicks were ≤ 15 d of age.

*"Quick" estimates of daily nest survival.* We used the "quick" method of Johnson and Klett (1985) to generate estimates of nest success for yearling and adult females in each region in each year. This method uses information about the average nest age when first discovered (*f*) and length of the incubation period (*h*) to estimate an approximate daily nest survival rate (*S*) as the (*h-f*) root of apparent nest success. From that, an approximate value for nest success is calculated as $S^h$. Because nests of radio-marked sage-grouse are typically discovered on the first visit after the start of incubation, we estimated average nest age when nests were discovered as one-half the length of the average monitoring interval in each year. In our study, these intervals were 5 d in 2003 and 3-4 d from 2004-2006.

*Nest, brood, and female spring-summer daily survival rates.* We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate sets of *a priori* candidate models describing variation in daily survival rate (DSR) of nests, of broods, and of females during the spring-summer season. We evaluated relative support for each candidate model using the generalized linear model method described by Rotella et al. (2004) in Statistical Analysis Software (SAS), version 9.1. For most models, we used the logit link to avoid convergence problems and constrain estimates to a (0, 1) interval (Rotella et al. 2004). However, we used the sine link in female survival models where

100% survival among a subset of individuals caused problems with convergence. This method allows staggered entry and right-censoring, variation in interval lengths between visits, and makes no assumptions about when nest failure, brood failure, or death of the female occur during an interval (Rotella et al. 2004). The method assumes: (1) homogenous DSRs within a set of covariate conditions; (2) fates are correctly classified; (3) visits do not influence survival; (4) fates are independent; (5) all visits in which fate is determined are recorded; (6) checks are conducted independently of fate, and (7) all nests, broods, and females are correctly aged (Dinsmore et al. 2002, Rotella et al. 2004). In each analysis, we assessed relative support for each model in the model set by comparing Akaike Information Criterion values adjusted for small sample size ($AIC_c$) and $AIC_c$ weights (Burnham and Anderson 2002). To assess support for different variables, we examined maximum-likelihood estimates of coefficients and associated standard errors for each model. Due to model uncertainty, we used model-averaging to obtain unconditional estimates and standard errors for regression coefficients. We used the ESTIMATE command within SAS PROC NLMIXED to calculate nest success as the product of all DSRs for specific models of interest over a 28-d incubation period for nests, a 35-d period for broods, and over the spring-summer period for females (Rotella et al. 2004). These commands generate an approximate standard error for nest and brood success based on the Delta method (Seber 1982, Billingsley 1986). Tests for goodness-of-fit and overdispersion are not yet available for these types of models (Rotella et al. 2007). We estimated annual female survival as the product of spring-summer and fall-winter survival rates. Season lengths for spring-summer and fall-winter varied slightly among years depending on nesting phenology. Because we wished to make inferences

regarding natural processes that influence nest failure, especially predation, we considered a nesting interval successful if the nest was intact at the end of the interval and the female was alive or had been killed while away from the nest. If the female was killed by a predator while on the nest, we classified the nest as having failed. To estimate what female survival would have been in the absence of WNv mortality, we ran the analysis again after removing all females known to have died from WNv. This may underestimate the effect of WNv because only 40% of mortalities during the WNv season yielded testable carcasses (Walker et al. 2004).

*Fall-winter female survival rates.* Due to relatively high fall-winter survival rates and long intervals between visits (45-90 d), maximum-likelihood methods failed to converge. Therefore, we estimated fall-winter female survival rates over the entire fall-winter period using Kaplan-Meier analysis (Winterstein et al. 2001) rather than estimating daily or monthly survival rates. Kaplan-Meier analysis allows staggered entry and right-censoring. We assumed that females died at the midpoint of the interval prior to detecting a mortality.

*Observer effects.* To meet assumption (3) in the nest-survival analysis, we excluded 14 nests (nine in 2003, three in 2005, and two in 2006) that were abandoned due to research activities. Also, brood fate could not be determined on all visits. Therefore, to meet assumption (2) in the brood-survival analysis, we eliminated from the analysis all visits in which brood fate could not be determined.

*Hypotheses.* Each of the candidate models in the model set represented a specific hypothesis for how female characteristics, season, and environmental variables, either alone or in combination, influenced daily nest, brood, and female survival. In the nest-

survival analysis, we constructed models as combinations of *Nest age*, *Hen age*, *Nest attempt*, *Julian date*, *Previous spring precipitation*, *Previous spring drought index*, *Region*, and *Year*. In the brood-survival analysis, we constructed models using *Brood age*, *Hen age*, *Nest attempt*, *Julian date*, *Spring precipitation*, *Region*, and *Year*. For the female survival analysis, we constructed models with effects of *Hen age*, *Nesting status, Brooding status, WNv season*, *Region*, and *Year*. We outline the biological hypotheses for running models with each of these variables below.

*Nest age*. Daily survival rate (DSR) of nests may increase with nest age for two reasons. Increasing grass and forb growth around nests over time (Hausleitner et al. 2005) may decrease the detectability of nests to predators and lead to a pattern of increasing DSR with nest age (Holloran et al. 2005, Moynahan et al. 2006*a*). Increasing nest survival with nest age may also result from heterogeneity among nests in detectability to predators because easily detected nests are likely to be depredated earlier (Klett and Johnson 1982, Martin et al. 2000, Dinsmore et al. 2002). To control for this phenomenon, we first examined the influence of *Nest age* on DSR. Because the relationship between DSR and Nest age may be non-linear, we also considered a model with both *Nest age* and *Nest age* + *Nest age*$^2$. We defined nest age as the number of days since the estimated start of incubation. Because females spend most of their time off the nest during laying (Schroeder et al. 1999), a behavior that may decrease detectability of nests and influence estimates of DSR, we estimated DSR during laying and during incubation separately.

*Brood age*. We hypothesized that DSR of broods would increase with brood age for the same reasons as nest age. In addition, broods become more mobile with age and

begin to fly at ~15 d (Schroeder et al. 1999). To allow for either linear or nonlinear responses of DSR to brood age, we considered models with *Brood age* and with *Brood age* + *Brood age*$^2$. We defined brood age as the number of days elapsed since the estimated hatch date.

*Hen age*. Age of breeding females influences reproductive effort and reproductive success in a broad array of bird species, including sage-grouse, with older birds often having higher nest survival than younger birds (e.g., Holloran 1999, Hausleitner 2003). Older, more experienced females may be better able to select safe nest and brood-rearing locations than naïve breeders (i.e., yearlings). Alternatively, because nesting may put females at greater risk, females that place nests and raise broods in safe locations may simply be more likely to survive their first breeding season and be recruited into the adult age class. Yearlings also spend more time off the nest, and leave the nest more frequently during the day than adults, which may expose nests to greater predation from diurnal predators, such as common ravens (*Corvus corax*) (Coates 2007). Thus, we hypothesized that older females would have a higher DSR than yearlings for nests and broods. In contrast, female survival in sage-grouse generally declines with increasing age (Zablan et al. 2003, Hagen et al. 2005), possibly due to trade-offs caused by greater reproductive effort. Zablan et al. (2003) estimated annual survival for yearlings as 0.72-0.75, compared with 0.57-0.61 for adults. Thus, we anticipated lower survival among adult females than among yearlings. We also estimated age-specific nest and brood survival estimates to produce estimates that could be included in age-structured population models.

*Season effects.* Previous studies of sage-grouse have documented that late-season nests have higher survival than early-season nests (Sveum 1995, Popham 2000, Moynahan et al. 2006*a*, Sika 2006). Although this pattern has not been documented for broods, both later nests and later broods may also show higher survival because of changes in predator abundance, shifts in predator foraging strategies, increasing abundance of alternative prey over the course of the nesting season, or because increased grass cover decreases predation risk later in the season (Schroeder et al. 1999). To examine the hypothesis that nest and brood DSR increases over the course of the season, we compared the predictive value of two different variables: (a) *Nest attempt* included as a categorical nest- or brood-specific covariate, and (b) *Julian date* as a time-specific covariate. We predicted that nest and brood survival would be higher for second nesting attempts and nesting attempts later in the season. To allow for the possibility of a non-linear relationship between DSR and Julian date in the nest-survival analyses, we also included models with *Julian date* + *Julian date*$^2$. Another possibility is that brood survival could decrease over the course of the season (after controlling for brood age), especially in dry years when a lack of precipitation dries up mesic sites on which broods depend for insects and forbs or forces females and their broods to concentrate in what suitable brood-rearing habitat remains (Moynahan 2004). Thus, brood survival may decrease with increasing Julian date, or perhaps only in dry years. To examine this possibility, we considered models with a *Julian date* * *Spring precipitation* interaction in the brood-survival analysis.

*Precipitation*. We considered three variables describing different mechanisms for how precipitation affects DSR of nests. Seven nests were known to have failed due to

flooding and mudslides following a major snowstorm in mid-May 2005. To control for this phenomenon, we included an effect of extreme precipitation events in all models. We also compared the effect of winter plus spring precipitation versus winter plus spring precipitation the previous year. Grass and forb growth in sagebrush-steppe habitat are largely controlled by winter and spring precipitation, with greater herbaceous production in wetter years (Skinner et al. 2002). Increased grass and forb growth is typically preferred by females for nesting and brood-rearing (Hagen et al. 2007) and is commonly associated with higher nest success (Schroeder et al. 1999; Connelly et al. 2000, 2004). Thus, above-average spring precipitation may lead to increased nest survival (Holloran et al. 2005, also see Martin 2007). However, because birds often begin nesting in April before most new grass and forb growth has occurred, residual cover from the previous year may be more important (Schultz 2004, Holloran et al. 2005). In the Powder River Basin, birds nest from early April through mid-June. Thus, we measured the influence of spring precipitation on nest DSR by including normalized February-May precipitation in the current year and normalized February-July precipitation in the previous year. In contrast, because broods appear well after grass and forb growth has started, brood survival should depend on current year precipitation rather than residual grass cover. Thus, we only considered current spring precipitation in brood survival models. We calculated percent normal precipitation for each region in each year of our study (2003-2006) by dividing precipitation totals for each time period (Feb-May and Feb-July) by the long-term averages for those same periods based on precipitation data from 1957-2006 (Western Regional Climate Center, Reno, Nevada, USA). For the Decker region, we used precipitation data from the Sheridan Field Station, WY weather station (no.

488160). For the Buffalo region, we used data from the Buffalo, WY station (no. 481165). For the Spotted Horse region, we used precipitation data from the Clearmont, WY station (no. 481816).

*Reproductive status*. We hypothesized that female survival may depend on current or previous reproductive effort. Breeding-survival trade-offs are common in birds (Martin 1995, Clark and Martin 2008). In sage-grouse, nesting females are sometimes depredated while on nests (Schroeder et al. 1999), and previous studies have documented lower survival among nesting vs. non-nesting females (Sika 2006, *contra* Moynahan et al. 2006*b*). Females also actively defend young broods against predators with conspicuous and potential risky behaviors such as wing-dragging displays and active aggression (Schroeder et al. 1999). The tendency of brooding females to seek out wet meadows with high forb and insect abundance in mid-summer may also expose them to higher predation or mosquitos that vector WNv. Finally, residual effects of breeding may decrease subsequent survival if individuals that bred are in poorer body condition and consequently spend more time foraging than being vigilant. To test these ideas, we included two different reproductive effort terms in the female survival analysis. We coded intervals during the breeding season according to whether a female was or was not incubating a nest (*OnNest*) and whether a female was or was not with a brood younger than 35 d old (*WBrood*), with the expectation that nesting and brood-rearing females would have lower survival than non-breeding females.

*Region.* Nest, brood, and female survival may vary geographically due to ecological differences between study regions that we did not or could not measure (e.g., predator communities, grazing pressure), differences in life-history strategies (i.e., resident vs.

migratory populations), or differences in land use that influence risk of mortality (e.g., extent of coal-bed natural gas development, agricultural development, roads and powerlines, etc.) (Connelly et al. 2000, Zou et al. 2006*a*, Walker et al. 2007*a*). Therefore, we included a dummy-coded, group-level covariate for *region* to account for geographical variation unexplained by differences in other variables.

*West Nile virus.* We included a WNv variable in the female survival analysis. Sage-grouse are highly susceptible to WNv (Clark et al. 2006). The *WNv* variable denotes whether each day during the interval was, or was not, during the WNv transmission period for that region in that year based on temperature. West Nile virus transmission is regulated on an annual basis by temperature and the availability of suitable breeding areas for mosquitos (Reisen et al. 2006, Zou et al. 2006*a*). Zou et al. (2006*b*) developed a degree-day model to predict WNv transmission events based on temperature. However, the model underpredicted WNv transmission in our area because temperatures at the weather stations were lower than those at our study sites. Therefore, we revised the model to be more inclusive based on the earliest and latest confirmed WNv-related mortalities at our study sites (i.e., only a 64 degree-day threshold required for WNv transmission), then estimated the WNv transmission period in each year at each site using the revised criterion. We do not suggest that only 64 degree-days are required for within-host WNv amplification and transmission, only that a 64 degree-day threshold at the closest weather stations (10-40 miles away) coincided with WNv transmission events on our study sites. We included a *WNv*Region* interaction to allow the severity of WNv mortality to vary among regions because of greater availability of surface water from coal-bed natural gas development and irrigated agriculture in the Spotted Horse and

Buffalo regions than near Decker (Walker et al. 2004, Zou et al. 2006*a*, Doherty 2007). We also included models with a *WNv*WBrood* interaction to test whether females with broods were more vulnerable during the WNv transmission season than because broods typically require more mesic habitats in late summer than non-brooding females.

*Year*. Nest, brood, and female survival in sage-grouse can vary dramatically on an annual basis (Schroeder et al. 1999; Moynahan et al. 2006 *a*, *b*). Therefore, we included an effect of *Year* to account for annual variation in nest, brood, and female survival unexplained by other year-specific covariates (e.g., precipitation).

## Results

*Nest initiation, renesting rate, clutch size, and hatching success.* Females typically began laying in late March or early April (Table 1). The latest date a nest was initiated in any year was 2 June. Nest initiation rates were consistently high (range = 0.89-1.00) across all sites, years, and age classes (Table 2 *a*). In almost all cases, the only females not found on nests were those that were not adequately monitored during the nesting season. Adults and yearlings showed similar rates of nest initiation rate (0.99 ± 0.008 SE for adults vs. 0.97 ± 0.013 SE for yearlings). Renesting rate was higher for adults (0.54 ± 0.054 SE) than for yearlings (0.19 ± 0.049 SE) (Table 2 *a, b*). Renesting rates were lower for both adults and yearlings in 2004. Over the course of four years, one of 14 adult females whose second nest failed attempted a third nest, whereas no yearling females attempted a third nest. Mean clutch size of first nests was consistently higher than that of renests, and clutch size was consistently higher for adults than for yearlings (Table 3). Observed clutch size varied from as many as 14 eggs (in an adult's first nest)

to only 2 eggs (in a yearling's renest). Hatching success was uniformly high, varying from 0.87-1.00 across all regions, years, and age classes (Table 3). There was no obvious relationship between hatching success and hen age or between hatching success and nest attempt (Table 3).

*Apparent nest success and causes of nest failure.* Apparent nest success varied by region and year from 0.46 to 0.85 (Table 4). Fifteen nests (ten in 2003, three in 2005, and two in 2006) were abandoned after the hen was flushed from the nest by observers during laying or early in incubation. Seventy-eight percent of 175 nests that failed due to natural causes were depredated (Table 5). Nest predators could not be identified in most cases, but mammals, birds, and snakes were all known to have depredated nests based on sign at nests. A major snowstorm on 11-12 May 2005 caused seven females to abandon first nests due to drifting snow, flooding, and mudslides (Table 5). Natural abandonment was otherwise uncommon; only three other nests were abandoned, all for unknown reasons. Mortality of females during incubation was the cause of failure for approximately 11% of 175 nests that failed due to natural causes (Table 5). Of these, only seven female were killed while on the nest. In these cases, the nest was also depredated. In contrast, 11 females were killed during the incubation period while away from their nests, which remained intact. The cause of failure for 10 nests was unknown. Quick estimates of nest success for each region, year, and age class were similar to maximum-likelihood estimates, except when sample sizes were low (Table 6).

*Hatching dates, apparent brood success, and apparent chick survival.* Almost one-quarter of females with broods in the Buffalo region could not be monitored for 35-d post-hatch because they crossed onto inaccessible property or moved long-distance and

could not be relocated, so the fate of many broods and chicks was unknown (Table 7). Therefore, inferences regarding brood and chick survival are based on only a subset of those broods that hatched. We did not monitor broods in Spotted Horse in 2004 because the only nest monitored at that site in 2004 failed. Hatching dates across regions ranged from 9 May through 3 July (Table 7). Apparent brood success ranged from 0.66-0.93 and was similar among regions (Table 7). Apparent chick survival ranged from 0.33-0.55 (Table 7), and was lowest in 2004 (0.33-0.38), highest in 2005 (0.51-0.55), and intermediate in 2006 (0.40-0.48).

*Causes of female mortality.* We could not determine cause of death for 40% of 217 hens that died during the study (Table 8). Among the remaining mortalities, suspected proximate causes of death, in order from most common to least common, included predation (104), infection with WNv (19), collisions with vehicles and power lines (4), other diseases (2), and legal harvest (1) (Table 8).

*Daily nest survival during laying.* We estimated DSR during laying using data from 34 nests found prior to the start of incubation. Only one nest failed during this period. Due to small sample size, we estimated survival from a constant-survival model only. Daily survival rate during laying was estimated as 0.993 ± 0.007 (mean ± SE). Assuming females 2 eggs every 3 days (Schroeder et al. 1999), we estimated nest success for a 12-d laying period as 0.916 ± 0.08 (mean ± SE). Thus, we estimated that approximately 8% of nests were depredated during laying.

*Daily nest survival during incubation.* We included 428 nests from 289 individual females in the nest-survival analysis (Table 9). All eight models for DSR of nests with model weight >0.01 (i.e., those within 5 AIC*c* units of the best-approximating

model) included a *Region* by *Year* interaction (Table 10). Because coefficients for *Region*Year* effects in the top 6 models were similar, we illustrate them using results from the best-approximating model (Figure 2). Daily nest survival estimates from the Decker region were higher than in Spotted Horse in 2003 and similar to those near Buffalo in 2004, but much lower than near Buffalo in 2005 and 2006 (Figure 2). *Hen age* was in four of six models within 2.8 AIC units of the best approximating model (Table 10). As predicted, daily nest survival was higher among adults than among yearlings (Figure 3). A seasonal effect was also strongly supported, with all models within 2.2 AIC units including a positive effect of either *Julian date* or *Nest attempt*. As predicted, nests initiated earlier in the season (i.e., first nests) had lower survival than those initiated later (i.e., renests) (Figure 3). Previous spring precipitation had a positive effect on DSR in all cases (model-averaged ß ± SE = 0.79 ± 0.28), but compared to models with unspecified region and year effects, those with precipitation terms received essentially no support (>19 $AIC_c$ units lower). The *Region*Year* interaction in the top model masks the effects of previous spring precipitation because these effects are confounded (i.e., previous spring precipitation is both region- and year-specific). Current spring precipitation showed no relationship with daily nest survival. The effects of *Nest age* were unexpected; nests had higher survival early and late during the incubation period rather than simply increasing with *Nest age* (Figure 4). A *Region*Year*Hen age+Nest attempt* model was used to produce estimates of nest success for comparison with other methods and for use in population modeling (Figure 5, Table 6).

*Daily brood survival.* We included 246 broods from 206 individual females in the brood-survival analysis (Table 9). As predicted, brood survival increased with brood age

(Figure 6). All models for DSR of broods within 8 AIC*c* units of the best-approximating model included an effect of *Region* (Table 11), and estimates indicated higher brood survival in the Buffalo region than near Decker (Figure 6). Brood survival was also higher in Spotted Horse, but the effect was imprecisely estimated (Figure 6). The second-best approximating model ($\Delta AIC_c = 0.40$) included a *Region*Year* interaction. Results from this model suggest that the Buffalo region experienced intermediate brood survival in 2004 (0.68) and high brood survival in 2005 (0.92) and 2006 (0.93) (Figure 7). In the Decker region, brood survival was intermediate in 2003 (0.63), high in 2004 (0.84), intermediate in 2005 (0.67) and 2006 (0.52), whereas the only estimate for Spotted Horse suggested high brood survival in 2003 (0.82) (Figure 7). Effects of spring precipitation and hen age on brood survival were positive in all models but were imprecisely estimated. There were no obvious effects of year, Julian date, or spring drought indices on brood survival.

*Daily spring-summer female survival.* We censored four females that incurred potentially life-threatening injuries during rocket-net captures (e.g., internal bleeding) and six females that were never relocated following capture prior to analyses. In total, we included 343 individuals in the spring-summer female survival analysis (Table 9). All five models within 2 ΔAIC units of the best approximating model included a *Region*WNV* interaction (Table 12). Results from these models highlight the extremely low survival rates documented as a result of WNv mortality in Spotted Horse in 2003 (Figure 8). Model coefficients also suggest lower survival during 2003, during the WNv season, and in the Buffalo region, but all effects were imprecisely estimated. The top model also included a weak positive effect on DSR of being with a young brood, but

because hens only have young broods for short periods of time (<35d), the influence on season-long survival was minimal (Figure 7). There was no clear relationship between DSR and hen age or whether the hen was on a nest.

Re-running the analysis without the 19 confirmed WNv mortalities resulted in a top model with *Region + Year* effects, plus a positive but poorly estimated effect of having a young brood (Table 12). Results from this model indicate that, even in the absence of WNv impacts, female survival was lower near Buffalo than near Decker or Spotted Horse. A *Region*Year*Hen age* model was used to produce region-, year-, and age-specific estimates (Figure 9, Table 13).

*Fall-winter female survival.* We included 233 individuals in the fall-winter Kaplan-Meier female survival analysis (Table 9). Fall-winter survival for both age classes in the Buffalo region averaged lower in 2005-2006 than in other years. Juvenile survival near Decker in 2003-2004 and 2004-2005 was comparable with that of yearlings and adults. All yearlings near Decker in 2005-2006 and all adults near Buffalo in 2004-2005 survived the fall and winter. High fall-winter survival in Spotted Horse may be an artifact of small sample sizes (n = 1-4) in both years.

*Annual female survival.* Mortality associated with WNv reduced survival estimates in Spotted Horse in 2003 and in the Buffalo region in 2004 (Table 15). Effects of WNv mortality on survival were not detected in our sample of marked birds near Decker in 2003 or 2005, despite the documented outbreak near Spotted Horse. Effects of WNv on survival were detected in all years (2004-2006) near Buffalo.

## Discussion

*Nest initiation, renesting rate, clutch size, and hatching success.* High nest initiation rates in this study (0.97-0.99) contrast with substantially lower rates reported in several other parts of their range, particularly for yearlings (Wallestad and Pyrah 1974, Connelly et al. 1993, Heath et al. 1998, Lyon and Anderson 2003, Moynahan et al. 2006*a*, Sika 2006, Robinson 2007), but are consistent with high initiation rates reported over 4 years in Washington (Schroeder 1997). In some cases, this discrepancy may be due to other studies not monitoring birds early enough during the season (Connelly et al. 1993) or intensively enough during the nesting season (Lyon and Anderson 2003, Sika 2006) and therefore, having a higher likelihood of missing nests during laying or early in incubation. However, it may also be due to natural annual or geographic variation in environmental conditions that influenced pre-laying forage quality, body condition, or both (Barnett and Crawford 1994, Gregg et al. 2006). Estimates of nest initiation, including those reported here, are typically biased low because nests depredated during laying or during the first few days of incubation likely go undetected. Similarly, nests of females killed during laying or early incubation may also have gone undetected. Higher observed renesting rates among adults match findings from several previous studies (Sveum 1995, Heath et al. 1997, Moynahan et al. 2006*a*, Sika 2006, Gregg et al. 2006), suggesting that yearling reproductive effort is somehow constrained by developmental, physiological, or evolutionary factors.

Similar year-to-year patterns in renesting rates between two geographically disjunct regions suggests that ecological processes occurring over large scales, such as regional precipitation patterns, drive annual variation in renesting rate. Renesting was

low in 2004 in both the Decker and Buffalo regions, the only year with below-average winter-spring precipitation during the course of our study, yet higher in all other years (except when precluded by high first nest survival). Studies of radio-marked greater sage-grouse farther north in Montana also documented low renesting rates in years with below-average winter-spring precipitation (2001 and 2004) and higher renesting rates in wetter years with greater grass and forb production (2002 and 2005) (except when high survival of first nests precluded renesting) (Moynahan 2004, Sika 2006).

Clutch sizes in this study were consistent with range-wide estimates for this species, but we documented individual cases of larger clutch size (14 eggs; first nest) and smaller clutch size (2; renest) than previously reported (Schroeder et al. 1999, Connelly et al. 2004). As in other studies, our data also indicate that, on average, adults lay ~0.5 more eggs per clutch than yearlings (Petersen 1980, Moynahan 2004, Sika 2006) and that clutch sizes of first nests average ~1.5 eggs larger than renests (Moynahan 2004, Sika 2006). Hatching success in the Powder River Basin (0.92) was within the normal range for the species (0.76-0.99) (Schroeder et al. 1999).

*Nest and brood survival*. Our estimate of DSR during laying (0.993) was generally higher than estimates of DSR during incubation – with the exception of the Buffalo region in 2005 and 2006 – and higher than DSRs reported during incubation in other studies (~0.96-0.97, Moynahan 2004, Fig. 3; ~0.96-0.98, Sika 2006). This supports the hypothesis that nests generally are at lower risk of predation during laying than during incubation, perhaps due to reduced scent or activity at the nest. Like waterfowl, some female sage-grouse also sometimes cover their nests with feathers and dried grass prior to clutch completion (unpub. data), a behavior that may reduce detectability to predators.

Estimates of daily nest survival in our study (~0.963-0.979) were comparable to those reported previously by Moynahan et al. (2006*a*) and Sika (2006), again with the exception of Buffalo in 2005 (0.988) and 2006 (0.996). Our estimate of nest success for first nests of adults over a 28-day period in Buffalo in 2006 (0.945) was the highest ever reported for this species.

Estimates of daily brood survival are difficult to compare with studies that estimated survival over shorter or longer time periods (e.g., 28 d, 30 d, 56 d) because DSR increased with brood age (this study, Moynahan 2004). Estimates of annual brood success to 35 d in our study (mean = 0.75, range = 0.52-0.93 across sites and years) were comparable with estimates to 35 d reported from Alberta based on radio-marked chicks (0.63; Aldridge 2005) but generally higher than those reported from central Montana based on day-time flush counts (~0.21-0.76; Moynahan 2004). Our estimates were similar to those from south-central Montana that were based on a combination of day-time flush counts and night-time spotlight counts (0.71-0.84; Sika 2006). Our estimates of brood survival to 35 d near Buffalo in 2005 (0.92) and 2006 (0.93) are the two highest ever reported for this species. Holloran (2005) also reported relatively high rates of brood survival (0.48-0.73) for broods 45-90 d of age (i.e., from hatch through 15 August).

Estimates of apparent chick survival are tentative because we were unable to follow all broods to 35 d and unable to estimate detectability. Estimates are likely biased low due to undercounting of chicks and because we were unable to conduct night-time counts on all brood hens. In contrast, values for apparent chick survival may overestimate true values due to non-independence of fates among chicks within a brood (Aldridge 2005). Our estimates of chick survival (range 0.33-0.55) were generally higher

than those reported from previous studies using radio-marked chicks. Burkepile et al. (2002) reported 21-32% survival of chicks marked with 1.0 g transmitters to 28 d. Aldridge (2005, Figure 3-1) reported ~35% chick survival to 35 d, not accounting for non-independent fates. Brood mixing is unlikely to have influenced estimates because brood switching is relatively uncommon during early brood-rearing (<1% ; Gregg et al. 2007). Apparent chick survival was lowest in both regions in 2004 (0.33-0.38), the only drought year during our study. This matches the findings of Moynahan (2004), who found that very few chicks survived to 30 d during a severe summer drought in 2001. However, due to uncertainty in our estimates of chick survival, we were unable to test whether chick survival parallels that of brood survival within each region over time.

Parallel, but opposite patterns of nest and brood survival within each region across years during our study suggest that substantial overlap occurs in nest and brood predators [American badger (*Taxidea taxus*), coyote (*Canis latrans*), weasels, common raven (*Corvus corax*), and snakes)], that nest and brood survival are both influenced by ecological processes that mediate predation, or both. For example, environmental conditions that promote high nest survival, such as high previous spring precipitation and greater residual grass cover, may also promote high brood survival. Predation was the major cause of nest failure in our study, and it is typically the major cause of nest and brood failure for this species range-wide (Schroeder et al. 1999).

*Causes of mortality and female survival*. As in most other studies, the proximate cause of most mortality was predation. However, the second most important documented cause of mortality (approximately 9% of all mortalities) was WNv, which reinforces the idea that the virus is a significant new source of mortality in susceptible populations.

Documentation of only one legally harvested sage-grouse indicates that hunting was not a major mortality factor in our study area from 2003-2006. This finding is consistent with a concurrent study that found little support for harvest as a major source of mortality further north in Montana in 2004-2005 (Sika 2006). Unlike other studies, no deaths were reported from stock tank drowning (Sika 2006) or poisoning (Blus et al. 1989).

The positive effect of having a young brood on female survival was contrary to our prediction that defending a brood increases risk for females. However, because it resulted in only a marginal increase in season-long survival, this effect may not be biologically meaningful. It is possible that females with broods could experience higher survival if predation risk diminishes as group size increases, particularly if surrounding individuals (chicks) are more vulnerable to predators (Pulliam 1973). Females capable of successfully raising broods may also be of higher quality or in better condition.

*Sources of mortality and female survival.* Effects of WNv led to substantially lower estimates of female spring-summer survival, and effects of WNv on survival were apparent for adults and yearlings, in all three regions, and in all four years of the study. Overall, WNv mortality reduced annual survival of females by 4.7% (range 0-21%) for yearlings and 5.2% (range 0-27%) for adults. The WNv outbreak near Spotted Horse in 2003 resulted in the lowest estimate of spring-summer survival for adult females ever reported for this species (0.13 ± 0.09 SE) (Walker et al. 2004). Annual female survival rates in the Buffalo and Decker regions were reduced by similar amounts due to WNv-related mortality, although pending WNv test results on 4 birds may increase our estimate of WNv-related mortality from Buffalo in 2006. Other sage-grouse studies have also

documented substantial negative effects of WNv on survival rates in late summer (Naugle et al. 2004, 2005; Moynahan et al. 2006*b*, Sika 2006, Kaczor 2008).

Our study reinforced previous studies showing higher survival in fall-winter than in spring-summer (Moynahan et al. 2006*b*). However, moderate spring-summer survival in Buffalo in 2005 (0.58± 0.08 SE) combined with low fall-winter survival (0.61 ± 0.02 SE) led to the lowest region- and year-specific estimate of annual survival ever reported for this species, excluding those attributed to outbreaks of WNv (Walker et al. 2004, Moynahan et al. 2006*b*). However, the cause of low fall-winter survival remains unknown. The winter of 2005-2006 was mild, with above average temperatures and below average snowfall (Western Regional Climate Center data, Reno, NV), and fall-winter survival rates in the Decker region were relatively high in 2005 (1.00 for 16 yearlings, 0.77 ± 0.01 SE for 40 adults). The pattern is also inconsistent with a reproductive trade-off hypothesis. Females in the Buffalo region had high reproductive effort and high nest and brood success in both 2005 and 2006, yet fall-winter survival was only lower in 2005-2006. We were unable to assess impacts of snow depth or winter storm events on overwinter female survival, even though these factors likely are important (Moynahan et al. 2006*b*). All of our fall-winter survival estimates came from years with mild winters and no unusual snowfall or temperature events that would have restricted access to sagebrush for forage or cover. Residual effects of WNv infection from the previous summer could have been one factor reducing overwinter survival of infected individuals in 2005-2006, but estimated infection rates in summer 2005 were relatively low (<10%) (Walker et al. 2007*b*).

The best-approximating models of nest, brood, and female survival rates all showed a large effect of region. However, patterns of nest, brood, and female survival within each region were clearly different, with higher female survival in the Decker region (even after excluding WNv-related mortalities) and higher nest and brood survival in the Buffalo region. Vital rates in the Decker region were close to range-wide averages, whereas in the Buffalo region, nest survival was the highest ever reported and female survival was one the lowest ever reported. This raises the question of which ecological processes are influencing vital rates in dramatically different ways near Buffalo. Data on local-scale vegetation characteristics and landscape-scale habitat and land-use patterns may help explain additional annual and geographic variation in vital rates. Data on how nest, brood, and adult predators are responding to anthropogenic changes associated with energy development would also be valuable, but may be logistically difficult to obtain at scales appropriate for studies of sage-grouse.

## Management Implications

Minimal differences between quick and maximum-likelihood estimates of nest success with sample sizes >10 suggests that the "quick" method of estimating nest success is a valuable tool for adjusting previously published data on apparent nest success. Increased monitoring effort (i.e., decreased monitoring intervals) during the nesting period will result in improved estimates of nest initiation and renesting rates, and may reveal that sage-grouse initiate nests at higher rates than previously suspected. Parallel increases and decreases in annual renesting rates across regions and across studies suggest that renesting effort is strongly influenced by large-scale ecological

processes (e.g., regional precipitation patterns) that may be beyond the control of wildlife managers. Parallel patterns of annual nest and brood success within regions across years suggest that nest and brood predators of this species either show substantial overlap in the Powder River Basin, or that predation on nests and broods is influenced in similar ways by temporal variation in precipitation or understory productivity. Our finding of a positive effect of previous spring precipitation is consistent with previous recommendations to maintain residual grass cover as a way to improve habitat for nesting females and increase nest success (Connelly et al. 2000, Holloran et al. 2005, Hagen et al. 2007). Higher renesting rates, larger clutch sizes, and higher nest success among adult females, in combination with higher success of renests, underscores the importance of adult females for population growth. Management to improve spring-summer survival of adult females at both a local and a landscape scale would likely be more beneficial demographically than managing habitat for other life stages (e.g., broods). Management to reduce habitat for sage-grouse predators (e.g., powerlines for raptors) may also be beneficial, as predators were the main source of mortality for all life stages. Our findings suggest that reducing mortality due to WNv, particularly from anthropogenic sources (e.g., irrigated fields, coal-bed natural gas ponds, stock tanks and impoundments), is an important management concern in the Powder River Basin. The persistent, and in some cases, severe negative effects of WNv on sage-grouse in our study indicate that habitat "improvements" that create surface water in sage-grouse summer habitat may instead be detrimental to sage-grouse populations.

## Literature Cited


Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation. University of Alberta, Edmonton, Alberta, Canada.

Barnett, J. F., and J. A. Crawford. 1994. Pre-laying nutrition of sage grouse hens in Oregon. Journal of Wildlife Management 47:114-118.

Billingsley, P. 1986. Probability and Measure. 2nd Edition, John Wiley and Sons, Inc., New York, New York, USA.

Blus, L. J., C. S. Staley, C. J. Henny, G. W. Pendleton, T. H. Craig, E. H. Craig, and D. K. Halford. 1989. Effects of organophosphorus insecticides on sage grouse in southeastern Idaho. Journal of Wildlife Management 53:1139–1146.

Burkepile, N. A., J. W. Connelly, D. W. Stanley, and K. P. Reese. 2002. Attachment of radiotransmitters to one-day-old sage grouse chicks. Wildlife Society Bulletin 30:93-96.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multi–model inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York, New York, USA.

Clark, L., J. Hall, R. McLean, M. Dunbar, K. Klenk, R. Bowen, and C. A. Smeraski. 2006. Susceptibility of greater sage-grouse to experimental infection with West Nile virus. Journal of Wildlife Diseases 42:14-22.

Clark, M. E. and T. E. Martin. 2008. Modeling tradeoffs in avian life history traits and consequences for population growth. Ecological Modelling 209:110-120.

Coates, P. S. 2007. Greater sage-grouse (*Centrocercus urophasianus*) nest predation and incubation behavior. Dissertation. Idaho State University, Pocatello, Idaho, USA.

Connelly, J. W., R. A. Fischer, A. D. Apa, K. P. Reese, and W. L. Wakkinen. 1993. Renesting of sage grouse in southeastern Idaho. Condor 95: 1041-1043.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage-grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Crunden, C. W. 1963. Age and sex of grouse from wings. Journal of Wildlife Management 27:846-849.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476-3488.

Doherty, M. K. 2007. Mosquito populations in the Powder River Basin, Wyoming: a comparison of natural, agricultural and effluent coal-bed natural gas aquatic habitats. M. S. Thesis. Montana State University, Bozeman, Montana, USA.

Doherty, K. E., D. E. Naugle, and B. L. Walker. 2008. Sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187-195.

Eng, R. L. 1955. A method for obtaining Sage Grouse age and sex ratios from wings. Journal of Wildlife Management 19:267-272.

Geisen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224-231.

Gregg, M. A., M. R. Dunbar, J. A. Crawford, and M. D. Pope. 2006. Total plasma protein and renesting by greater sage-grouse. Journal of Wildlife Management 70:472-478.

Gregg, M. A., M. R. Dunbar, and J. A. Crawford. 2007. Use of implanted radiotransmitters to estimate survival of greater sage-grouse chicks. Journal of Wildlife Management 71:646-651.

Hagen, C. A., J. C. Pitman, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2005. Age-specific variation in apparent survival rates of male lesser prairie-chickens. Condor 107:78-86.

Hagen, C.A., J. W. Connelly, and M.A. Schroeder. 2007. A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. Wildlife Biology 13(S1):27-35.

Hausleitner, D. 2003. Population dynamics, habitat use and movements of greater sage-grouse in Moffat County, Colorado. M. S. Thesis. University of Idaho, Moscow, Idaho, USA.

Heath, B., R. Straw, S. Anderson, and J. Lawson. 1997. Sage grouse productivity, survival, and seasonal habitat use near Farson, Wyoming. Wyoming Game and Fish Department Completion Report, Cheyenne, Wyoming, USA.

Heath, B., R. Straw, S. Anderson, J. Lawson, and M. Holloran. 1998. Sage-grouse productivity, survival, and seasonal habitat use among three ranches with different livestock grazing, predator control, and harvest management practices. Wyoming Game and Fish Department Completion Report, Cheyenne, Wyoming, USA.

Holloran, M. J. 1999. Sage-grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. M.S. Thesis. University of Wyoming, Laramie, Wyoming, USA.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation. University of Wyoming, Laramie, Wyoming, USA.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638-649.

Huwer, S. L. 2004. Evaluating greater sage-grouse brood habitat using human-imprinted chicks. M. S. Thesis. Colorado State University, Fort Collins, Colorado, USA.

Johnson, D. H., and A. T. Klett. 1985. Quick estimates of success rates of duck nests. Wildlife Society Bulletin 13:51-53.

Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection of greater sage-grouse in northwestern South Dakota. M.S. Thesis. South Dakota State University, Brookings, South Dakota, USA.

Klebenow, D.A. 1969. Sage grouse nesting and brood habitat in Idaho. Journal of Wildlife Management 33: 649-661.

Klett, A. T., and D. H. Johnson. 1982. Variability in nest survival rates and implications to nesting studies. Auk 99:77-87.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage-grouse nest initiation and movement. Wildlife Society Bulletin 31:486-491.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecological Monographs 65: 101-127.

Martin, T. E. 2007. Climate correlates of 20 years of trophic changes in a high elevation riparian system. Ecology 88:367-380.

Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proceedings of the Royal Society of London, Series B 267:2287-2294.

Moynahan, B. J. 2004. Landscape-scale factors affecting population dynamics of greater sage-grouse (*Centrocercus urophasianus*) in north-central Montana, 2001-2004.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, J. W. Thomas. 2006*a*. Factors affecting nest survival of greater-sage-grouse in northcentral Montana. Journal of Wildlife Management .

Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2006*b*. Factors contributing to process variance in annual survival of female greater sage-grouse in north-central Montana. Ecological Applications 16:1529-1538.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: pending crisis for Greater Sage-grouse. Ecology Letters: 7:704-713.

Naugle, D. E., C. L. Aldridge, B. L. Walker, K. E. Doherty, M. R. Matchett, J. McIntosh, T. E. Cornish, M. S. Boyce. 2005. West Nile virus and sage-grouse: what more have we learned? Wildlife Society Bulletin: 33:1-8.

Petersen, B. E. 1980. Breeding and nesting ecology of female sage grouse in North Park, Colorado. M.S. Thesis. Colorado State University, Fort Collins, Colorado, USA.

Popham, G. P. 2000. Sage grouse nesting habitat in northeastern California. M.S. Thesis. Humboldt State University, Arcata, California, USA.

Pulliam, H. R. 1973. On the advantages of flocking. Journal of Theoretical Biology 38: 419-422.

Reisen, W. K., Y. Fang, V. M. Martinez. 2006. Effects of temperature on the transmission of West Nile virus by *Culex tarsalis* (Diptera: Culicidae). Journal of Medical Entomology 43:309-317.

Robinson, J. D. 2007. Ecology of two geographically distinct greater sage-grouse populations inhabiting Utah's West Desert. Thesis. Utah State University, Logan, Utah, USA.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187-205.

Rotella, J. J., M. L. Taper, S. Stephens, and M. S. Lindberg. 2007. Extending methods for modeling heterogeneity in nest-survival data using generalized mixed models. Studies in Avian Biology 34:34-44.

Schroeder, M. A., and C. E. Braun. 1991. Walk-in traps for capturing greater prairie-chickens on leks. Journal of Field Ornithology 62:378-385.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillian, New York, New York, USA.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526-540.

Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99:933-941.

Schroeder, M. A. , and C. E. Braun. 1991. Walk-in traps for capturing greater prairie-chickens on leks. Journal of Field Ornithology 62:378-385.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage Grouse (*Centrocercus urophasianus*). *In* A. Poole and F. Gill [eds.], The birds of North America, No. 425. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.

Schultz, B. 2004. Analysis of studies used to develop herbaceous height and cover guidelines for sage grouse nesting habitat. Cooperative Extension Special Publication SP-04-11, University of Nevada, Reno.

Skinner, R. H., J. D. Hanson, G. L. Hutchinson, and G. E. Schuman. 2002. Response of $C_3$ and $C_4$ grasses to supplemental summer precipitation. Journal of Range Management 55:517-522.

Sika, J. L. 2006. Breeding ecology, survival rates, and causes of mortality of hunted and nonhunted greater sage-grouse in central Montana. M.S. Thesis. Montana State University, Bozeman, Montana, USA.

Sveum, C. M. 1995. Habitat selection by sage grouse hens during the breeding season in south-central Washington. M.S. Thesis. Oregon State University, Corvallis, Oregon, USA.

Wakkinen, W.L., K.P. Reese, J.W. Connelly, R.A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425-426.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2004. Outbreak of West Nile virus in greater sage-grouse and guidelines for monitoring, handling, and submitting dead birds. Wildlife Society Bulletin 32:1000-1006.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007*a*. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644-2654.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2007*b*. West Nile virus and greater sage-grouse: estimating infection rate in a wild bird population. Avian Diseases 51:691-696.

Wallestad, R. and D. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management. 38:630-633.

Winterstein, S. R., K. H. Pollock, and C. M. Bunck. 2001. Analysis of survival data from radio-telemetry studies. Pages 351-380 *in* Radio tracking and animal populations. J. J. Millspaugh and J. M. Marzluff, eds. Academic Press, San Diego, California, USA.

Zablan, M. A., C. E. Braun, and G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal of Wildlife Management 67:144-154.

Zou, L., S. N. Miller, E. T. Schmidtmann. 2006*a*. Mosquito larval habitat mapping using remote sensing and GIS: implications of coalbed methane development and West Nile virus. Journal of Medical Entomology 43:1034-1041.

Zou, L., S. N. Miller, E. T. Schmidtmann. 2006*b*. A GIS tool to estimate West Nile virus risk based on a degree-day model. Environmental Modeling and Assessment. Published on-line: DOI 10.1007/s10661-006-9373-8.

Table 1. Timing of clutch initiation and clutch completion for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Values presented as mean (range).

| | Clutch initiation date | | | | Clutch completion date | | | |
|---|---|---|---|---|---|---|---|---|
| | AD | | YR | | AD | | YR | |
| Region - Year | 1st nests | Re-nests[a] | 1st nests | Re-nests | 1st nests | Re-nests[a] | 1st nests | Re-nests |
| Decker - 2003 | 4/11 (4/06-4/23) | 5/11 (4/25-5/27) | 4/16 (4/06-5/08) | 5/09 (4/30-5/15) | 4/24 (4/18-5/03) | 5/21 (5/06-6/04) | 4/28 (4/21-5/19) | 5/18 (5/08-5/26) |
| Decker - 2004 | 4/08 (3/30-5/01) | 4/29 | 4/10 (4/02-4/22) | - | 4/20 (4/11-5/12) | 5/10 | 4/20 (4/13-5/03) | - |
| Decker - 2005 | 4/14 (3/28-5/04) | 5/14 (4/25-5/27) | 4/19 (4/04-5/06) | 5/16 | 4/25 (4/09-5/16) | 5/24 (5/07-6/05) | 4/29 (4/15-5/12) | 5/24 |
| Decker - 2006 | 4/12 (4/04-4/29) | 5/7 (5/01-5/17) | 4/18 (4/09-4/26) | 5/03 (4/25-5/10) | 4/24 (4/15-5/10) | 5/16 (5/12-5/27) | 4/29 (4/21-5/06) | 5/12 (5/06-5/19) |
| Buffalo - 2004 | 4/5 (3/29-4/14) | 4/29 | 4/12 (4/02-4/27) | - | 4/18 (4/11-4/26) | 5/10 | 4/23 (4/16-5/04) | - |

Table 1 (cont.). Timing of clutch initiation and clutch completion for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Values presented as mean (range).

| | Clutch initiation date | | | | Clutch completion date | | | |
|---|---|---|---|---|---|---|---|---|
| | AD | | YR | | AD | | YR | |
| Region - Year | 1st nests | Re-nests[a] | 1st nests | Re-nests | 1st nests | Re-nests[a] | 1st nests | Re-nests |
| Buffalo - 2005 | 4/10 (3/31-5/03) | 5/07 (4/30-5/20) | 4/18 (4/04-5/03) | 5/15 (5/14-5/17) | 4/23 (4/12-5/15) | 5/17 (5/11-5/26) | 4/29 (4/16-5/18) | 5/22 (5/20-5/25) |
| Buffalo - 2006 | 4/12 (4/08-4/23) | 5/02 | 4/15 (4/06-5/01) | 4/12 | 4/23 (4/19-5/05) | 5/13 | 4/26 (4/18-5/12) | 4/23 |
| SH - 2003 | 4/20 (4/11-4/26) | 5/07 (5/03-5/11) | 4/20 (4/14-4/30) | - | 5/03 (4/25-5/11) | 5/14 (5/06-5/22) | 5/02 (4/26-5/11) | - |

[a] One successful third nest is included in adult renests from the Decker region in 2005.
[b] Totals also include hatched nests from breeding females of undetermined age (i.e., after-hatching-year birds).

Table 2a. Nest initiation rates ± SE, renesting rates ± SE, and second renesting rates ± SE for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Sample size is in parentheses.

| | Nest initiation rate | | | Renesting rate | | | Second renesting rate | | |
|---|---|---|---|---|---|---|---|---|---|
| Region – Year | AD | YR | All | AD | YR | All | AD | YR | All |
| Decker - 2003 | 1.00 ± 0.00 (20) | 0.89 ± 0.07 (19) | 0.95 ± 0.04 (40) | 0.67 ± 0.14 (12) | 0.56 ± 0.17 (9) | 0.62 ± 0.11 (21) | 0.00 ± 0.00 (1) | 0.00 ± 0.00 (3) | 0.00 ± 0.00 (4) |
| Decker - 2004 | 0.94 ± 0.04 (31) | 0.94 ± 0.05 (18) | 0.94 ± 0.03 (49) | 0.09 ± 0.09 (11) | 0.00 ± 0.00 (8) | 0.05 ± 0.051 (19) | 0.00 ± 0.00 (1) | - | 0.00 ± 0.00 (1) |
| Decker - 2005 | 0.98 ± 0.02 (53) | 1.00 ± 0.00 (15) | 0.99 ± 0.02 (68) | 0.58 ± 0.10 (26) | 0.10 ± 0.10 (10) | 0.44 ± 0.08 (36) | 0.33 ± 0.22 (3) | 0.00 ± 0.00 (1) | 0.25 ± 0.18 (4) |
| Decker - 2006 | 1.00 ± 0.00 (47) | 1.00 ± 0.00 (21) | 1.00 ± 0.00 (68) | 0.56 ± 0.18 (18) | 0.33 ± 0.16 (9) | 0.48 ± 0.10 (27) | 0.00 ± 0.00 (3) | 0.00 ± 0.00 (2) | 0.00 ± 0.00 (5) |
| Decker - TOTAL | 0.98 ± 0.01 (151) | 0.96 ± 0.02 (73) | 0.97 ± 0.01 (225) | 0.51 ± 0.06 (67) | 0.25 ± 0.07 (36) | 0.42 ± 0.05 (103) | 0.13 ± 0.12 (8) | 0.00 ± 0.00 (6) | 0.07 ± 0.07 (14) |
| Buffalo - 2004 | 1.00 ± 0.00 (12) | 1.00 ± 0.00 (35) | 1.00 ± 0.00 (48) | 0.50 ± 0.35 (2) | 0.00 ± 0.00 (15) | 0.06 ± 0.06 (17) | 0.00 ± 0.00 (1) | - | 0.00 ± 0.00 (1) |

Table 2a (cont.). Nest initiation rates ± SE, renesting rates ± SE, and second renesting rates ± SE for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Sample size is in parentheses.

| | Nest initiation rate | | | Renesting rate | | | Second renesting rate | | |
|---|---|---|---|---|---|---|---|---|---|
| Region – Year | AD | YR | All | AD | YR | All | AD | YR | All |
| Buffalo - 2005 | 1.00 ± 0.00 (36) | 0.94 ± 0.04 (31) | 0.97 ± 0.02 (68) | 0.80 ± 0.13 (10) | 0.33 ± 0.19 (6) | 0.63 ± 0.12 (16) | 0.00 ± 0.00 (1) | - | 0.00 ± 0.00 (1) |
| Buffalo - 2006 | 1.00 ± 0.00 (21) | 0.98 ± 0.03 (40) | 0.98 ± 0.02 (61) | 0.50 ± 0.36 (2) | 0.25 ± 0.22 (4) | 0.33 ± 0.19 (6) | 0.00 ± 0.00 (3) | 0.00 ± 0.00 (2) | 0.00 ± 0.00 (5) |
| Buffalo - TOTAL | 1.00 ± 0.00 (69) | 0.97 ± 0.02 (106) | 0.98 ± 0.01 (177) | 0.71 ± 0.12 (14) | 0.12 ± 0.07 (25) | 0.33 ± 0.08 (39) | 0.00 ± 0.00 (5) | 0.00 ± 0.00 (2) | 0.00 ± 0.00 (7) |
| SH - 2003 | 1.00 ± 0.00 (8) | 1.00 ± 0.00 (4) | 1.00 ± 0.00 (12) | 0.50 ± 0.25 (4) | 0.00 ± 0.00 (3) | 0.29 ± 0.17 (7) | 0.00 ± 0.00 (1) | - | 0.00 ± 0.00 (1) |
| TOTAL | 0.99 ± 0.01 (228) | 0.97 ± 0.01 (173) | 0.98 ± 0.01 (414) | 0.54 ± 0.05 (85) | 0.19 ± 0.05 (64) | 0.39 ± 0.04 (149) | 0.07 ± 0.07 (14) | 0.00 ± 0.00 (8) | 0.05 ± 0.04 (22) |

Table 2b. Renesting rates ± SE (proportion of females that had an unsuccessful first nest and survived detected on a second nest) for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003, excluding birds that abandoned nests due to investigator disturbance. Sample size is in parentheses.

| Region - Year | AD | YR | Combined |
|---|---|---|---|
| Decker - 2003 | 0.50 ± 0.18 (8) | 0.33 ± 0.19 (6) | 0.43 ± 0.13 (14) |
| Decker - 2004 | 0.09 ± 0.087 (11) | 0.00 ± 0.00 (8) | 0.05 ± 0.051 (19) |
| Decker - 2005 | 0.58 ± 0.097 (26) | 0.10 ± 0.095 (10) | 0.44 ± 0.083 (36) |
| Decker - 2006 | 0.56 ± 0.18 (18) | 0.25 ± 0.15 (8) | 0.46 ± 0.098 (26) |
| Decker - TOTAL | 0.48 ± 0.063 (63) | 0.16 ± 0.064 (32) | 0.37 ± 0.050 (95) |
| Buffalo - 2004 | 0.50 ± 0.35 (2) | 0.00 ± 0.00 (15) | 0.06 ± 0.06 (17) |
| Buffalo - 2005 | 0.78 ± 0.14 (9) | 0.20 ± 0.18 (5) | 0.57 ± 0.13 (14) |
| Buffalo - 2006 | 0.50 ± 0.36 (2) | 0.00 ± 0.00 (3) | 0.20 ± 0.18 (5) |
| Buffalo - TOTAL | 0.69 ± 0.13 (13) | 0.04 ± 0.043 (23) | 0.28 ± 0.075 (36) |
| SH - 2003 | 0.50 ± 0.25 (4) | 0.00 ± 0.00 (2) | 0.33 ± 0.19 (6) |
| TOTAL | 0.51 ± 0.056 (80) | 0.11 ± 0.041 (57) | 0.34 ± 0.041 (137) |

Table 3. Clutch size and hatching success for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Clutch size values presented as mean ± SE (except where n = 1). Hatching success data presented as a proportion (no. eggs hatched in successful nests of known clutch size / no. eggs laid in successful nests with known clutch size).

| | Clutch size | | | | Hatching success | | | |
|---|---|---|---|---|---|---|---|---|
| | AD | | YR | | AD | | YR | |
| Region - Year | 1st nests | Re-nests | 1st nests | Re-nests[a] | 1st nests | Re-nests | 1st nests | Re-nests |
| Decker - 2003 | 8.68 ± 0.21 | 6.63 ± 0.65 | 8.31 ± 0.26 | 6.00 ± 0.58 | 0.79 (62/69)[b] | 0.90 (27/30) | 0.92 (57/62) | 0.77 (10/13) |
| Decker - 2004 | 8.00 ± 0.20 | - | 7.33 ± 0.29 | - | 0.97 (125/129) | - | 0.97 (34/35) | - |
| Decker - 2005 | 7.75 ± 0.25 | 6.53 ± 0.27 | 6.67 ± 0.60 | 5.00 | 0.88 (153/174) | 0.93 (64/69) | 0.95 (21/22) | - |
| Decker - 2006 | 8.37 ± 0.21 | 6.30 ± 0.40 | 8.08 ± 0.40 | 6.50 ± 0.50 | 0.97 (161/166) | 0.88 (35/40) | 0.97 (86/89) | 1.0 (7/7) |

Table 3 (cont.). Clutch size and hatching success for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Clutch size values presented as mean ± SE (except where n = 1). Hatching success data presented as a proportion (no. eggs hatched in successful nests of known clutch size / no. eggs laid in successful nests with known clutch size).

| | Clutch size | | | | Hatching success | | | |
|---|---|---|---|---|---|---|---|---|
| | AD | | YR | | AD | | YR | |
| Region - Year | 1st nests | Re-nests | 1st nests | Re-nests[a] | 1st nests | Re-nests | 1st nests | Re-nests |
| Buffalo - 2004 | 8.56 ± 0.41 | - | 7.40 ± 0.38 | - | 0.90 (64/71) | - | 0.95 (74/78) | - |
| Buffalo - 2005 | 8.55 ± 0.37 | 6.50 ± 0.56 | 7.50 ± 0.39 | 4.00 | 0.93 (148/159) | 0.8 (28/35) | 0.86 (112/130) | 0.89 (8/9) |
| Buffalo - 2006 | 7.00 ± 0.29 | 7.00 | 7.13 ± 0.18 | 7.00 | 0.89 (119/133) | 1.0 (7/7) | 0.93 (200/214) | 1.0 (7/7) |
| SH - 2003 | 8.67 ± 0.42 | 4.50 ± 2.50 | 8.33 ± 0.33 | - | 0.94 (32/34) | 1.0 (2/2) | 0.75 (6/8) | - |

[a] Sample size n =1 for yearling renests with known clutch size for Decker in 2005 and Buffalo in 2005.
[b] This estimate includes data from one nest that was incubated for 50+ days in which all 9 eggs failed to hatch.

Table 4. Apparent nest success and number and fate for nests of adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003. Apparent nest success is presented as a proportion (successful nests/total nests).

| | AD | | YR | | Combined |
|---|---|---|---|---|---|
| Region - Year | 1st nests | Re-nests[a] | 1st nests | Re-nests | Annual total |
| Decker - 2003 | 0.38 (8/21) | 0.88 (7/8) | 0.41 (7/17) | 0.40 (2/5) | 0.47 (24/51) |
| Decker - 2004 | 0.62 (18/29) | 0.00 (0/1) | 0.41 (7/17) | - | 0.53 (25/47) |
| Decker - 2005 | 0.45 (23/51) | 0.69 (11/16) | 0.27 (4/15) | 0.00 (0/1) | 0.46 (38/83) |
| Decker - 2006 | 0.48 (21/44) | 0.60 (6/10) | 0.60 (12/20) | 0.33 (1/3) | 0.52 (40/77) |
| Decker - TOTAL | 0.48 (70/145) | 0.69 (24/35) | 0.43 (30/69) | 0.33 (3/9) | 0.49 (127/258) |
| Buffalo - 2004 | 0.75 (9/12) | 0.00 (0/1) | 0.50 (17/34) | - | 0.56[b] (27/48) |

Table 4 (cont.). Apparent nest success and number and fate for nests of adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003. Apparent nest success is presented as a proportion (successful nests/total nests).

| | AD | | YR | | Combined |
|---|---|---|---|---|---|
| Region - Year | 1st nests | Re-nests[a] | 1st nests | Re-nests | Annual total |
| Buffalo - 2005 | 0.64 (23/36) | 0.88 (7/8) | 0.69 (20/29) | 1.00 (2/2) | 0.70[b] (53/76) |
| Buffalo - 2006 | 0.95 (19/20) | 1.00 (1/1) | 0.79 (31/39) | 1.00 (1/1) | 0.85 (52/61) |
| Buffalo - TOTAL | 0.75 (51/68) | 0.80 (8/10) | 0.67 (68/102) | 1.00 (3/3) | 0.71[b] (132/185) |
| Spotted Horse - 2003 | 0.50 (4/8) | 0.50 (1/2) | 0.25 (1/4) | - | 0.43 (6/14) |
| TOTAL | 0.57 (125/220) | 0.70 (33/47) | 0.57 (99/175) | 0.50 (6/12) | 0.57[b] (265/457) |

[a] One successful third nest from the Decker region in 2005 is included in renests.
[b] Totals include successful nests of unknown-aged females (i.e., after-hatching-year) near Buffalo in 2004 (n=1) and 2005 (n=1).

Table 5. Apparent proximate cause of failure for nests of adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003.

| | | Cause of nest failure | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | ♀ killed | | | |
| Region - Year | No. failed nests / total nests | Predation | Weather | Abandoned | on / off nest | Research | Did not hatch | Unknown |
| Decker - 2003 | 27 / 51 | 10 | 0 | 0 | 1 / 2 | 9 | 1 | 4 |
| Decker - 2004 | 22 / 47 | 18 | 0 | 1 | 0 / 2 | 0 | 0 | 1 |
| Decker - 2005 | 45 / 83 | 31 | 7 | 1 | 2 / 3 | 1 | 0 | 0 |
| Decker - 2006 | 37 / 77 | 28 | 0 | 1 | 1 / 3 | 1 | 0 | 3 |
| Decker - TOTAL | 131 / 258 | 87 | 7 | 3 | 4 / 10 | 11 | 1 | 8 |
| Buffalo - 2004 | 21 / 48 | 21 | 0 | 0 | 0 | 0 | 0 | 0 |
| Buffalo - 2005 | 23 / 76 | 19 | 1 | 0 | 0 | 2 | 0 | 1 |
| Buffalo - 2006 | 9 / 61 | 3 | 0 | 0 | 3 / 1 | 1 | 1 | 0 |
| Buffalo - TOTAL | 53 / 185 | 43 | 1 | 0 | 3 / 1 | 3 | 1 | 1 |
| SH - 2003 | 8 / 14 | 6 | 0 | 0 | 0 | 1 | 0 | 1 |
| TOTAL | 192/457 | 136 | 8 | 3 | 7, 11 | 15 | 2 | 10 |

Table 6. Comparison of "quick" estimates of nest success and nest success estimated from maximum-likelihood estimates of daily survival rate based on a *Region*Year*Hen age + Nest attempt* model for adult (AD) and yearling (YR) female greater sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. "Quick" nest success estimates (Johnson and Klett 1985) are for the incubation period only.

| | "Quick" estimate | | | | Maximum-likelihood estimate (mean ± SE) | | | | Absolute Difference | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | AD | | YR | | AD | | YR | | AD | | YR | |
| Region - Year | 1st nests | Re-nests[a] | 1st nests | Re-nests | 1st nests | Re-nests[a] | 1st nests | Renests | 1st nests | Re-nests[a] | 1st nests | Re-nests |
| Decker - 2003 | 0.35 | 0.86 | 0.38 | 0.37 | 0.72 ±0.11 | 0.82 ±0.08 | 0.48 ±0.15 | 0.65 ±0.13 | -0.37 | 0.04 | -0.10 | -0.28 |
| Decker - 2004 | 0.60 | 0.00[b] | 0.39 | - | 0.61 ±0.09 | - | 0.55 ±0.12 | - | -0.01 | - | -0.16 | - |
| Decker - 2005 | 0.43 | 0.67 | 0.24 | 0.00[b] | 0.47 ±0.07 | 0.64 ±0.08 | 0.29 ±0.11 | - | -0.03 | 0.03 | -0.05 | -0.47[b] |
| Decker - 2006 | 0.45 | 0.58 | 0.58 | 0.31[b] | 0.52 ±0.08 | 0.68 ±0.09 | 0.51 ±0.12 | 0.67 ±0.11 | -0.07 | -0.10 | 0.07 | -0.36[b] |

Table 6 (cont.). Comparison of "quick" estimates of nest success and nest success estimated from maximum-likelihood estimates of daily survival rate based on a *Region*Year*Hen age + Nest attempt* model for adult (AD) and yearling (YR) female greater sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. "Quick" nest success estimates (Johnson and Klett 1985) are for the incubation period only.

| | "Quick" estimate | | | | Maximum-likelihood estimate (mean ± SE) | | | | Absolute difference | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | AD | | YR | | AD | | YR | | AD | | YR | |
| Region - Year | 1st nests | Re-nests[a] | 1st nests | Re-nests | 1st nests | Re-nests[a] | 1st nests | Re-nests | 1st nests | Re-nests[a] | 1st nests | Re-nests |
| Buffalo - 2004 | 0.74 | 0.00[b] | 0.48 | - | 0.72 ±0.14 | - | 0.49 ±0.09 | - | 0.02 | - | -0.01 | - |
| Buffalo - 2005 | 0.62 | 0.88[b] | 0.67 | 1.00[b] | 0.69 ±0.08 | 0.80 ±0.07 | 0.79 ±0.08 | 0.87 ±0.06 | -0.07 | 0.07[b] | -0.12 | 0.13[b] |
| Buffalo - 2006 | 0.95 | 1.00[b] | 0.78 | 1.00[b] | 0.95 ±0.05 | 0.97 ±0.03 | 0.88 ±0.06 | 0.92 ±0.04 | 0.00 | -0.03 | -0.10 | 0.08[b] |
| SH - 2003 | 0.47[b] | 0.47[b] | 0.22[b] | - | 0.56 ± 0.19 | 0.71 ±0.15 | 0.28 ±0.25 | - | -0.09[b] | -0.24[b] | -0.06[b] | - |

[a] One successful third nest from the Decker region in 2005 is included in renests.
[b] Values are based on sample sizes of nests ≤ 9.

Table 7. Earliest and latest hatching dates, apparent brood survival, number and fate of broods, apparent chick survival, and minimum no. chicks surviving to 35d for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Brood data presented as no. successful broods / no. broods of known fate / no. broods of unknown fate. Chick data presented as no. chicks that survived to 35d / no. chicks hatched in broods of known fate / no. chicks hatched in broods of unknown fate.

| Region - Year | Hatching date | | | Apparent brood success | | | Apparent chick survival | | |
|---|---|---|---|---|---|---|---|---|---|
| | AD | YR | All | AD | YR | All[a] | AD | YR | All[b] |
| Decker - 2003 | 5/15-7/03 | 5/19-6/25 | 5/15-7/03 | 0.71 (10/14/1) | 0.56 (5/9/0) | 0.67 (16/24/1) | 0.54 (54/100/3) | 0.28 (19/67/0) | 0.43 (75/174/3) |
| Decker - 2004 | 5/11-6/10 | 5/13-5/28 | 5/11-6/10 | 0.89 (16/18/0) | 1.00 (6/6/1) | 0.91 (21/23/2) | 0.32 (40/125/6) | 0.58 (22/38/5) | 0.38 (62/163/11) |
| Decker - 2005 | 5/10-7/03 | 5/18-6/12 | 5/10-7/03 | 0.77 (24/31/4) | 1.00 (4/4/0) | 0.80 (28/35/4) | 0.47 (93/197/27) | 0.78 (18/23/0) | 0.50 (111/220/27) |
| Decker - 2006 | 5/13-6/23 | 5/20-6/03 | 5/13-6/23 | 0.81 (17/21/6) | 0.75 (8/12/0) | 0.76 (25/33/6) | 0.42 (61/145/30) | 0.38 (33/88/0) | 0.40 (94/233/30) |

Table 7 (cont.). Earliest and latest hatching dates, apparent brood survival, number and fate of broods, apparent chick survival, and minimum no. chicks surviving to 35d for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Brood data presented as no. successful broods / no. broods of known fate / no. broods of unknown fate. Chick data presented as no. chicks that survived to 35d / no. chicks hatched in broods of known fate / no. chicks hatched in broods of unknown fate.

| | Hatching date | | | Apparent brood survival | | | Apparent chick survival | | |
|---|---|---|---|---|---|---|---|---|---|
| Region - Year | AD | YR | All | AD | YR | All[a] | AD | YR | All[b] |
| Buffalo - 2004 | 5/09-5/24 | 5/14-5/29 | 5/09-5/29 | 0.88 (7/8/1) | 0.58 (7/12/5) | 0.71 (15/21/6) | 0.41 (29/70/0) | 0.26 (20/78/30) | 0.33 (51/156/30) |
| Buffalo - 2005 | 5/10-6/23 | 5/14-6/20 | 5/10-6/23 | 0.96 (27/28/3) | 0.95 (18/19/3) | 0.96 (46/48/6) | 0.51 (84/164/Unk) | 0.63 (67/107/13+) | 0.55 (152/277/21+) |
| Buffalo - 2006 | 5/19-6/06 | 5/16-6/06 | 5/16-6/06 | 0.88 (7/8/12) | 0.92 (22/24/8) | 0.91 (29/32/20) | 0.43 (24/56/70) | 0.50 (78/155/48) | 0.48 (102/211/118) |
| SH - 2003 | 5/23-6/08 | 5/31 | 5/23-6/08 | 0.80 (4/5/0) | 1.00 (1/1/0) | 0.83 (5/6/0) | 0.54 (19/35/0) | 0.50 (3/6/0) | 0.54 (22/41/0) |

[a] Totals also include broods from females of undetermined age (i.e., after-hatching-year).
[b] Totals also include chicks from females of undetermined age (i.e., after-hatching-year).

Table 8. Suspected cause of death of radio-collared female sage-grouse near Decker, MT from 2003-2007, Buffalo, WY from 2004-2007, and Spotted Horse (SH), WY in 2003-2004.

| | | Suspected proximate cause of death | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Region - Year | No. mortalities | Raptor kill | Mammal kill | Unknown predator | WNv | Vehicle collision | Powerline collision | Other disease | Legal harvest | Unknown |
| Decker 2003-2004 | 21 | 1 | 0 | 13 | 0 | 0 | 1 | 0 | 0 | 6 |
| Decker 2004-2005 | 27 | 4 | 1 | 10 | 3[a] | 0 | 0 | 0 | 0 | 9 |
| Decker 2005-2006 | 24 | 3 | 2 | 5 | 0 | 0 | 0 | 1[b] | 0 | 13 |
| Decker 2006-2007 | 34 | 1 | 0 | 13 | 3 | 0 | 0 | 1[c] | 0 | 16 |
| Buffalo 2004-2005 | 23 | 8 | 4 | 6 | 1 | 0 | 0 | 0 | 1 | 3 |
| Buffalo 2005-2006 | 39 | 7 | 4 | 9 | 3 | 2 | 0 | 0 | 0 | 14 |
| Buffalo 2006-2007 | 39 | 3 | 0 | 7 | 3[d] | 0 | 0 | 1 | 0 | 25[d] |
| SH 2003-2004 | 10 | 1 | 0 | 2 | 6 | 0 | 1 | 0 | 0 | 1 |
| All regions - all years | 217 | 28 | 11 | 65 | 19[d] | 2 | 2 | 2 | 1 | 87[d] |

[a] Two of the three mortalities positive for West Nile virus near Decker in 2004 occurred in alfalfa fields irrigated with water from coal-bed natural gas development.
[b] Aspergillosus.
[c] Metastatic mineralization of the kidney reported, cause unknown.
[d] Four mortalities listed here as unknown cause of death may have died from West Nile virus and are currently being tested at the Wyoming State Veterinary Laboratory.

Table 9. Sample sizes for nest, brood, and female survival analyses and interval lengths (d) for female survival analyses in three regions of the Powder River Basin, 2003-2006. Spring-summer survival was measured from the beginning of nesting (30 Mar - 6 Apr, depending on the year) to 10 Sept. Fall-winter survival was measured from 10 Sept to the beginning of nesting the following spring.

| | | | Spring-summer | | | Fall-winter | | | |
|---|---|---|---|---|---|---|---|---|---|
| Region - Year | No. nests | No. broods | No. yearlings | No. adults | Interval length (d) | No. juveniles | No. yearlings | No. adults | Interval length (d) |
| Decker 2003 | 40 | 25 | 21 | 27 | 160 | 13 | 15 | 22 | 202 |
| Decker 2004 | 46 | 25 | 31 | 42 | 164 | 11 | 19 | 35 | 208 |
| Decker 2005 | 82 | 36 | 16 | 60 | 157 | 0 | 16 | 40 | 206 |
| Decker 2006 | 73 | 36 | 26 | 50 | 159 | 0 | 18 | 26 | 202 |
| Buffalo 2004 | 46 | 23 | 39 | 12 | 166 | 0 | 28 | 8 | 199 |
| Buffalo 2005 | 72 | 52 | 34 | 40 | 166 | 0 | 23 | 23 | 208 |
| Buffalo 2006 | 58 | 43 | 52 | 23 | 157 | 0 | 25 | 14 | 208 |
| SH 2003 | 11 | 6 | 4 | 10 | 162 | 0 | 2 | 1 | 203 |
| SH 2004 | 0 | 0 | 1 | 4 | 162 | 0 | 1 | 3 | 203 |
| All regions - all years | 428 | 246 | 219 | 254 | | 24 | 147 | 172 | |
| No. individuals | 289 | 206 | 343 (spring-summer) | | | 233 (fall-winter) | | | |

Table 10. *A priori* models of daily survival rate for greater sage-grouse nests in the Powder River Basin, 2003-2006. Models are ranked by $\Delta AIC_c$ values.

| No. | Model[1] | $K$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|---|
| 1 | Region*Year+Hen Age+Julian Date | 13 | 1020.046 | 0.000 | 0.333 |
| 2 | Region*Year+Hen Age+Attempt | 13 | 1021.552 | 1.506 | 0.157 |
| 3 | Region*Year+Julian Date | 12 | 1021.887 | 1.841 | 0.132 |
| 4 | Region*Year+Attempt | 12 | 1022.155 | 2.109 | 0.116 |
| 5 | Region*Year+Hen Age | 12 | 1022.651 | 2.606 | 0.090 |
| 6 | Region*Year+Hen Age+Julian Date+Julian Date$^2$ | 14 | 1022.833 | 2.787 | 0.083 |
| 7 | Region*Year | 11 | 1023.990 | 3.944 | 0.046 |
| 8 | Region*Year+Julian Date+Julian Date$^2$ | 13 | 1025.051 | 5.006 | 0.027 |
| 9 | Region+Year+Hen Age+Julian Date | 11 | 1029.546 | 9.500 | 0.003 |
| 10 | Region*Year*Hen Age+Julian Date | 20 | 1029.962 | 9.916 | 0.002 |
| 11 | Region+Year+Hen Age+Attempt | 11 | 1030.545 | 10.499 | 0.002 |
| 12 | Region+Year+Hen Age | 10 | 1030.915 | 10.869 | 0.001 |
| 13 | Region*Year*Hen Age+Attempt | 20 | 1031.201 | 11.155 | 0.001 |
| 14 | Region+Year+Attempt | 10 | 1031.403 | 11.358 | 0.001 |
| 15 | Region+Year+Julian Date | 10 | 1031.462 | 11.417 | 0.001 |
| 16 | Region+Year*Hen Age+Julian Date | 14 | 1031.880 | 11.834 | 0.001 |

| | | | | | |
|---|---|---|---|---|---|
| 17 | Region*Year*Hen Age | 19 | 1032.220 | 12.174 | 0.001 |
| 18 | Region+Year*Hen Age+Attempt | 14 | 1032.746 | 12.701 | 0.001 |
| 19 | Region+Year+Hen Age+Julian Date+Julian Date$^2$ | 12 | 1032.882 | 12.836 | 0.001 |
| 20 | Region*Year*Hen Age+Julian Date+Julian Date$^2$ | 21 | 1032.956 | 12.910 | 0.001 |
| 21 | Region+Year*Hen Age | 13 | 1033.316 | 13.270 | 0.000 |
| 22 | Region+Year*Hen Age+Julian Date+Julian Date$^2$ | 15 | 1035.146 | 15.100 | 0.000 |
| 23 | Region+Year+Julian Date+Julian Date$^2$ | 11 | 1035.284 | 15.239 | 0.000 |
| 24 | Julian Date+Julian Date$^2$+PrevSprPrecip | 7 | 1038.522 | 18.477 | 0.000 |
| 25 | Hen Age+Julian Date+Julian Date$^2$+PrevSprPrecip | 8 | 1040.175 | 20.129 | 0.000 |
| 26 | Julian Date+PrevSprPrecip | 6 | 1040.673 | 20.627 | 0.000 |
| 27 | Attempt+PrevSprPrecip | 6 | 1040.951 | 20.905 | 0.000 |
| 28 | Attempt*PrevSprPrecip | 7 | 1041.604 | 21.558 | 0.000 |
| 29 | Hen Age+Julian Date+PrevSprPrecip | 7 | 1041.771 | 21.726 | 0.000 |
| 30 | Julian Date*PrevSprPrecip | 7 | 1042.259 | 22.213 | 0.000 |
| 31 | Hen Age+Attempt+PrevSprPrecip | 7 | 1042.495 | 22.449 | 0.000 |
| 32 | Hen Age+Attempt*PrevSprPrecip | 8 | 1043.110 | 23.064 | 0.000 |
| 33 | Hen Age+PrevSprPrecip | 6 | 1043.389 | 23.343 | 0.000 |
| 34 | Hen Age+Julian Date*PrevSprPrecip | 8 | 1043.396 | 23.350 | 0.000 |
| 35 | NestAge+NestAge$^2$+ExtremePrecip | 4 | 1044.653 | 24.608 | 0.000 |

| | | | | | |
|---|---|---|---|---|---|
| 36 | Hen Age+Julian Date+Julian Date$^2$ | 7 | 1045.364 | 25.319 | 0.000 |
| 37 | Julian Date+Julian Date$^2$+SprPrecip | 7 | 1045.388 | 25.342 | 0.000 |
| 38 | Hen Age+Julian Date | 6 | 1045.954 | 25.908 | 0.000 |
| 39 | Attempt*SprPrecip | 7 | 1046.154 | 26.108 | 0.000 |
| 40 | Julian Date+SprPrecip | 6 | 1046.177 | 26.131 | 0.000 |
| 41 | Attempt+SprPrecip | 6 | 1046.316 | 26.270 | 0.000 |
| 42 | Hen Age+Attempt | 6 | 1046.355 | 26.309 | 0.000 |
| 43 | Hen Age+Julian Date+Julian Date$^2$+SprPrecip | 8 | 1047.361 | 27.315 | 0.000 |
| 44 | Julian Date*SprPrecip | 7 | 1047.500 | 27.454 | 0.000 |
| 45 | Hen Age+Julian Date+SprPrecip | 7 | 1047.924 | 27.878 | 0.000 |
| 46 | Hen Age+SprPrecip | 6 | 1048.049 | 28.003 | 0.000 |
| 47 | Hen Age+Attempt*SprPrecip | 8 | 1048.088 | 28.042 | 0.000 |
| 48 | Hen Age+Attempt+SprPrecip | 7 | 1048.242 | 28.197 | 0.000 |
| 49 | Hen Age+Julian Date*SprPrecip | 8 | 1049.254 | 29.208 | 0.000 |

[1] All models include effects of *nest age* + *nest age*$^2$ and *extreme precipitation*.

Table 11. *A priori* models of daily survival rate for greater sage-grouse broods in the Powder River Basin, 2003-2006. Models are ranked by $\Delta AIC_c$ values.

| No. | Model | *K* | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|---|
| 1 | Brood Age+Region | 4 | 304.106 | 0.000 | 0.225 |
| 2 | Brood Age+Region*Year | 9 | 304.509 | 0.403 | 0.184 |
| 3 | Brood Age+Region+Hen Age | 5 | 304.820 | 0.714 | 0.157 |
| 4 | Brood Age+Region*Year+Hen Age | 10 | 305.480 | 1.374 | 0.113 |
| 5 | Brood Age+Region+Julian Date | 5 | 306.061 | 1.955 | 0.085 |
| 6 | Brood Age+Region*Year+Julian Date | 10 | 306.494 | 2.388 | 0.068 |
| 7 | Brood Age+Region+Hen Age+Julian Date | 6 | 306.745 | 2.639 | 0.060 |
| 8 | Brood Age+Region*Year+Hen Age+Julian Date | 11 | 307.464 | 3.358 | 0.042 |
| 9 | Brood Age+Region+Year | 7 | 309.365 | 5.259 | 0.016 |
| 10 | Brood Age+Region+Year+Hen Age | 8 | 310.427 | 6.321 | 0.010 |
| 11 | Brood Age+Region+Year+Julian Date | 8 | 311.148 | 7.042 | 0.007 |
| 12 | Brood Age+Region+Year*Julian Date | 11 | 311.647 | 7.542 | 0.005 |
| 13 | Brood Age+Region+Year+Hen Age+Julian Date | 9 | 312.203 | 8.097 | 0.004 |
| 14 | Brood Age | 2 | 312.264 | 8.159 | 0.004 |
| 15 | Brood Age+Region+Year*Julian Date+Hen Age | 12 | 312.302 | 8.197 | 0.004 |
| 16 | Brood Age+SprPrecip | 3 | 313.017 | 8.911 | 0.003 |

| | | | | | |
|---|---|---|---|---|---|
| 17 | Brood Age+Julian Date | 3 | 313.972 | 9.867 | 0.002 |
| 18 | Brood Age+Julian Date+SprPrecip | 4 | 314.163 | 10.057 | 0.001 |
| 19 | Brood Age+SprPMDI | 3 | 314.211 | 10.105 | 0.001 |
| 20 | Brood Age+Hen Age | 3 | 314.265 | 10.159 | 0.001 |
| 21 | Brood Age+Hen Age+SprPrecip | 4 | 314.980 | 10.874 | 0.001 |
| 22 | Brood Age+Region+Year*Hen Age | 11 | 315.073 | 10.967 | 0.001 |
| 23 | Global | 12 | 315.261 | 11.156 | 0.001 |
| 24 | Brood Age+Julian Date+SprPMDI | 4 | 315.755 | 11.649 | 0.001 |
| 25 | Brood Age+Hen Age+Julian Date | 4 | 315.975 | 11.869 | 0.001 |
| 26 | Brood Age+Julian Date*SprPrecip | 5 | 316.094 | 11.988 | 0.001 |
| 27 | Brood Age+Hen Age+Julian Date+SprPrecip | 5 | 316.127 | 12.021 | 0.001 |
| 28 | Brood Age+Year | 5 | 316.169 | 12.063 | 0.001 |
| 29 | Brood Age+Hen Age+SprPMDI | 4 | 316.209 | 12.103 | 0.001 |
| 30 | Brood Age+Hen Age*SprPrecip | 5 | 316.627 | 12.521 | 0.000 |
| 31 | Brood Age+Region+Year*Hen Age+Julian Date | 12 | 316.924 | 12.818 | 0.000 |
| 32 | Brood Age+Julian Date*SprPMDI | 5 | 317.356 | 13.250 | 0.000 |
| 33 | Brood Age+Hen Age*SprPMDI | 5 | 317.732 | 13.626 | 0.000 |
| 34 | Brood Age+Hen Age+Julian Date+SprPMDI | 5 | 317.754 | 13.648 | 0.000 |
| 35 | Brood Age+Year+Julian Date | 6 | 317.823 | 13.717 | 0.000 |

| | | | | | |
|---|---|---|---|---|---|
| 36 | Brood Age+Hen Age*SprPrecip+Julian Date | 6 | 317.832 | 13.726 | 0.000 |
| 37 | Brood Age+Julian Date*SprPrecip+Hen Age | 6 | 318.058 | 13.953 | 0.000 |
| 38 | Brood Age+Year+Hen Age | 6 | 318.168 | 14.062 | 0.000 |
| 39 | Brood Age+Year*Julian Date | 9 | 318.767 | 14.661 | 0.000 |
| 40 | Brood Age+Julian Date*SprPMDI+Hen Age | 6 | 319.352 | 15.246 | 0.000 |
| 41 | Brood Age+Hen Age*SprPMDI+Julian Date | 6 | 319.364 | 15.258 | 0.000 |
| 42 | Brood Age+Year+Hen Age+Julian Date | 7 | 319.820 | 15.714 | 0.000 |
| 43 | Brood Age+Year*Julian Date+Hen Age | 10 | 320.773 | 16.667 | 0.000 |
| 44 | Brood Age+Year*Hen Age | 9 | 321.354 | 17.248 | 0.000 |
| 45 | Brood Age+Year*Hen Age+Julian Date | 10 | 323.106 | 19.000 | 0.000 |

Table 12. *A priori* models of daily spring-summer female survival rate for greater sage-grouse in the Powder River Basin, spring 2003 - spring 2007. Models are ranked by $\Delta AIC_c$ values.

| No. | Model | $K$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|---|
| 1 | Region*WNV+Year+With Brood | 10 | 1611.503 | 0.000 | 0.221 |
| 2 | Region*WNV+Year | 9 | 1611.997 | 0.494 | 0.173 |
| 3 | Region*WNV+Year+On Nest | 10 | 1612.730 | 1.227 | 0.120 |
| 4 | Region*WNV+Year+Hen Age+With Brood | 11 | 1612.975 | 1.472 | 0.106 |
| 5 | Region*WNV+Year+Hen Age | 10 | 1613.595 | 2.091 | 0.078 |
| 6 | Region+Year+With Brood+WNV | 8 | 1614.247 | 2.744 | 0.056 |
| 7 | Region*WNV+Year+Hen Age+On Nest | 11 | 1614.391 | 2.887 | 0.052 |
| 8 | Region+Year+WNV | 7 | 1615.007 | 3.504 | 0.038 |
| 9 | Region+Year+On Nest+WNV | 8 | 1615.582 | 4.079 | 0.029 |
| 10 | Region+Year+With Brood*WNV | 9 | 1615.800 | 4.297 | 0.026 |
| 11 | Region+Year+Hen Age+With Brood+WNV | 9 | 1615.867 | 4.363 | 0.025 |
| 12 | Region+Year+Hen Age+WNV | 8 | 1616.739 | 5.235 | 0.016 |
| 13 | Global | 10 | 1617.267 | 5.764 | 0.012 |
| 14 | Region+Year+Hen Age+On Nest+WNV | 9 | 1617.366 | 5.862 | 0.012 |
| 15 | Region+Year+Hen Age+With Brood*WNV | 10 | 1617.427 | 5.924 | 0.011 |

| | | | | | |
|---|---|---|---|---|---|
| 16 | Region*Hen Age+Year+With Brood+WNV | 11 | 1618.077 | 6.574 | 0.008 |
| 17 | Region*Hen Age+Year+WNV | 10 | 1619.003 | 7.500 | 0.005 |
| 18 | Region*Hen Age+Year+With Brood*WNV | 12 | 1619.638 | 8.134 | 0.004 |
| 19 | Region*Hen Age+Year+On Nest+WNV | 11 | 1619.660 | 8.157 | 0.004 |
| 20 | Region+Year+With Brood | 7 | 1621.341 | 9.838 | 0.002 |
| 21 | Region+Year+Hen Age+With Brood | 8 | 1623.057 | 11.553 | 0.001 |
| 22 | Region+Year | 6 | 1623.579 | 12.075 | 0.001 |
| 23 | Region*Year | 10 | 1623.943 | 12.439 | 0.000 |
| 24 | Region+Year+Hen Age | 7 | 1625.413 | 13.909 | 0.000 |
| 25 | Region*Hen Age+Year+With Brood | 10 | 1625.503 | 14.000 | 0.000 |
| 26 | Region+Year+On Nest | 7 | 1625.542 | 14.039 | 0.000 |
| 27 | Region*Year+Hen Age+On Nest | 12 | 1626.598 | 15.094 | 0.000 |
| 28 | Region*Year*Hen Age | 20 | 1627.251 | 15.748 | 0.000 |
| 29 | Region+Year+Hen Age+On Nest | 8 | 1627.367 | 15.864 | 0.000 |
| 30 | Region*Hen Age+Year | 9 | 1627.938 | 16.435 | 0.000 |
| 31 | Region*Hen Age+Year+On Nest | 10 | 1629.882 | 18.378 | 0.000 |
| 32 | Region*Year+With Brood | 11 | 1670.830 | 59.327 | 0.000 |
| 33 | Region*Year+On Nest | 11 | 1677.943 | 66.439 | 0.000 |
| 34 | Region*Year*Hen Age+On Nest+WNV | 22 | 1720.185 | 108.682 | 0.000 |

| | | | | | |
|---|---|---|---|---|---|
| 35 | Region*Year+Hen Age | 11 | 1734.204 | 122.701 | 0.000 |
| 36 | Region*Year*Hen Age+On Nest | 21 | 1734.731 | 123.227 | 0.000 |
| 37 | Region*Year*Hen Age+With Brood*WNV | 23 | 1758.631 | 147.127 | 0.000 |
| 38 | Region*Year*Hen Age+WNV | 21 | 1770.376 | 158.873 | 0.000 |
| 39 | Region*Year+Hen Age+With Brood | 12 | 1782.309 | 170.806 | 0.000 |
| 40 | Region*Year*Hen Age+With Brood+WNV | 22 | 1785.598 | 174.095 | 0.000 |
| 41 | Region*Year+Hen Age+WNV | 12 | 1794.996 | 183.492 | 0.000 |
| 42 | Region*Year+Hen Age+With Brood*WNV | 14 | 1811.092 | 199.588 | 0.000 |
| 43 | Region*Year+Hen Age+On Nest+WNV | 13 | 1823.341 | 211.838 | 0.000 |
| 44 | Region*Year+Hen Age+With Brood+WNV | 13 | 1841.026 | 229.522 | 0.000 |

Table 13. *A priori* models of daily spring-summer female survival rate for greater sage-grouse in the Powder River Basin, spring 2003 - spring 2007, excluding mortalities confirmed positive for West Nile virus. Models are ranked by $\Delta AIC_c$ values.

| No. | Model[1] | $K$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|---|
| 1 | Region+Year+With Brood | 7 | 1454.115 | 0.000 | 0.312 |
| 2 | Region+Year | 6 | 1455.091 | 0.976 | 0.192 |
| 3 | Region+Year+Hen Age+With Brood | 8 | 1455.488 | 1.373 | 0.157 |
| 4 | Region+Year+Hen Age | 7 | 1456.617 | 2.502 | 0.089 |
| 5 | Region+Year+On Nest | 7 | 1456.762 | 2.647 | 0.083 |
| 6 | Global | 9 | 1457.452 | 3.337 | 0.059 |
| 7 | Region+Year+Hen Age+On Nest | 8 | 1458.329 | 4.214 | 0.038 |
| 8 | Region*Hen Age+Year+With Brood | 10 | 1458.972 | 4.857 | 0.028 |
| 9 | Region*Year | 10 | 1459.626 | 5.511 | 0.020 |
| 10 | Region*Hen Age+Year | 9 | 1460.129 | 6.014 | 0.015 |
| 11 | Region*Hen Age+Year+On Nest | 10 | 1461.857 | 7.741 | 0.007 |
| 12 | Region*Year*Hen Age+On Nest | 21 | 1466.915 | 12.800 | 0.001 |
| 13 | Region*Year*Hen Age | 20 | 1468.292 | 14.177 | 0.000 |
| 14 | Region*Year+With Brood | 11 | 1500.477 | 46.362 | 0.000 |
| 15 | Region*Year*Hen Age+With Brood | 21 | 1509.824 | 55.708 | 0.000 |

| | | | | | |
|---|---|---|---|---|---|
| 16 | Region*Year+On Nest | 11 | 1517.646 | 63.531 | 0.000 |
| 17 | Region*Year+Hen Age | 11 | 1549.517 | 95.402 | 0.000 |
| 18 | Region*Year+Hen Age+On Nest | 12 | 1568.049 | 113.933 | 0.000 |
| 19 | Region*Year+Hen Age+With Brood | 12 | 1605.581 | 151.466 | 0.000 |

Table 14. Spring-summer survival estimates ± SE for adult (AD) and yearling (YR) female greater sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003-2004, including and excluding mortalities confirmed positive for West Nile virus.

| | Survival (including WNv) | | Survival (excluding WNv) | |
|---|---|---|---|---|
| Region - Year | AD | YR | AD | YR |
| Decker - 2003 | 0.680 ± 0.099 | 0.593 ± 0.117 | 0.680 ± 0.099 | 0.593 ± 0.117 |
| Decker - 2004 | 0.808 ± 0.065 | 0.580 ± 0.100 | 0.808 ± 0.065 | 0.682 ± 0.099 |
| Decker - 2005 | 0.732 ± 0.061 | 1.000 | 0.732 ± 0.061 | 1.000 |
| Decker - 2006 | 0.637 ± 0.070 | 0.731 ± 0.087 | 0.671 ± 0.069 | 0.764 ± 0.084 |
| Buffalo - 2004 | 0.447 ± 0.216 | 0.644 ± 0.082 | 0.593 ± 0.231 | 0.668 ± 0.081 |
| Buffalo - 2005 | 0.582 ± 0.079 | 0.639 ± 0.086 | 0.627 ± 0.078 | 0.671 ± 0.085 |
| Buffalo - 2006 | 0.696 ± 0.103 | 0.589 ± 0.076 | 0.696 ± 0.103 | 0.647 ± 0.075 |
| SH - 2003 | 0.125 ± 0.087 | 0.482 ± 0.249 | 0.392 ± 0.184 | 0.693 ± 0.254 |
| SH - 2004 | 1.000 | 1.000 | 1.000 | 1.000 |

Table 15. Annual survival estimates for adult (AD) and yearling (YR) female greater sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003-2004, including and excluding mortalities confirmed positive for West Nile virus.

| | Annual survival (including WNv) | | Annual survival (excluding WNv) | |
|---|---|---|---|---|
| Region - Year | AD | YR | AD | YR |
| Decker - 2003 | 0.588 | 0.514 | 0.587 | 0.514 |
| Decker - 2004 | 0.740 | 0.519 | 0.740 | 0.610 |
| Decker - 2005 | 0.562 | 1.000 | 0.562 | 1.000 |
| Decker - 2006 | 0.563 | 0.606 | 0.594 | 0.634 |
| Buffalo - 2004 | 0.447 | 0.575 | 0.593 | 0.596 |
| Buffalo - 2005 | 0.354 | 0.472 | 0.381 | 0.496 |
| Buffalo - 2006 | 0.596 | 0.519 | 0.596 | 0.569 |
| SH - 2003 | 0.125 | 0.482 | 0.392 | 0.693 |
| SH - 2004 | 1.000 | 1.000 | 1.000 | 1.000 |

Figure 1. Expansion of coal-bed natural gas development in the Powder River Basin from 1997-2005. Approximate boundaries of study sites with radio-marked greater sage-grouse in the Powder River Basin, 2003-2006 are outlined with black dashed lines. Study regions are labeled in bold. Gray dots represent active coal-bed natural gas wells. County names are in small font.

Figure 2. Daily survival rate (DSR) of nests (with 95% CIs) in three regions of the Powder River Basin, 2003-2006. SH = Spotted Horse.

Figure 3. Daily survival rate (DSR) of nests (with 95% CIs) in relation to date and hen age based on nests in three regions of the Powder River Basin, 2003-2006.

Figure 4. Estimated daily survival rate (DSR) of nests during incubation (with 95% CIs) as nest age increases based on nesting data from three regions of the Powder River Basin, 2003-2006. We illustrate the effect with data from nests in the Decker region in 2003 that began incubation on May 12, the average date of clutch completion in that region in that year in that region.

Figure 5. Estimated nest success (with 95% CIs) in three regions of the Powder River Basin, 2003-2006 for first nests and renests of (a) yearlings and (b) adults based on a *Region*Year*Hen age* + *Attempt* model. SH = Spotted Horse.

Figure 6. Daily survival rate (DSR) of broods (with 95% CIs) in three regions of the Powder River Basin, 2003-2006. Point estimates start at brood age of 1 d and are shown

for every other day through 35 d. Point estimates and CIs are offset for clarity. SH = Spotted Horse.

Figure 7. Estimated brood success (with 95% CIs) in three regions of the Powder River Basin, 2003-2006 based on a *Region*Year* model.

Figure 8. Estimated spring-summer survival (with 95% CIs) for greater sage-grouse females without broods (i.e., non-nesting females and females with unsuccessful nests) and those that raised broods to 35 d in three regions of the Powder River Basin, 2003-2006, based on the best-approximating model (*Region*WNv+Year+WBrood*).

Figure 9. Spring-summer survival (with 95% CIs) for (a) yearling and (b) adult females in three regions of the Powder River Basin from 2003-2007, based on a *Region*Year*Hen age* model. Estimates presented include (white bars) or exclude (gray bars) mortalities confirmed positive for West Nile virus. SH = Spotted Horse.

Figure 10. Fall-winter juvenile, yearling, and adult female survival (with 95% CIs) in three regions of the Powder River Basin from 2003 - 2006. Estimates refer to survival from fall to the following spring (e.g., 2003 means fall 2003 - spring 2004). Survival data on juveniles were only collected in the Decker region in fall-winter 2003-2004 and 2004-2005. Survival estimates for Spotted Horse were based on only 2 individuals in 2003-2004 and 4 individuals in 2004-2005.

Figure 11. Estimated annual survival of (a) yearling and (b) adult females in three regions of the Powder River Basin, 2003 - 2006 based on a *Region*Year*Hen age* model. Estimates presented include (white bars) or exclude (gray bars) mortalities confirmed positive for West Nile virus. Estimates refer to survival from fall in that year through the following spring. Survival estimates for Spotted Horse were based on only 2 individuals in 2003-2004 and 4 individuals in 2004-2005.

Figure 1

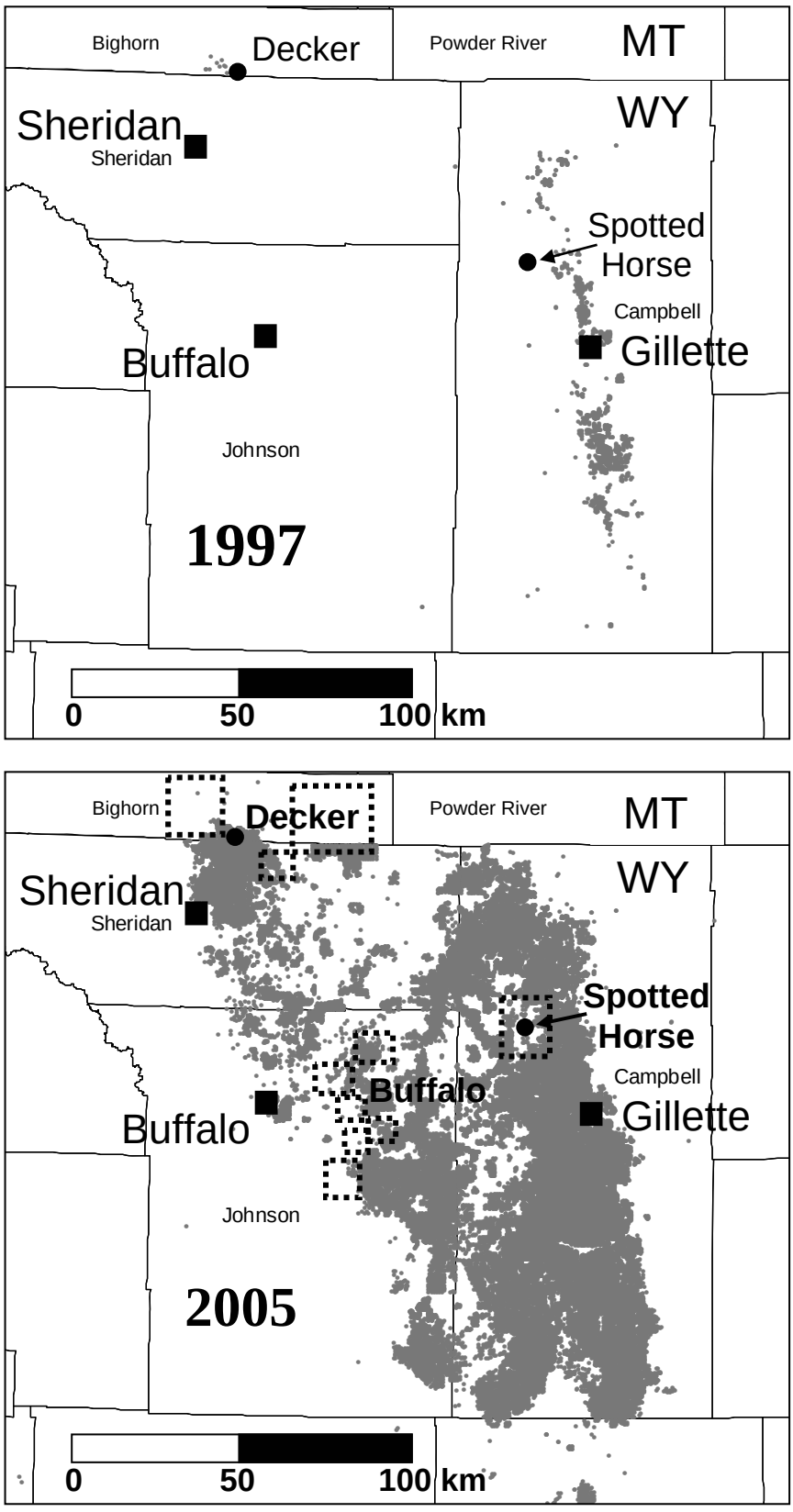

Bighorn
Decker
Powder River
MT
WY
Sheridan
Sheridan
Spotted
Horse
Campbell
Gillette
Buffalo
Johnson
1997
0
50
100 km
Bighorn
Decker
Powder River
MT
WY
Sheridan
Sheridan
Spotted
Horse
Buffalo
Campbell
Gillette
Buffalo
Johnson
2005
0
50
100 km

Figure 2.

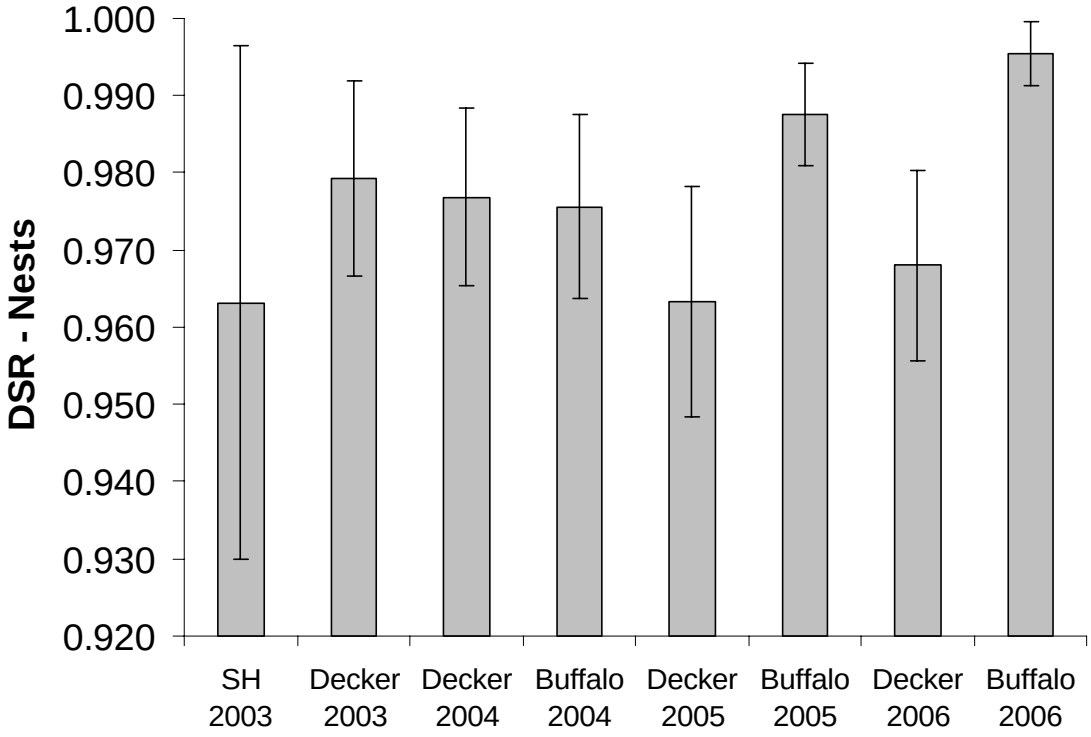

DSR - Nests
1.000
0.990
0.980
0.970
0.960
0.950
0.940
0.930
0.920
SH 2003
Decker 2003
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006

Figure 3.

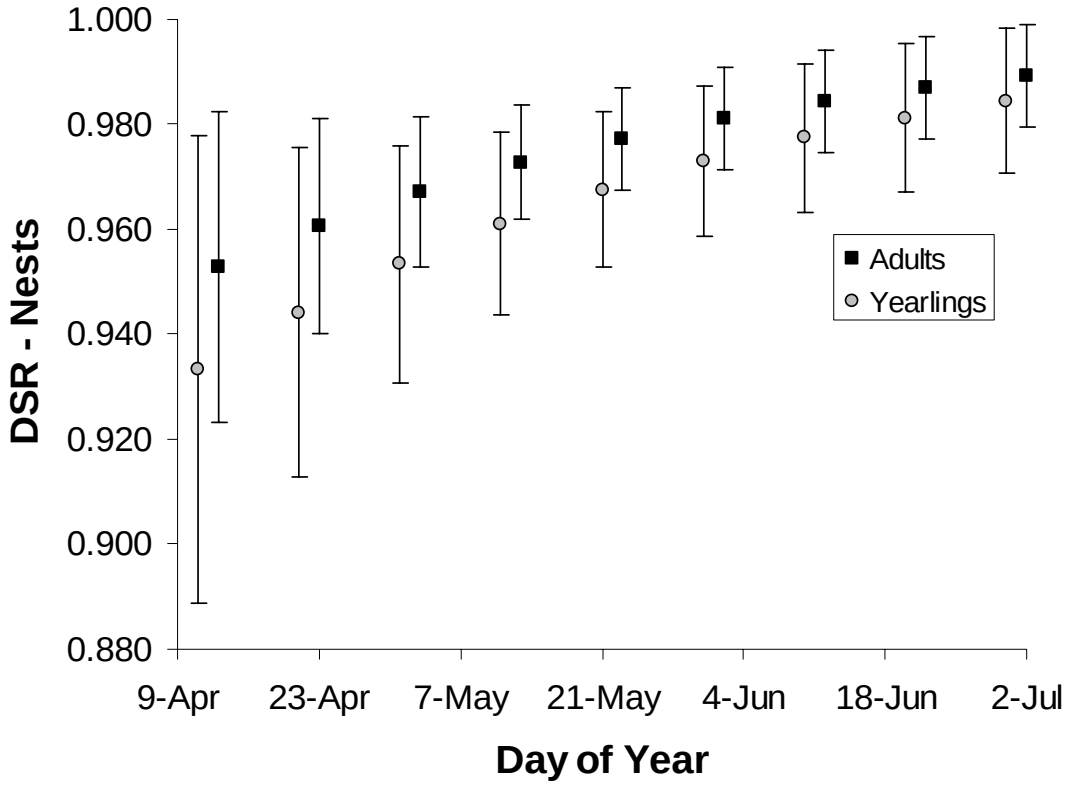

1.000
0.980
0.960
0.940
0.920
0.900
0.880
DSR - Nests
Adults
Yearlings
9-Apr
23-Apr
7-May
21-May
4-Jun
18-Jun
2-Jul
Day of Year

Figure 4.

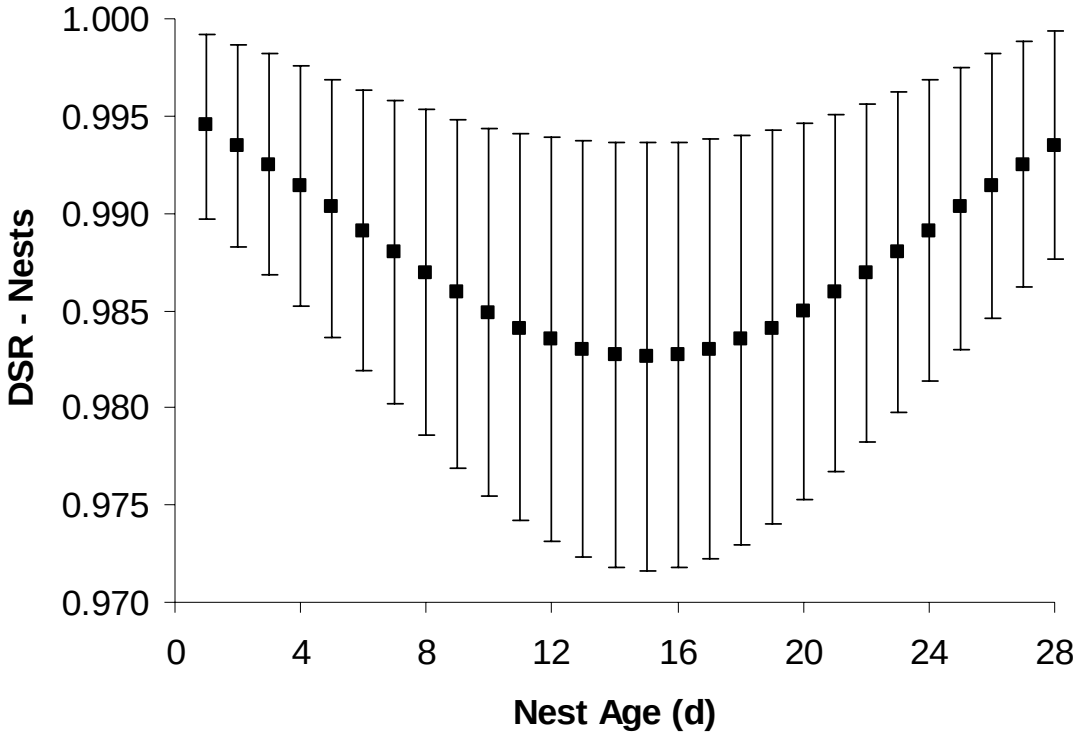
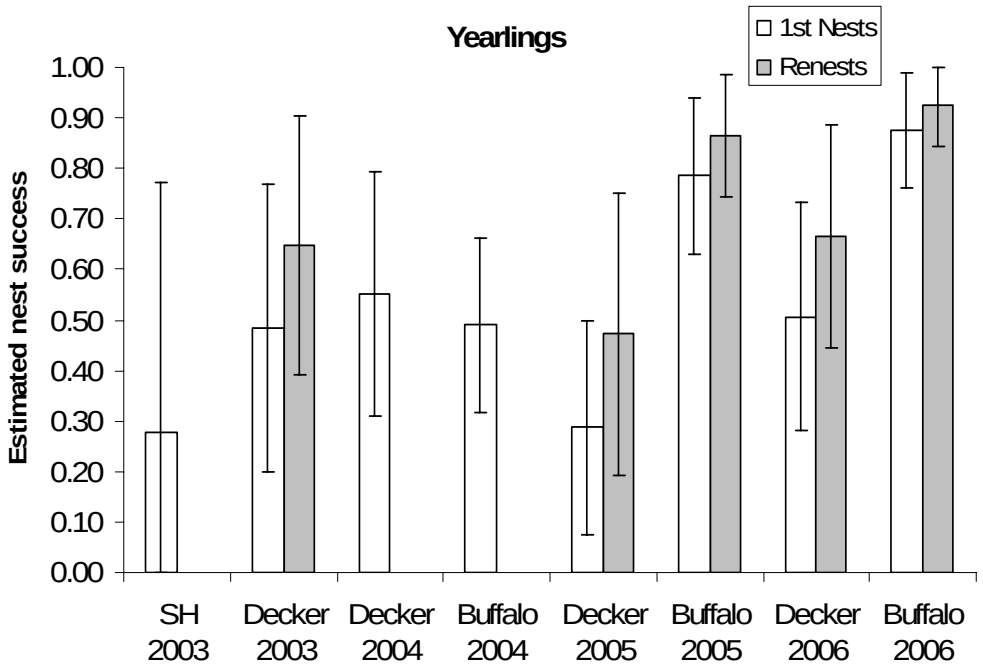

1.000
0.995
0.990
0.985
0.980
0.975
0.970
DSR - Nests
0
4
8
12
16
20
24
28
Nest Age (d)

Figure 5.

(a)


Yearlings
1st Nests
Renests
Estimated nest success
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
SH 2003
Decker 2003
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006

(b)

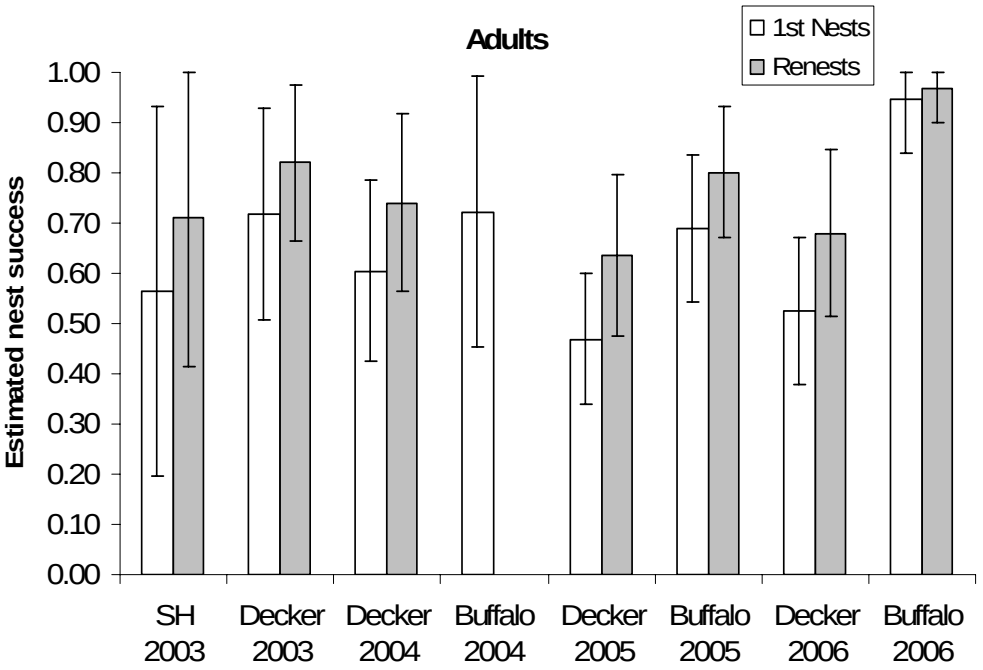

Adults
1st Nests
Renests
Estimated nest success
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
SH 2003
Decker 2003
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006

Figure 6.

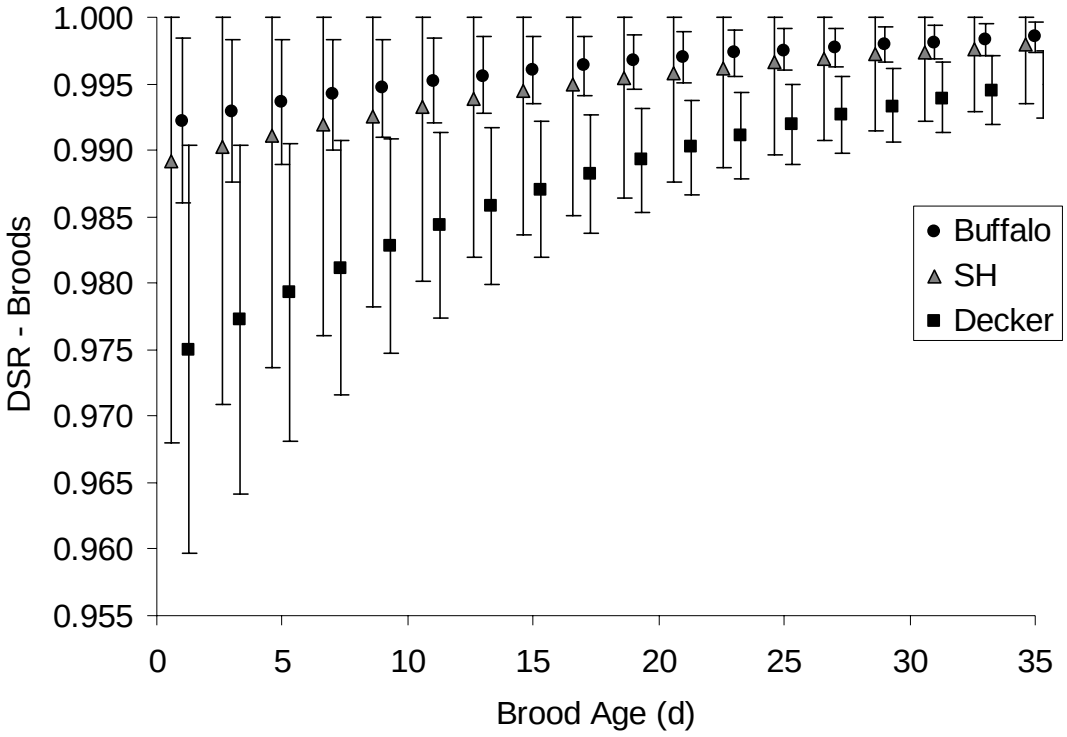

1.000
0.995
0.990
0.985
0.980
0.975
0.970
0.965
0.960
0.955
DSR - Broods
0
5
10
15
20
25
30
35
Brood Age (d)
Buffalo
SH
Decker

Figure 7.

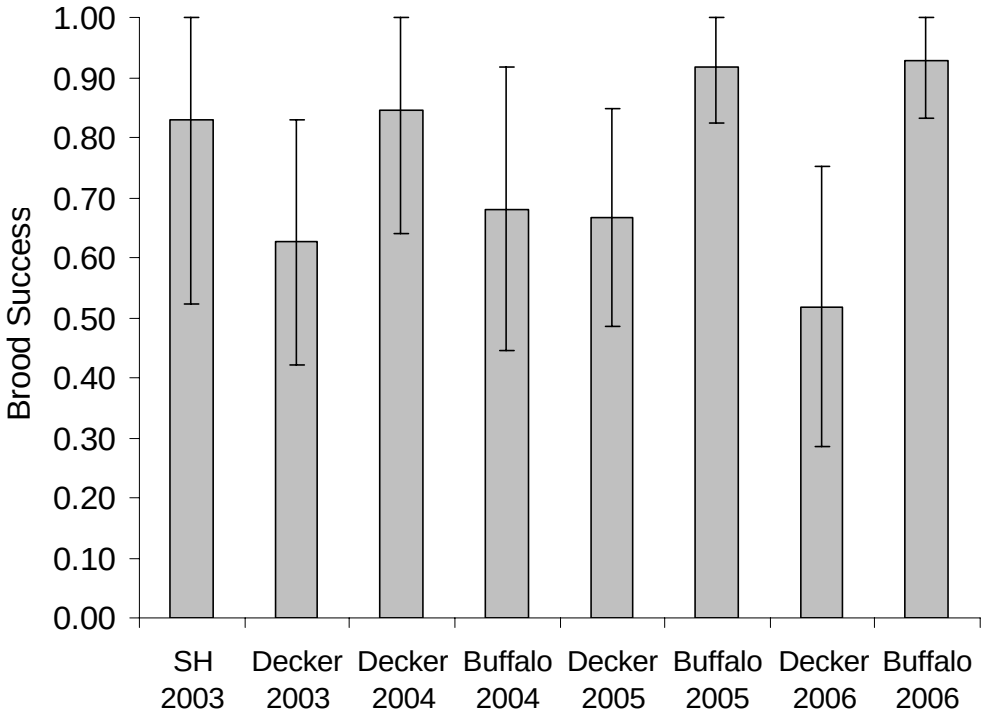

Brood Success
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
SH 2003
Decker 2003
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006

Figure 8.

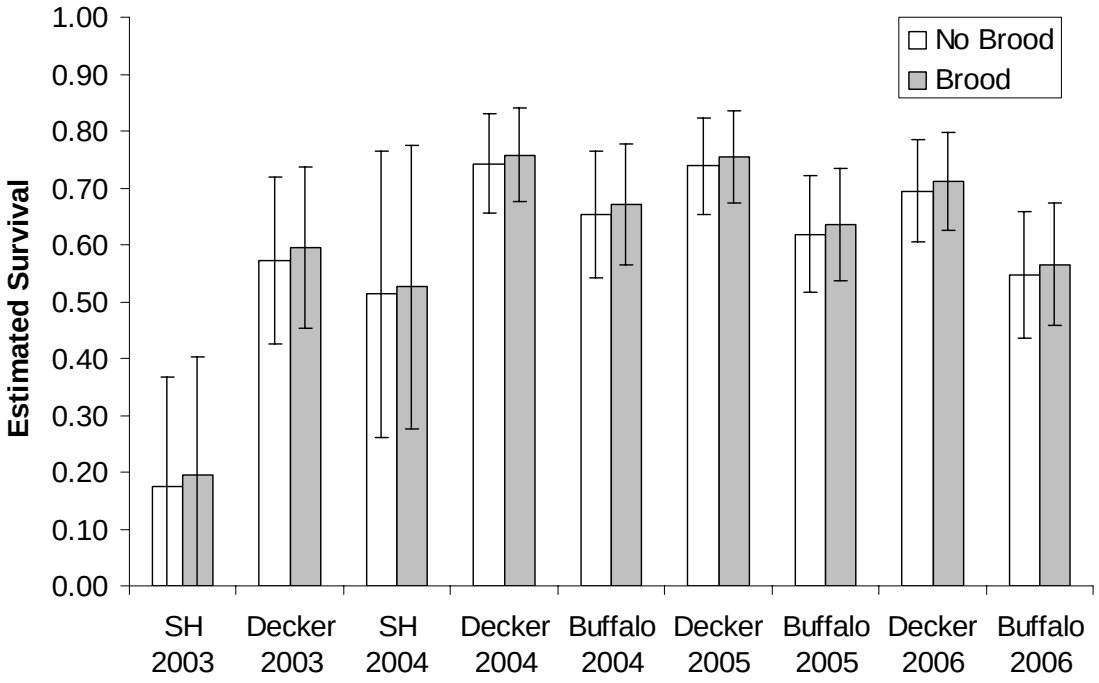
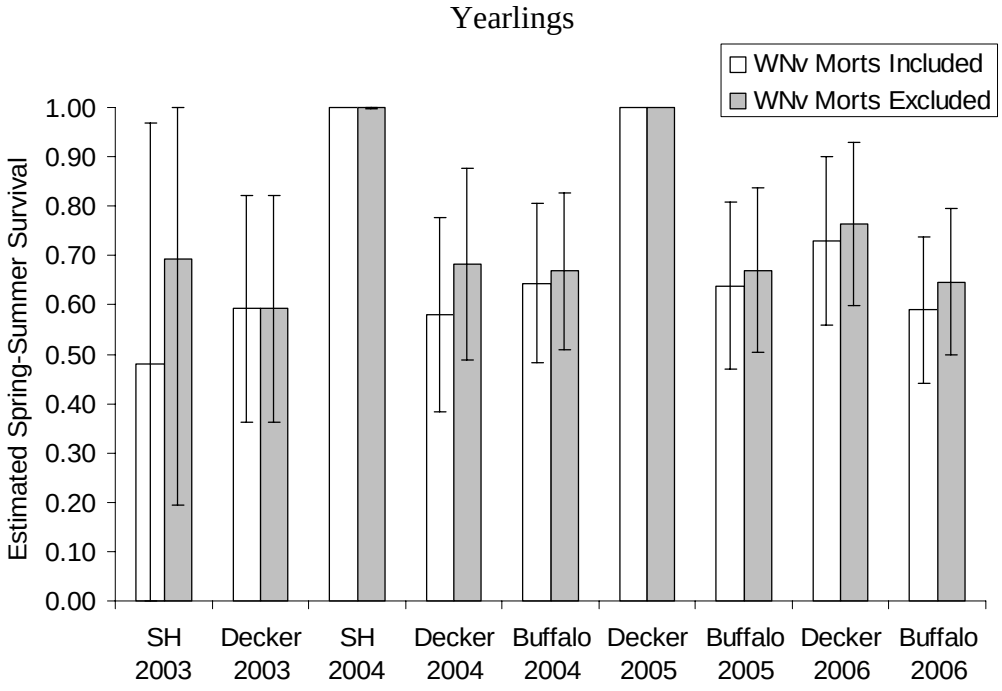

Estimated Survival
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
No Brood
Brood
SH 2003
Decker 2003
SH 2004
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006

Figure 9.

(a)


Yearlings
WNv Morts Included
WNv Morts Excluded
Estimated Spring-Summer Survival
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
SH 2003
Decker 2003
SH 2004
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006

(b)

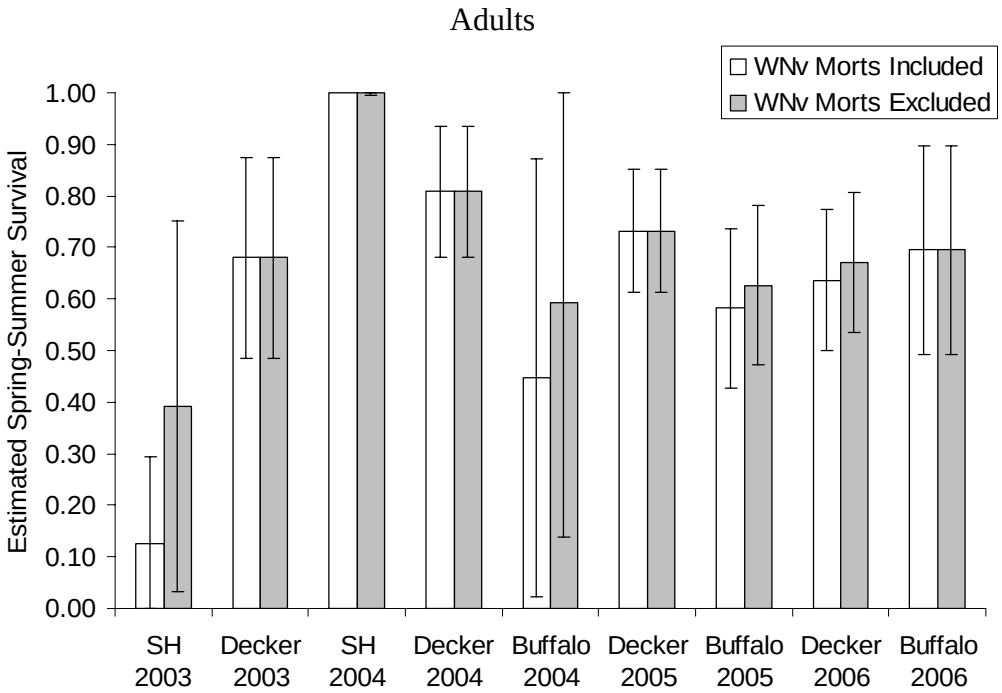

Adults
WNv Morts Included
WNv Morts Excluded
Estimated Spring-Summer Survival
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
SH 2003
Decker 2003
SH 2004
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006

Figure 10.

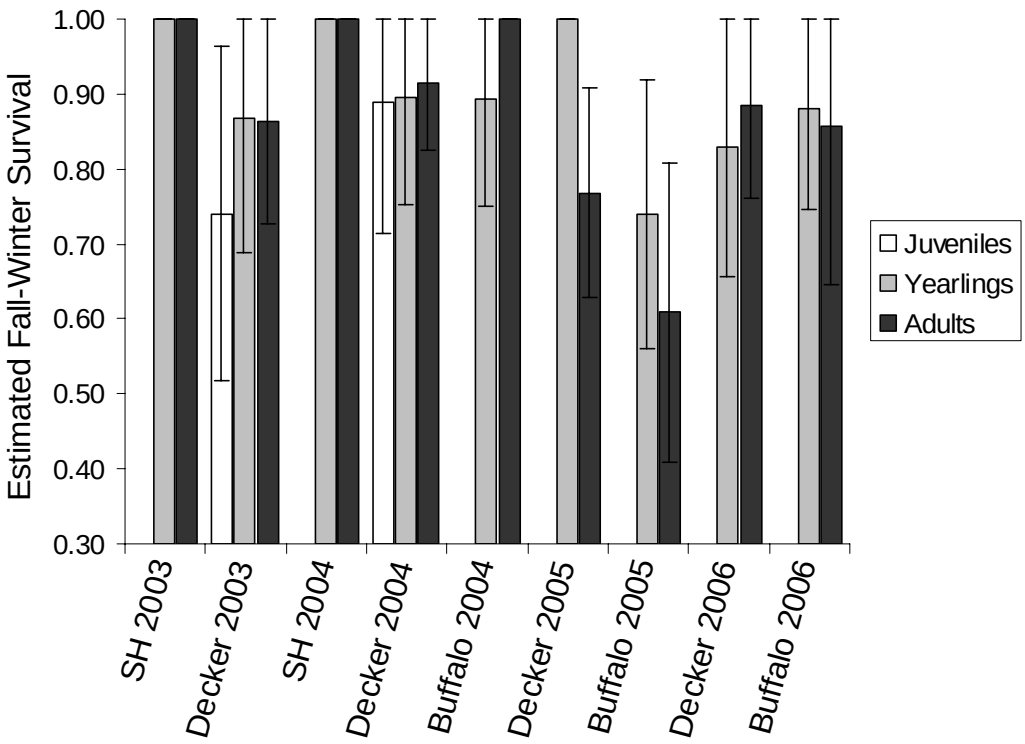
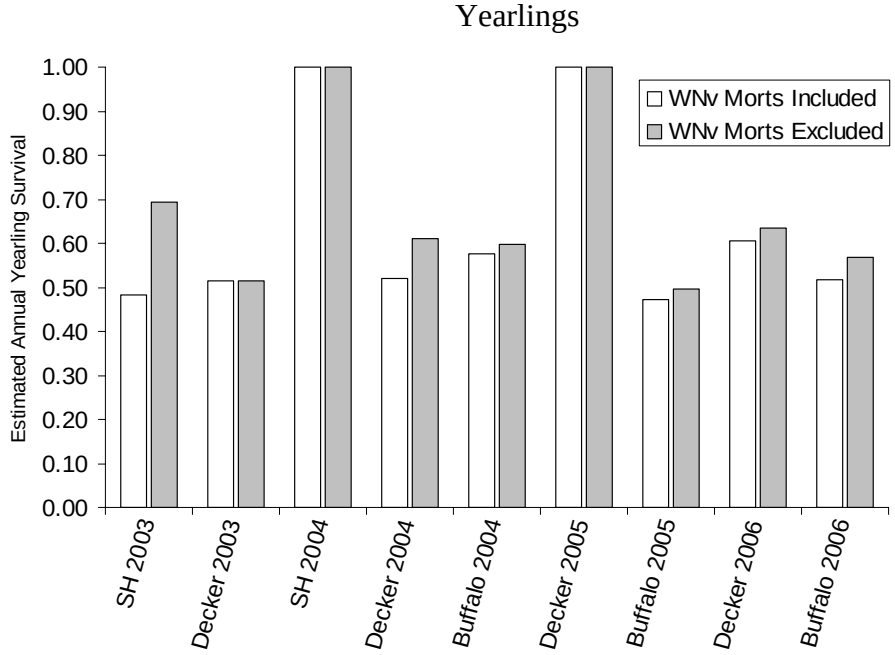
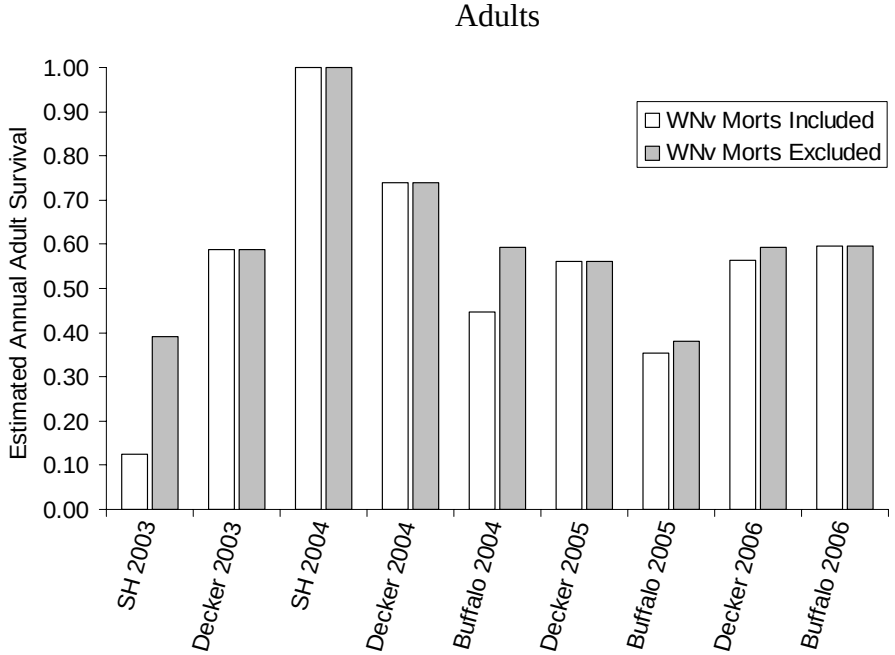

Estimated Fall-Winter Survival
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
SH 2003
Decker 2003
SH 2004
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006
Juveniles
Yearlings
Adults

Figure 11.

(a)


Yearlings
Estimated Annual Yearling Survival
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
WNv Morts Included
WNv Morts Excluded
SH 2003
Decker 2003
SH 2004
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006

(b)


Adults
Estimated Annual Adult Survival
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
WNv Morts Included
WNv Morts Excluded
SH 2003
Decker 2003
SH 2004
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006

# CHAPTER 5. IMPACTS OF WEST NILE VIRUS ON POPULATION GROWTH OF GREATER SAGE-GROUSE.

*Abstract.* A new concern for conservation of greater sage-grouse (*Centrocercus urophasianus*) in western North America is the arrival and spread of West Nile virus (Flaviviridae, *Flavivirus*) (WNv). Since 2003, declines in late-summer survival due to WNv-related mortality and mortality events have been reported in 11 of the 13 states within the species' current range, and laboratory studies have documented 100% mortality following infection. However potential long-term effects of WNv on populations have not been investigated. We used life-stage simulation analysis models and empirical data on WNv-related mortality and infection rates from radio-marked sage-grouse to explore potential impacts of WNv on population growth in the Powder River Basin of northeastern Wyoming and southeastern Montana, USA from 2003-2006. Observed levels of mortality indicate that WNv reduced estimates of population growth (i.e., finite rate of increase, $\lambda$) by -0.073 to -0.103 per year. Simulated impacts based on current estimates of WNv infection rate suggested an average decline in $\lambda$ of -0.073 to -0.075 due to WNv. Because of low annual infection rates, resistance to WNv disease was projected to increase gradually over time (assuming no changes in virulence). Severe outbreaks of WNv may result in increased resistance in the population, but may also simultaneously reduce local abundance below thresholds for population persistence. Residual or sublethal (i.e., carryover) effects of WNv infection in surviving individuals have the potential to hinder the evolution of resistance. Presently, carryover effects appear to have little influence on population growth because so few individuals survive

infection, but they may become relevant if infection rates or the proportion of resistant birds in the population increases. Changes in the virulence or epizootiology of WNv and in the distribution and management of surface water from coal-bed natural gas development will play an important role in long-term impacts on greater sage-grouse populations in the Powder River Basin.

***Keywords***: *Centrocercus urophasianus*, demographics, flavivirus, greater sage-grouse, population model, life-stage simulation analysis, Powder River Basin, sagebrush, vital rates, West Nile virus.

Emerging infectious diseases can act as important new sources of mortality for populations of sensitive and declining wildlife species. A major new concern for conservation of North American birds, including greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse"), in North America is the arrival and spread of West Nile virus (WNv; Flaviviridae, *Flavivirus*) (McLean 2006, Koenig et al. 2007, LaDeau et al. 2007). Recent studies have documented declines in sage-grouse survival attributable to WNv in wild (Naugle et al. 2004, 2005; Walker et al. 2004, 2007*b*) and laboratory populations (Clark et al. 2006). West Nile virus first arrived within the current range of sage-grouse in 2002 (Kilpatrick et al. 2007), and WNv-related mortality in sage-grouse was documented that year (Naugle et al. 2004). In 2003, WNv-related mortality reduced late-summer survival rate of females by ~25% across much of the eastern half of the species' range (Naugle et al. 2004), and resulted in near-extirpation of a local breeding population in northeastern Wyoming by spring 2004 (Walker et al. 2004). From

2004-2007, annual WNv-related mortality and localized severe mortality events have been reported throughout the species' range. By the end of 2007, WNv-positive mortalities had been documented in 11 of the 13 states and provinces where the species still occurs, with the exception of Washington and Saskatchewan (U. S. Geological Survey 2006; Walker 2006; Walker et al. 2007*b*). In northeastern Wyoming and southeastern Montana, WNv-related mortality during the summer resulted in an average decline in annual female survival of 5% (range 0-27%) from 2003-2006 (Chapter 4). Overall, estimates of WNv-related mortality among breeding-aged females during the summer WNv transmission period across the species' range varied from 0-71% (Walker et al. 2004, Naugle et al. 2005, USGS 2006, Kaczor 2008).

The spread and prevalence of resistance to WNv-induced disease over time also has important implications for effects of the virus on populations. West Nile virus is now considered the predominant endemic arthropod-borne disease in North America (Gubler 2007, Kramer et al. 2008), and it has been a persistent source of mortality in sage-grouse since 2003 (Walker 2006, Walker et al. 2007*b*). However, managing WNv risk for sage-grouse is a daunting task because of the scale at which reservoir and amplifying hosts (Kato et al. 2008), mosquito vectors (Doherty 2007), and sage-grouse are distributed during the summer transmission period (Connelly et al. 2000). For that reason, most wildlife managers must simply hope that resistance to disease will increase over time. To date, the combination of high mortality rates during severe WNv outbreaks, 100% mortality among experimentally infected birds from both eastern and western portions of the species' range, and low seroprevalence among survivors (0-10%), suggest that resistance to WNv-induced disease in sage-grouse generally is low (Naugle et al. 2004,

2005; Walker et al. 2004, 2007*b*; Clark et al. 2006). The first cases of sage-grouse surviving WNv infection were documented in 2005 and 2006 in northeastern Wyoming (Walker et al. 2007*b*), but live, seropositive birds have not yet been reported from other parts of the species' range. Exposure to the virus could increase resistance to WNv-induced disease over time at the population level and improve the likelihood of long-term population persistence, but changes in resistance depend on annual infection rates and the fitness of individuals that survive infection compared to uninfected birds.

Sublethal or residual (i.e., "carryover") effects of WNv infection may also be important in determining population-level impacts of the virus. As in other birds (e.g., raptors; Nemeth et al. 2006*a*, *b*) and in mammals (e.g., humans, horses; Hayes et al. 2005, Hayes and Gubler 2006), sage-grouse that survive WNv infection may nonetheless suffer persistent symptoms (Clark et al. 2006). In other species, non-lethal cases of WNv infection often result in chronic symptoms (e.g., reduced mobility, weakness, disorientation, muscle pain, etc.) and lengthy recovery periods (Marra et al. 2004, Hayes et al. 2005; Nemeth et al. 2006*a*, *b*). These symptoms in turn, may decrease nutritional or body condition of individuals and influence fall-winter survival, reproductive effort, or both following infection. In sage-grouse, nutritional condition prior to the breeding season is positively correlated with reproductive effort and success (Dunbar et al. 2005, Gregg et al. 2006). Carryover effects of WNv infection on sage-grouse have not been studied because low infection rates and high mortality have left few infected survivors for observation (Walker et al. 2007*b*). However, carryover effects might substantially influence population growth if the proportion of infected survivors increases over time.

Understanding the consequences of increased risk of WNv on populations due to

changes in land use is also crucial for projecting potential impacts of the virus. Anthropogenic changes may increase disease risk by directly or indirectly altering the abundance and habitat use of vectors, reservoirs, and hosts during the transmission period (McSweegan 1996). Of particular concern in the Powder River Basin are ponds associated with coal-bed natural gas (CBNG) development that increase the availability and distribution of larval habitat for mosquitos that vector WNv (Zou et al. 2006*a*, Doherty 2007) and increases in irrigated cropland and water impoundments for livestock due to increased availability of CBNG water. Additional water sources may simultaneously attract sage-grouse in late summer (Connelly and Doughty 1989, Schroeder et al. 1999, Connelly et al. 2000), concentrate potential WNv reservoirs and amplifying hosts, and increase mosquito abundance (Doherty 2007).

Understanding impacts of WNv on populations requires incorporating variation in all of these factors – mortality, resistance to disease, carryover effects, and anthropogenic changes to landscapes – into demographic models. Matrix models, in particular, are valuable for understanding how the influence of impacts on vital rates translates into consequences of potential stressors for population growth. Life-stage simulation analysis in particular, allows consideration of changes in both the mean and variance of specific vital rates on changes in population growth (Wisdom et al. 2000, Reed et al. 2002). However, assumptions associated with matrix models (e.g., populations at stable age distribution) suggest that such models are best used to identify changes in population growth rate under different scenarios, rather than absolute values for growth rates (Reed et al. 2002).

Overall, several lines of evidence suggest that WNv could be an important new stressor on sage-grouse populations, but the potential for long-term population-level effects of WNv has not been explored. We used population projection models, degree-day models for predicting WNv risk (Zou et al. 2006*b*), and empirical data on WNv-related mortality rates from radio-marked females to explore potential impacts of WNv on population growth in the Powder River Basin of northeastern Wyoming and southeastern Montana. We used stage-specific vital rates to parameterize a life-stage simulation analysis model to predict long-term population growth under eight different scenarios: (1) no WNv mortality, (2) observed WNv mortality; (3) simulated current WNv mortality; (4) simulated current WNv mortality with increasing resistance to WNv-induced disease over time; (5) simulated current WNv mortality with increasing resistance to disease and carryover effects on infected survivors; (6) simulated elevated WNv mortality due to expansion of CBNG development; (7) simulated elevated WNv mortality with increasing resistance; and (8) simulated elevated WNv mortality with increasing resistance and carryover effects.

## Methods

*Analyses.* We conducted both analytical sensitivity and elasticity analyses and life-stage simulation analysis to test the importance of mean vital rate values and their variability in predicting $\lambda$ for the Powder River Basin (Mills et al. 1999, Wisdom et al. 2000,. We then generated and compared means for $\lambda$ for each impact scenario based on 1000 simulations in MATLAB (version R2007a, The Mathworks, Inc., Natick, Massachusetts, USA).

*Correlation among vital rates*. We used correlations between vital rates to generate sets of correlated random vital rates for simulations (Box 8.6 in Morris and Doak 2002). We conducted analyses both with and without correlations to see how correlation structure influenced estimates of λ and interpretation of sensitivities, elasticities, and $r^2$ values. Incorporating correlation structure is important for generating realistic combinations of vital rates for simulations that are representative of typical values for the population of interest (Wisdom et al. 2000, Mills and Lindberg 2002, Morris and Doak 2002). Estimating correlations among vital rates requires estimates of each vital rate over multiple years, preferably for as many years as there are vital rates (Morris and Doak 2002). We were unable to generate a meaningful correlation matrix from the Powder River Basin data due to the short time-frame of the study (2003-2006) and because not all vital rates were estimated in all years. Instead, we assigned pairs of vital rates a correlation coefficient of none (0.00), low (0.25), moderate (0.50), or high (0.75) based on whether published data indicated that both vital rates were regulated by the same biological mechanism(s) (Appendix A). We also examined correlation coefficients between vital rates in the range-wide data to check for evidence for or against hypothesized correlations. We then tested to make sure the final correlation matrix was valid (i.e., positive semi-definite) (Box 8.8 in Morris and Doak 2002).

*Sampling vs. process variance*. Total variance in survival and productivity estimates is comprised of an unknown mix of temporal, spatial, and sampling variation. Because variance can strongly influence population model results and interpretation (Wisdom et al. 2000), sampling variance must be removed from total variance to obtain an estimate of actual spatial and temporal (i.e., process) variance in each vital rate.

Because sampling variance was unlikely to be equal across years or across studies, we used the variance discounting method of White (2000) to remove sampling variance from total variance estimates for Powder River Basin and range-wide data. In that analysis, estimates of variance for binomially-distributed vital rates in each year were estimated from the theoretical variance of a proportion ($\sigma^2 = pq/n$), where $p$ = proportion that survived, $q = 1 - p$, and $n$ = number of sample units included in the analysis.

*Model structure.* We used a two-stage, female-based life-cycle model to summarize stage-specific rates of fertility and survival (Figure 1). We used vital rates for each stage to calculate fertility and survival estimates for parameterizing a 2 x 2 stage-specific population projection model (i.e., Lefkovitch matrix model) based on a pre-breeding, birth-pulse census and a one-year projection interval, with birds "censused" on ~1 April just prior to the initiation of nesting. The two stages are yearlings (YR) and older adults (AD). Stage-specific survival and fecundity values were considered the same for all individuals within each stage. Female sage-grouse commonly breed as yearlings, so yearling females were allowed to reproduce in the model. Variables in the projection matrix included:

$f_{yr}$: fertility of yearlings (no. female juveniles produced per yearling female),

$f_{ad}$: fertility of adults (no. female juveniles produced per adult female),

$s_{yr}$: annual survival of yearlings from the start of the breeding season (~1 April) in their second calendar year through the start of the breeding season in their third calendar year,

$s_{ad}$: annual survival of adults from the start of the breeding season (~1 April) through the start of the breeding season in following calendar year.

*Vital Rates.* Whenever possible, we used mean vital rates and their associated variances from the Powder River Basin (Chapter 4) in the projection model. However, because vital rates vary both temporarily and spatially, a 4-year study is insufficient to adequately characterize means and variances. Moreover, data were not available for all vital rates in all years (e.g., juvenile survival, renest success). Therefore, we also summarized year- and site-specific estimates of vital rates from published and unpublished literature sources from across the species' range for comparison (Appendix B). In the range-wide data, estimates based on combined data from several years were treated as a single estimate for that study location. Estimates from the same study location in the same year were included only once, even if they appeared in more than one publication. We excluded data that did not use reliable methods for obtaining or estimating vital rates and those with sample sizes <10 (Appendix B). When data from the Powder River Basin were unavailable or too sparse to reliably estimate means or variances, we used range-wide means, variances, or both. We also used range-wide data to establish upper and lower bounds and to identify appropriate sampling distributions for each vital rate.

Nest initiation rate ($INIT_1$) was defined as the proportion of females in each stage (i.e., yearling or adult) that were adequately monitored during the nesting season and initiated at least one nest (i.e., laid at least one egg). Renesting rate ($INIT_2$) is defined as the proportion of females whose first nests were unsuccessful that survived, were adequately monitored, and initiated a second nesting attempt. Second renesting rate ($INIT_3$) is defined as the proportion of females whose first and second nests were unsuccessful that survived, were adequately monitored, and initiated a third nesting

attempt. Although rates of nest initiation and renesting are likely biased low because some nests fail before they can be discovered, no method exists to correct this bias.

Clutch size was defined as the number of female eggs laid in the nest. On average, adults lay ~0.5 eggs per clutch more than yearlings in first nests, and first nests (8.3) average ~1.5 eggs per clutch more than renests (Petersen 1980, Schroeder 1997, Moynahan 2004, Chapter 4). Due to a lack of data on third nests, we assumed that clutch sizes of third nests (adults only) averaged one egg fewer than second nests. Data on sex ratio at hatch were unavailable. Therefore, instead of including sex ratio as a separate vital rate with unknown mean and variance, we instead assumed an equal ratio of males to females at hatch and multiplied clutch size means by 0.5 to generate stage-specific estimates of clutch size for female eggs only ($CLUTCH_1$, $CLUTCH_2$, and $CLUTCH_3$).

Nest success ($SUCC_1$, $SUCC_2$) was defined as the probability of a nest surviving from laying through hatching. We considered a nest successful if ≥1 egg hatched. We used exponentiated estimates of daily survival rates (DSR) of nests to estimate region, year, and stage-specific nest success for first and second nesting attempts for each region and year in the Powder River Basin (Chapter 4) and then calculated mean values across regions and years. Data from second nesting attempts included one successful third nest of one female in 2005. Yearlings have never been recorded attempting a third nest (Appendix B), so third nests were excluded from yearling fertility calculations. For range-wide data, we estimated nest success during incubation by adjusting reported rates of apparent nest success using the "quick" method of Johnson and Klett (1985). Apparent nest success was defined as the proportion of nests that hatched at least one egg. The "quick" method uses the average age of when nests are found (*f*) and average

age of nests at hatch ($h$) to calculate an approximate daily nest survival rate ($S$) as the ($h$-$f$) root of apparent nest success. Nest success is then calculated as $S^h$. Nests of radio-marked female sage grouse are typically found during the first visit following the start of incubation (Schroeder et al. 1999, Chapter 4). Thus, we estimated the average age at which nests were found for each study as one-half the reported monitoring interval, where day 1 represented the first day of incubation (i.e., the date of clutch completion). Quick estimates of nest success during incubation were then multiplied by estimated nest success during laying, based on a daily survival estimate of 0.997 during laying (Chapter 4) and laying intervals that varied by age and nest attempt (10.5 d and 9 d for yearling first nests and renests and 12 d and 10.5 d for adult first nests and renests, respectively).

Hatchability (HATCH) was defined as the mean proportion of eggs that hatched across regions and years (i.e., no. of eggs in all clutches of known size divided by the no. of eggs that hatched from all clutches of known size). For range-wide data, there were no published estimates of differences in hatchability of eggs between yearlings and adults, between first nests and renests, or between male and female eggs, so we used the same value (0.923) in all calculations.

Chick survival (CHSURV) was defined as the proportion of chicks that survived from hatch to 35d based on a combination of night-time spotlight counts and day-time flush counts (i.e., apparent chick survival). We were unable to distinguish between male and female chicks, so we assumed that chick survival estimates were representative of females. Males are thought to survive at lower rates than females as juveniles (Swenson 1986), but data on sex-specific survival of chicks <35 d old are not available. Chick

survival estimates from range-wide data also did not distinguish males from females (e.g., Burkepile et al. 2002, Aldridge 2005, Gregg 2006, Gregg et al. 2007, Chapter 4).

Juvenile survival was defined as the proportion of females that survive from ~35 days old to the start of the breeding season (~1 April) in their second calendar year. Estimates of survival for juveniles produced by yearling vs. adult females were unavailable, so we used the same juvenile survival estimates in calculations for both stages. Because the interval length for juvenile survival depends on when the chick hatches, we used data on average hatch dates for first and subsequent nesting attempts to calculate the approximate interval length required for first nests (9.1 mo [$JUVSURV_{91}$]) and for renests (8.3 mo [$JUVSURV_{83}$]). In the Powder River Basin, estimates of juvenile survival were for the 6.67-month interval from 10 Sept through ~1 April. Data on juvenile survival from 35 d of age through 10 Sept were unavailable. Range-wide estimates of juvenile survival were only reported for 5-7 month long intervals (Sept-Nov through March). Because most chick mortality occurs prior to 35 d (Burkepile et al. 2002, Aldridge 2005, Gregg et al. 2007), we assumed that monthly survival rates for juveniles from 35 d of age to 10 Sept were similar to those over the fall and winter.

*Fertility and survival calculations.* Stage-specific fertility for yearlings ($f_{yr}$) was calculated as:

$[INIT_{1YR} \times FCLUTCH_{1YR} \times SUCC_{1YR} \times HATCH \times CHSURV_{YR} \times JUVSURV_{91}] +$

$[INIT_{1YR} \times (1\text{-}SUCC_{1YR}) \times INIT_{2YR} \times FCLUTCH_{2YR} \times SUCC_{2YR} \times HATCH \times CHSURV_{YR} \times JUVSURV_{83}].$

Stage-specific fertility ($f_{yr}$) for yearlings in the Powder River Basin averaged 0.569. Stage-specific fertility for adults ($f_{ad}$) was calculated as:

$[INIT_{1AD} \times FCLUTCH_{1AD} \times SUCC_{1AD} \times HATCH \times CHSURV_{AD} \times JUVSURV_{91}] +$

$[INIT_{1AD} \times (1\text{-}SUCC_{1AD}) \times INIT_{2AD} \times FCLUTCH_{2AD} \times SUCC_{2AD} \times HATCH \times CHSURV_{AD} \times JUVSURV83] +$

$[INIT_{1AD} \times (1\text{-}SUCC_{1AD}) \times INIT_{2AD} \times (1\text{-}SUCC_{2AD}) \times INIT_{3AD} \times FCLUTCH_{3AD} \times SUCC_{2AD} \times HATCH \times CHSURV_{AD} \times JUVSURV_{83}]$.

Stage-specific fertility ($f_{ad}$) for adults in the Powder River Basin averaged 0.846.

Yearling survival ($s_{yr}$) was defined as the proportion of yearling (i.e., "second-year") females that survived from the start of the breeding season (~ 1 April) in their second calendar year (i.e., their first breeding season) to the start of the breeding season (~ 1 April) in their third calendar year. Yearling survival in the Powder River Basin averaged 0.639.

Adult survival ($s_{ad}$) was defined as the proportion of adult (i.e., "after-second-year") females that survived from the start of the breeding season (~1 April) to the start of the breeding season (~ 1 April) the following year. Adult survival in the Powder River Basin averaged 0.556. In the range-wide survival data, we excluded estimates from studies that estimated annual survival rates from poncho or wing-tagged birds, as those types of marks likely increase detectability to predators and bias survival estimates. We was unable to include data from studies that analyzed yearling and adult daily or monthly survival rates but failed to report stage-specific survival estimates.

*WNv impact scenarios*. Each scenario required adjusting juvenile, yearling, and adult survival rates to account for to WNv-related mortality. Most chicks reach the juvenile stage (i.e., > 35 d old) prior to the onset of WNv transmission season in early July (particularly in years with high success of first nests and low renesting rates), so we made no adjustments to chick survival estimates. This results in a conservative estimate of the impact of WNv. Mortality from WNv may reduce chick survival directly, and

non-independent chicks and juveniles whose mothers die of WNv may also experience higher mortality. Calculations for each scenario were as follows:

(1) *No impact.* We based estimated means and variances of juvenile survival and annual yearling and adult female survival on the Powder River Basin dataset that excluded WNv-related mortalities (Chapter 4).

(2) *Observed WNv mortality*. We based estimated means and variances of juvenile survival and annual yearling and adult female survival on the Powder River Basin dataset that included WNv-related mortalities (Chapter 4). Juveniles are confirmed to have died from WNv (Naugle et al. 2004, Aldridge 2005), but we had too few juveniles collared during the WNv season in each year to estimate WNv-related mortality. Because juveniles flock together with yearlings and adults during the summer, we assumed they would all experience similar exposure to WNv. Therefore, we used observed reductions in adult and yearling spring-summer survival due to WNv (mean 5.3%, range 0.0 - 26.7%) to adjust estimates of juvenile survival for each region in each year as follows:

$$JUVSURV83_{adj} = (JUVSURV83^{(0.12)})^{(6.67)} \times ((JUVSURV83^{(0.12)})^{(1.63)} \times (1\text{-WNv mortality rate}))$$

$$JUVSURV91_{adj} = (JUVSURV91^{(0.11)})^{(6.67)} \times ((JUVSURV91^{(0.12)})^{(2.43)} \times (1\text{-WNv mortality rate}))$$

We then calculated a mean and variance for juvenile survival from adjusted estimates.

(3) *Current WNv mortality*. In all remaining scenarios, we based estimated means and variances of juvenile, yearling, and adult survival on the Powder River Basin dataset that excluded WNv-related mortalities. We then simulated impacts of WNv using empirical data on infection rates, WNv-related mortality rates, and predicted WNv transmission events from the Powder River Basin to adjust juvenile, yearling, and survival rates in response to WNv mortality. West Nile virus infection rate is

regulated by temperature (Reisen et al. 2006, Zou et al. 2006*b*), distribution and abundance of breeding sites for mosquito vectors (Zou et al. 2006*a, b*; Doherty 2007), and distribution and abundance of infected reservoir and amplifying hosts (Kato et al. 2008). To estimate adjustments to survival rates due to WNv, we first examined relationships between annual WNv severity predicted from temperature data (Western Regional Climate Center, Reno, Nevada, USA) using a degree-day model (Zou et al. 2006*b*) and actual reductions in annual survival due to WNv mortality for each of the three regions in the Powder River Basin from 2003-2006. However, these relationships were inconsistent (Figure 2*a*, *b*), suggesting that temperature is not the only predictor of WNv severity in the Powder River Basin (Zou et al. 2006*a*, Doherty 2007). Instead, we randomly selected infection rates from a stretched beta distribution (mean = 0.07, SD = 0.0548, minimum = 0.005, maximum = 1.0; Box 8.3 in Morris and Doak 2002) so that median infection rates matched the midpoint (~0.058) of observed annual minimum and maximum rates (Walker et al. 2007*b*). This SD allows most years to have low rates of WNv infection (e.g., median 0.055) and mortality (median 0.053). The relatively low SD produces some years with extreme values for infection rate, but data from 10,000 simulations indicate that values generally do not exceed ~0.50. This distribution resulted in a mean simulated annual infection rate of 0.069, a median simulated annual infection rate of 0.055 (range 0.005-0.515), and a conservative distribution of infection rates (Figure 3). The distribution of simulated infection rates contrasts with the distribution of annual predicted number of WNv events according to the degree-day model of Zou et al. (2006*b*) and a modified degree-day model based on actual dates of bird mortality

(Figure 4). Mortality due to WNv (M) was calculated from infection rate (I) and resistance to WNv-induced disease (R) as: $M = I – (I * R)$, which represents the proportion of the population infected minus the proportion infected but resistant. In this scenario, we maintained resistance constant at 0.04, the mean spring seroprevalence value measured over three years of study (Walker et al. 2007*b*).

(4) *Current WNv mortality with increasing resistance to WNv disease*. We assessed how an increase in resistance to WNv-induced disease would change population growth rate by calculating changes in the proportion of resistant individuals in the population under simulated vital rates and rates of WNv infection and WNv mortality. Because not all birds that are exposed to the virus become infected, we define "resistance" as the ability to survive exposure, infection, or both, and we assume the individuals with neutralizing antibodies to WNv were at minimum, exposed to the virus. Under this definition, resistant individuals may nonetheless experience sublethal or residual effects of WNv infection. We assumed that resistance to infection and disease was heritable and that all female offspring of a resistant female inherited traits that conferred resistance (i.e., heritability of resistance = 1). Seroprevalence data indicated that, on average, only 0.04 (range 0.00-0.10) of birds captured in spring had survived WNv infection from previous years (Walker et al. 2007*b*). Therefore, we used 0.04 as our starting value for resistance. We ran each simulation with 20 replicates to simulate responses within a reasonable management timeframe of 20 years, then ran the simulation 1000 times to generate means and standard deviations for $\lambda$ over the 20-year period.

(5) *Current WNv mortality with resistance and carryover effects*. We assessed how residual effects on overwinter survival and sublethal effects on reproductive effort might influence population growth rate by calculating changes in the proportion of resistant individuals in the population over time and by then reducing overwinter survival by 5%, nest initiation by 5% (adults) or 10% (yearlings), renesting rate by 10% (adults) or 20% (yearlings), and all clutch sizes by ~1 egg (~0.5 female eggs) for surviving infected individuals. We then ran each simulation with 20 replicates (i.e., 20 years) and ran the simulation 100 times to generate means and SDs for λs over the 20-year period.

(6) *Elevated WNv mortality (with and without resistance and carryover effects)*. We estimated changes in population growth for a scenario in which average WNv-related mortality increases due to the expansion of CBNG development. Coal-bed natural gas development is increasing the number and distribution of surface water ponds within sage-grouse habitat in the Powder River Basin (Zou et al. 2006*a*), and these ponds support breeding populations of the mosquito *Culex tarsalis* (Doherty 2007), a common, highly competent vector of WNv (Goddard et al. 2002, Turell et al. 2005). Zou et al. (2006*a*) estimated that CBNG development increased larval habitat for *C. tarsalis* by ~75% over a 21,000 $km^2$ area between 1999-2004. Coal-bed natural gas ponds likely increase exposure of sage-grouse to WNv in areas that otherwise would show low infection rates (Chapter 3, Walker et al. 2007*b*). In 2003, WNv mortality in the Spotted Horse region, an area with abundant CBNG ponds (Doherty 2007), was much higher (~75%) than in undeveloped areas near Decker (0%) (Walker et al. 2004), even though high summer temperatures predicted high rates of WNv

transmission throughout the Powder River Basin (Zou et al. 2006*b*). Furthermore, five of six WNv-positive mortalities at that time occurred next to CBNG ponds. In 2004, a year of relatively low and later WNv mortality, two of three WNv-positive mortalities in the Decker region occurred in alfalfa fields irrigated with water from CBNG development (Table 7, Chapter 4). Although mosquito control has been recommended for CBNG ponds (Doherty 2007, Walker et al. 2007*b*), there is no guarantee that control efforts will be consistently and appropriately implemented on all public and private lands. For this reason, we simulated elevated mortality due to CBNG by increasing the mean of the beta distribution used to estimate WNv infection rates (mean = 0.10, SD = 0.0548). This resulted in an average simulated annual WNv infection rate of 0.100 (range 0.007-0.380), a median simulated annual infection rate of 0.090, and average simulated annual WNv mortality of 0.096 (range 0.007-0.365). Although other, more complex CNBG scenarios are possible, an increase in average WNv-related mortality to ~10% throughout the Powder River Basin is plausible, and possibly too conservative, considering the established mechanistic links between CBNG, mosquitos, and WNv (Zou et al. 2006*a*, Doherty 2007, Walker et al. 2007*b*), the proximity of previous WNv-positive mortalities to CBNG water, the rapid spread and large scale of development (Walker et al. 2007*b*), and documented population declines in areas with CBNG development (Walker et al. 2004, 2007*a*).

## Results

*Vital rates and their importance in population growth.* Vital rate means and process variance from the Powder River Basin were similar to range-wide values, with a few exceptions (Appendix B). Results of life-stage simulation analysis suggested that different vital rates were important for λ than those based on analytical elasticity values (Figure 5). Mean elasticity values suggested that rates of nest initiation, clutch size, and hatchability had an equally important influence on λ as nest success, and chick, juvenile, yearling, and adult survival. However, because nest initiation, clutch size, and hatchability showed little variation in the Powder River Basin, life-stage simulation analysis identified other vital rates with greater potential to influence λ (Figure 6). Vital rates most important for population growth identified using life-stage simulation analysis included nest success, chick survival, juvenile survival, yearling survival, and adult survival, in that order (Figures 5, 6). Because vital rates require different management strategies, we also grouped vital rates subject to similar management actions (Figure 5). life-stage simulation analysis results for the Powder River Basin were similar to those from range-wide data (Figure 6).

*WNv impact scenarios.* The addition of WNv mortality resulted in a reduction in average estimated λ of -0.059 to -0.076 under scenarios with current mortality rates when vital rates were correlated and from -0.075 to -0.103 when vital rates were uncorrelated (Table 1). For the most part, excluding correlations among vital rates had only minor effects on estimates of how WNv influences λ (Table 1) and did not change our overall finding of substantially lower values for λ due to WNv mortality. Reductions in λ under scenarios with observed WNv mortality versus simulated WNv mortality were the same

(-0.73), suggesting that the distribution we selected for simulating infection rates was representative of actual WNv mortality. Elevated levels of WNv mortality, as expected, resulted in substantially larger decreases in estimated λ, ranging from -0.085 to -0.119 for scenarios with correlated vital rates, and -0.97 to -0.115 to scenarios with uncorrelated vital rates. However, substantial annual variation in vital rates resulted in wide variation in simulated values for λ in all scenarios (Figure 7). Thus, population growth rates can vary substantially from year to year.

Resistance to WNv disease was projected to increase only slightly during the 20-year period we examined. Low WNv infection rates, and consequently, low WNv mortality in most years, resulted in too few individuals exposed to the virus to quickly select for increased resistance. Resistance was projected to increase from 0.04 (our starting value) to 0.151 (range 0.082 - 0.374) over 20 years under current estimates of infection rate (Figure 8 *a*, *b*) and to 0.245 (range 0.125 - 0.514) under scenarios with elevated mortality. Increased resistance reduced annual WNv mortality rates from an average of 0.067 to 0.060 after 20 years (Figure 9) under current infection rates and from 0.097 to 0.075 under elevated infection rates. Increased resistance also reduced average declines in λ due to WNv (Table 1).

Carryover effects on fall-winter survival and subsequent reproductive effort slightly eroded gains in resistance to WNv disease (Figure 8 *a* ,*b*) because infected individuals survived at lower rates and produced fewer offspring. Resistance estimates at year 20 in the presence of carryover effects was 0.126 (range 0.074 - 0.253) under current infection rates and 0.198 (range 0.104 - 0.391) under elevated infection rates. However, on average, carryover effects influenced < 1% of all individuals in the population in any

given year over the 20-year period we examined (Figure 10). Carryover effects were projected to have only minor impacts on λ, and resulted in only slightly greater declines in λ (-0.01 to -0.02) than resistance-only scenarios (Table 1).

## Discussion

West Nile virus was a persistent new source of mortality in greater sage-grouse in the Powder River Basin that has the potential to reduce annual population growth and cause severe local population declines during outbreaks. Mortality from WNv resulted in a reduction in λ, regardless of whether impacts were based on observed or simulated WNv mortality rates. However, in any given year, declines in λ caused by WNv can be masked by naturally large annual variation in vital rates. For that reason, changes in lek counts are likely to detect only severe population reductions due to WNv (Walker et al. 2004), and monitoring impacts of low to moderate levels of WNv mortality on populations will require tracking and testing of radio-marked individuals during the transmission season (Walker et al. 2004). Without monitoring radio-marked individuals, impacts of WNv mortality, and even severe outbreaks, may go undetected and lead to the misperception among managers and policy-makers that WNv is no longer an issue for greater sage-grouse in the Powder River Basin. Moreover, in the absence of radio-marked birds, population declines due to severe or persistent WNv mortality may be incorrectly attributed to other potential stressors (e.g., weather, range management) and lead to inappropriate policy and management decisions.

In our study, mortalities from WNv were an order of magnitude more common than power line collisions, vehicle collisions, or harvest (Chapter 4). However,

occasional severe local outbreaks of WNv throughout the species' range appear to have impacts of a magnitude similar to organophosphate pesticide poisoning (Blus et al. 1989) and intensive, active energy development (Holloran 2005, Walker et al. 2007*a*). Whether populations heavily impacted by WNv (e.g., Spotted Horse, Wyoming) (Walker et al. 2004) can recover to previous levels will not be known for several years.

Resistance to WNv disease in simulations increased relatively slowly over time, in part because annual infection rates were low in most areas in most years. Estimating change in resistance to disease over time is complicated by several factors, including the potential for competition among viral strains (Davis et al. 2005) and rapid selection for changes in virulence (Davis et al. 2004). Paradoxically, the phenomenon that would promote increased resistance – high rates of WNv infection – can also lead to large reductions in local population size, which in some cases, may be problematic for population persistence. A parallel is found in insects in agricultural systems, in which only massive mortality events (e.g., pesticide spraying) that select for resistant individuals are capable of promoting the rapid spread of pesticide resistance. Even so, low rates of WNv transmission and infection in undeveloped sage-grouse habitats have almost certainly prevented more severe outbreaks and local extirpations. Naturally high variation in population growth rates in this species may allow populations to rebound quickly from impacts of WNv if consecutive years have high survival, high productivity, or both as seen in portions of the Powder River Basin from 2003-2006. The impact of WNv during a string of low-survival or low-productivity years may be severe.

Carryover effects are unlikely to substantially influence population growth except under conditions of high infection rates or high levels of resistance. Because carryover

effects were simulated based on best guess estimates rather than empirical data, they may or may not represent realistic values. Even so, it appears that so few infected individuals typically survive infection, such that resistant infected birds constitute only a small fraction of the fall or spring population in any given year. Carryover effects of WNv infection may be more important in areas with high infection rates (i.e., high exposure) caused by differences in land use (e.g., irrigated agriculture, CBNG development; Zou et al. 2006 *a*, Doherty 2007, Walker 2007*b*) or they may become more important several decades from now if resistance to WNv increases within and among sage-grouse populations.

Our model for the Powder River Basin may over- or underestimate impacts of WNv on populations in the Powder River Basin. Sage-grouse mortalities from WNv have occurred as early as 14 June in the Powder River Basin, which overlaps with chick survival from renests (Chapter 4). If mortality due to WNv commonly occurs among late-hatched chicks <35 d of age, among brooding females, or both, the scenarios presented may have substantially underestimated WNv impacts. Positive or negative density-dependent effects not included in our model could also influence impacts of WNv on population growth. In sage-grouse, the potential for negative density-dependent effects on population growth has been recognized (Connelly et al. 2003, LaMontagne et al. 2002, Sedinger and Rotella 2005), but no empirical evidence exists to evaluate whether the phenomenon occurs. Negative density-dependence may allow populations to recover more quickly from annual effects of WNv mortality. Positive density-dependence may also be an issue. For example, survival and population growth may be inhibited if severe WNv outbreaks greatly reduce local abundance, or if population size is

already reduced by other stressors (e.g., habitat loss and fragmentation, fire, weeds; Connelly et al. 2004). Positive density-dependent effects may occur if smaller flock sizes result in reduced overwinter survival (Courchamp et al. 1999, Stephens and Sutherland 1999), or if reduced lek size due to WNv mortality is associated with reduced female attendance (Kokko 1997), increased emigration, or delayed or reduced reproductive effort. Considering both forms density-dependence may be valuable in viability analyses for specific populations of known population size and carrying capacity. Impacts of WNv will likely be less severe for sage-grouse populations that summer at higher elevations than those in the Powder River Basin (e.g., southwestern Montana, extreme northwestern Colorado, western Wyoming, etc.). Lower temperatures at high elevations shorten periods of mosquito activity, increase larval development times, and reduce rates of virus amplification (i.e., longer extrinsic incubation periods) (Reisen et al. 2006).

*Managing WNv impacts.* Potential management strategies to reduce impacts of WNv in the Powder River Basin and elsewhere are limited. First, we know too little about which hosts initiate and maintain WNv transmission cycles (Kato et al. 2008). Even when key hosts have been identified (e.g., American robin [*Turdus migratorius*]; Kilpatrick et al. 2006), they typically cannot be managed at appropriates scales within sage-grouse habitat. Thus, most management for WNv involves attempts to reduce mosquito populations. Man-made water sources known to support breeding *Culex tarsalis* in sage-grouse habitat include overflowing stock tanks, stock ponds (especially seep and overflow areas and muddy shorelines with hoof prints), irrigated agricultural fields, and ponds constructed for CBNG development (Zou et al. 2006*a*, Doherty 2007). New water sources can be constructed in ways that discourage breeding mosquitos (e.g.,

steep-sided bare edges, restricted livestock access points, overbuilding ponds to prevent backup of water into standing vegetation, fluctuating water levels, overflow prevention) (Doherty 2007). Mosquito populations may also be managed using biological controls such as mosquitofish [*Gambusia* sp.] or native fish species, using biological or chemical larvicides, or by spraying for adults, but only if such methods are consistently and appropriately implemented by qualified mosquito control personnel (Doherty 2007). Mosquito control programs appear effective for reducing WNv risk in other habitats (Gubler et al. 2000, Reisen and Brault 2007) but the costs and benefits of control need to be weighed against potential detrimental effects of widespread spraying (Marra et al. 2004). Requiring infectious disease impact statements as part of planned, large-scale changes in land use (e.g., energy development, grazing plans) (McSweegan 1996) may also improve coordinated management of WNv risk in sage-grouse summer habitat.

Analytical elasticity and life-stage simulation analysis suggest that several different vital rates could respond to improved range and land management to offset impacts of WNv on $\lambda$. Increasing forb abundance during the pre-laying period is anticipated to increase female nutritional condition and renesting rate (Dunbar et al. 2005, Gregg et al. 2006). Similarly, increasing grass and sagebrush height is likely to improve nest success. Greater sage-grouse females clearly prefer nests sites with taller sagebrush and grass (Hagen et al. 2007), and taller grass height around nests has been documented to increase nest success in several different parts of the species' range (Holloran and Anderson 2005, Rebholz 2007). Chick survival may be increased by increasing forb and grass cover (Dahlgren et al. 2006, Hagen et al. 2007). Although broods use areas with less sagebrush than is available, decreasing sagebrush height or cover via spraying,

burning, or mowing would likely decrease nest success and overwinter survival (Swenson et al. 1987, Leonard et al. 2000, Smith et al. 2005) and is not recommended. Increasing the size and extent of undeveloped sagebrush landscapes and the amount of tall sagebrush cover would likely simultaneously increase juvenile, yearling, and adult survival. Although no studies have clearly linked female survival to landscape-scale habitat conditions, wintering birds prefer areas with large expanses of sagebrush cover and areas away from energy development (Homer et al. 1993, Doherty et al. 2008) and breeding populations are more likely to persist in areas with higher proportions of sagebrush habitat within 6.4 km of leks (Walker et al. 2007*a*). Selection for wintering areas with greater exposed sagebrush cover and taller sagebrush (Connelly et al. 2000) also suggests a benefit of increasing mature sagebrush cover, particularly during severe winters (Moynahan et al. 2006). Removing roads and power lines in sage-grouse habitat would decrease mortality from power line collisions, vehicle collisions, and avian predators that nest and hunt from power lines (Knight and Kawashima 1993, Steenhof et al. 1993).

The emergence of WNv as a new stressor on greater sage-grouse populations highlights the current impasse in sage-grouse management and conservation. Historic stressors such as fires and invasive weeds continue to cause habitat loss and fragmentation, and new stressors such as West Nile virus and rapidly increasing energy development are known to cause population declines, yet potential solutions for offsetting those losses conflict with livestock grazing and energy production, two of the most culturally and economically important land uses within sage-grouse habitat.

## Literature Cited

Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation, University of Alberta, Edmonton, Alberta, Canada.

Blus, L. J., C. S. Staley, C. J. Henny, G. W. Pendleton, T. H. Craig, E. H. Craig, and D. K. Halford. 1989. Effects of organophosphorus insecticides on sage grouse in southeastern Idaho. Journal of Wildlife Management 53:1139-1146.

Burkepile, N. A., J. W. Connelly, D. W. Stanley, and K. P. Reese. 2002. Attachment of radiotransmitters to one-day-old sage grouse chicks. Wildlife Society Bulletin 30:93-96.

Clark, L., J. Hall, R. McLean, M. Dunbar, K. Klenk, R. Bowen, and C. A. Smeraski. 2006. Susceptibility of greater sage-grouse to experimental infection with West Nile virus. Journal of Wildlife Diseases 42:14-22.

Connelly, J. W., and L. A. Doughty. 1989. Sage grouse use of wildlife water developments in southeastern Idaho. Pages 167-172 *in* G. K. Tsukamoto and S. J. Stiver (eds.). Wildlife water development: a proceedings of the wildlife water development symposium. Nevada Department of Fish and Game, Reno, NV.

Connelly, J. W., M.A. Schroeder, A R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Connelly, J. W., K. P. Reese, E. O. Garton, and M. L. Commons-Kemner. 2003. Response of greater sage-grouse *Centrocercus urophasianus* populations to different levels of exploitation in Idaho, USA. Wildlife Biology 9:335-340.

Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. Trends in Ecology and Evolution 14:405-410.

Dahlgren, D. K., R. Chi, and T. A. Messmer. 2006. Greater sage-grouse response to sagebrush management in Utah. Wildlife Society Bulletin 34:975-985.

Davis, C. T., D. W. C. Beasley, H. Guzman, M. Siirin, R. E. Parsons, R. B. Tesh, and A. D. T. Barrett. 2004. Emergence of attenuated West Nile virus variants in Texas, 2003. Virology 330: 342-350.

Davis, C. T., G. D. Ebel, R. S. Lanciotti, A. C. Brault, H. Guzman, M. Siirin, A. Lambert, R. E. Parsons, D. W. C. Beasley, et al. 2005. Phylogenetic analysis of North American West Nile virus isolates, 2001-2004: evidence for the emergence of a dominant genotype. Virology 342: 252-265.

Doherty, K. E., D. E. Naugle, and B. L. Walker. 2008. Sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187-195.

Doherty, M. K. 2007. Mosquito populations in the Powder River Basin, Wyoming: a comparison of natural, agricultural and effluent coal-bed natural gas aquatic habitats. Thesis. Montana State University, Bozeman, Montana, USA.

Dunbar, M. R. M. A. Gregg, J. A. Crawford, M. R. Giordano, and S. J. Tornquist. 2005. Normal hematologic and biochemical values for prelaying greater sage-grouse (*Centrocercus urophasianus*) and their influence on chick survival. Journal of Zoo and Wildlife Medicine 36:422-429.

Goddard, L.B., A. E. Roth, W. K. Reisen, and T. W. Scott. 2002. Vector competence of California mosquitoes for West Nile virus. Emerging Infectious Disease 8:1385-1391.

Gregg, M. A. 2006. Greater sage-grouse reproductive ecology: linkages among habitat resources, maternal nutrition, and chick survival. Dissertation. Oregon State University. Corvallis, Oregon, USA.

Gregg, M. A., M. R. Dunbar, J. A. Crawford, and M. D. Pope. 2006. Total plasma protein and renesting by greater sage-grouse. Journal of Wildlife Management 70:472-78.

Gregg, M. A., M. R. Dunbar, and J. A. Crawford. 2007. Use of implanted radiotransmitters to estimate survival of greater sage-grouse chicks. Journal of Wildlife Management 71:646-651.

Gubler, D. J. 2007. The continuing spread of West Nile virus in the western hemisphere. Emerging Infections 45:1039-46.

Gubler, D.J., G. L. Campbell, R. Nasci, N. Komar, L. Petersen, and J. T. Roehrig. 2000. West Nile virus in the United States: guidelines for detection, prevention, and control. Viral Immunology 13:469-75.

Hayes, E. B. and D. J. Gubler. 2006. West Nile virus: epidemiology and clinical features of an emerging epidemic in the United States. Annual Review of Medicine 57:181-94.

Hayes, E. B., J. J. Sejvar, S. R. Zaki, R. S. Lanciotti, A. V. Bode, and G. L. Campbell. 2005. Virology, pathology, and clinical manifestations of West Nile virus disease. Emerging Infectious Disease 11:1174-1179.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation. University of Wyoming, Laramie, Wyoming, USA.

Holloran, M. J. and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742-752.

Homer, C. G., T. C. Edwards, Jr., R. D. Ramsey, and K. P. Price. 1993. Use of remote sensing methods in modeling sage grouse winter habitat. Journal of Wildlife Management 57:78–84.

Johnson, D. H., and A. T. Klett. 1985. Quick estimates of success rates of duck nests. Wildlife Society Bulletin 13:51-53.

Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection of greater sage-grouse in northwestern South Dakota. M.S. Thesis. South Dakota State University, Brookings, South Dakota, USA.

Kato, C. Y., A. W. Fabian, E. T. Schmidtmann, G. D. Johnson, D. E. Naugle, and R. T. Mayer. 2008. Cytochrome *b* analyses of mosquito blood meals: identifying wildlife reservoirs of West Nile virus in sagebrush habitats of western North America. Journal of Wildlife Diseases. In press.

Kilpatrick A. M, L. D. Kramer, M. J. Jones, P. P. Marra, and P. Daszak. 2006. West Nile virus epidemics in North America are driven by shifts in mosquito feeding behavior. PLoS Biology 4:e82.

Kilpatrick, A. M., S. L. LaDeau, and P. P. Marra. 2007. Ecology of West Nile virus transmission and its impact on birds in the western hemisphere. The Auk 124:1121-1136.

Knight, R. L., and J. Y. Kawashima. 1993. Responses of raven and red-tailed hawk populations to linear right-of-ways. Journal of Wildlife Management 57:266–271.

Koenig, W. D., L. Marcus, T. W. Scott, and J. L. Dickinson. 2007. West Nile virus and California breeding bird declines. EcoHealth 4:18–24.

Kokko, H. 1997. The lekking game: can female choice explain aggregated male displays? Journal of Theoretical Biology 187:46-53.

Kramer, L. D., L. M. Styer, and G. D. Ebel. 2008. A global perspective on the epidemiology of West Nile virus. Annual Review of Entomology 53: 4.1-4.21.

LaDeau, S. L., A. M. Kilpatrick, and P. P. Marra. 2007. West Nile virus emergence and large-scale declines of North American bird populations. Nature on-line: doi:10.1038/nature05829.

LaMontagne, J. M., R. L. Irvine, and E. E. Crone. 2002. Spatial patterns of population regulation in sage grouse (*Centrocercus* spp.) population viability analysis. Journal of Animal Ecology 71:672-682.

Leonard, K. M., K. P. Reese, and J. W. Connelly. 2000. Distribution, movements and habitats of sage grouse, *Centrocercus urophasianus*, on the Upper Snake River Plain of Idaho: changes from the 1950's to the 1990's. Wildlife Biology 6:265–270.

Marra, P. P., S. Griffing, C. Caffrey, A. M. Kilpatrick, R. McLean, and C. Brand. 2004. West Nile virus and wildlife. BioScience 54:393-402.

McLean, R. G. 2006. West Nile virus in North American birds. Ornithological Monographs 60:44-64.

McSweegan, E. 1996. The infectious diseases impact statement: a mechanism for addressing emerging diseases. Emerging Infectious Diseases 2:103-108.

Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. The reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology 13:815-829.

Mills, L. S., and M. S. Lindberg. 2002. Sensitivity analysis to evaluate the consequences of conservation actions. Pages 338–366 in S. R. Beissinger and D. R. McCullough, editors. Population viability analysis. University of Chicago, Chicago, Illinois, USA.

Morris, W. F. and D. Doak 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Inc. Sunderland, Massachusetts, USA.

Moynahan, B. J. 2004. Landscape-scale factors affecting population dynamics of greater sage-grouse (*Centrocercus urophasianus*) in north-central Montana, 2001-2004. Dissertation, University of Montana, Missoula, Montana, USA.

Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2006. Factors contributing to process variance in annual survival of female greater sage-grouse in north-central Montana. Ecological Applications 16:1529-1538.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: pending crisis for Greater Sage-grouse. Ecology Letters: 7:704-713.

Naugle, D. E., C. L. Aldridge, B. L. Walker, K. E. Doherty, M. R. Matchett, J. McIntosh, T. E. Cornish, M. S. Boyce. 2005. West Nile virus and sage-grouse: what more have we learned? Wildlife Society Bulletin: 33:1-8.

Nemeth, N. M., D. Gould, R. Bowen, and N. Komar. 2006*a*. Natural and experimental West Nile virus infection in five raptor species. Journal of Wildlife Diseases 42:1-13.

Nemeth, N. M., D. C. Hahn, D. H. Gould, and R. A. Bowen. 2006*b*. Experimental West Nile virus infection in eastern screech owls (*Megascops asio*). Avian Diseases 50:252-258.

Petersen, B. E. 1980. Breeding and nesting ecology of female sage grouse in North Park, Colorado. M.S. Thesis. Colorado State University, Fort Collins, Colorado, USA.

Rebholz, J. L. 2007. Influence of habitat characteristics on greater sage-grouse reproductive success in the Montana Mountains, Nevada. M. S. Thesis. Oregon State University, Corvallis, Oregon, USA.

Reed, J. M., L. S. Mills, J. B. Dunning, Jr., E. S. Menges, K. S. McKelvey, R. Frye, S. Beissinger, M.-C. Anstett, and P. Miller. 2002. Emerging issues in population viability analysis. Conservation Biology 16:7-19.

Reisen, W. K. and A. C. Brault. 2007. West Nile virus in North America: perspectives on epidemiology and intervention. Pest Management Science 63:641-646.

Reisen, W. K., Y. Fang, V. M. Martinez. 2006. Effects of temperature on the transmission of West Nile virus by *Culex tarsalis* (Diptera: Culicidae). Journal of Medical Entomology 43:309-317.

Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99:933-941.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Pages 1-28 in A. Poole and F. Gill, editors. The Birds of North America, Number 425. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.

Sedinger, J. S. and Rotella, J. J. 2005. Effect of harvest on sage-grouse populations: what can we learn from the current data? Wildlife Biology 11: 371-375.

Smith, J. T., L. D. Flake, K. F. Higgins, G. D. Kobriger, and C. G. Homer. 2005. Evaluating lek occupancy of greater sage-grouse in relation to landscape cultivation in the Dakotas. Western North American Naturalist 65:310–320.

Steenhof, K., M. N. Kochert, and J. A. Roppe. 1993. Nesting by raptors and common ravens on electrical transmission line towers. Journal of Wildlife Management 57:272-281.

Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology and Evolution 14:401-405.

Swenson, J. E. 1986. Differential survival by sex in juvenile Sage Grouse and Gray Partridge. Ornis Scandinavica 17:14-17.

Swenson, J. E., C. A. Simmons, and C. D. Eustace. 1987. Decrease of sage grouse Centrocercus urophasianus after ploughing of sagebrush steppe. Biological Conservation 41:125–132.

Turell M. J., D. J. Dohm, M. R. Sardelis, M. L. O'Guinn, T. G. Andreadis, and J. A. Blow. 2005. An update on the potential of North American mosquitoes (Diptera: Culicidae) to transmit West Nile virus. Journal of Medical Entomology 42:57-62.

U. S. Geological Survey, Wildlife health bulletin 06-08. West Nile virus in Greater Sage-grouse [Internet]. [modified 6 Nov 2006; accessed 14 Nov 2006]. Available from: http://www.nwhc.usgs.gov/publications/wildlife_health_bulletins/WHB_06_08.jsp.

Walker, B. L. 2006. West Nile and sage-grouse update. Sagemap website: <www.usgs.gov/sagemap>. Accessed 29 November 2007.

Walker, B. L., D. E. Naugle, K. E. Doherty, T. E. Cornish. 2004. From the field: outbreak of West Nile virus in Greater Sage-grouse and guidelines for monitoring, handling, and submitting dead birds. Wildlife Society Bulletin 32:1000-1006.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007*a*. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644-2654.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2007*b*. West Nile virus and greater sage-grouse: estimating infection rate in a wild bird population. Avian Diseases 51:691-696.

White, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pages 288-331 *in* L. Boitani and T. K. Fuller (eds.), Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, New York, New York, USA.

Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life state simulation analysis: estimating vital rate effects on population growth for species conservation. Ecology 81:628-641.

Zou, L., S. N. Miller, E. T. Schmidtmann. 2006*a*. Mosquito larval habitat mapping using remote sensing and GIS: implications of coalbed methane development and West Nile virus. Journal of Medical Entomology 43:1034-1041.

Zou, L., S. N. Miller, E. T. Schmidtmann. 2006*b*. A GIS tool to estimate West Nile virus risk based on a degree-day model. Environmental Modeling and Assessment. Published on-line: DOI 10.1007/s10661-006-9373-8.

Table 1. Estimated average reduction in annual population growth (i.e., finite rate of increase, λ) under various West Nile virus (WNv) impact scenarios relative to no WNv mortality based on life-stage simulation analysis using vital rates for female greater sage-grouse in the Powder River Basin, Montana and Wyoming, 2003-2006. Results are based on 1000 life-stage simulation analysis simulation replicates. Reductions in λ due to WNv mortality may be masked in any given year by annual fluctuations in vital rates influential for population growth (e.g., nest success, chick survival, juvenile survival, survival of breeding-aged females).

| | Correlated | Uncorrelated |
|---|---|---|
| Scenario | Δλ | Δλ |
| No WNv | 0.000 | 0.000 |
| Observed WNv | -0.073 | -0.103 |
| Current WNv | -0.073 | -0.075 |
| Current WNv - resistance | -0.059 | -0.084 |
| Current WNv - resistance and carryover effects | -0.076 | -0.088 |
| Elevated WNv | -0.119 | -0.115 |
| Elevated WNv - resistance | -0.085 | -0.097 |
| Elevated WNv - resistance and carryover effects | -0.097 | -0.110 |

Figure 1. Life-cycle and stage-based projection matrix for a 2-stage, pre-breeding, birth-pulse model for female greater sage-grouse in the Powder River Basin, Montana and Wyoming, USA. Stage 1 consists of yearlings (YR) and stage 2 consists of older adults (AD).

Figure 2. Relationships between predicted no. days with West Nile virus transmission events based on a degree-day model (Zou et al. 2006*b*) and absolute decreases in (a) spring-summer survival and (b) annual survival due to WNv-related mortality in three regions of the Powder River Basin, Montana and Wyoming, USA, 2003-2006.

Figure 3. An example of the distribution of simulated WNv infection rates for female greater sage-grouse in the Powder River Basin, Montana and Wyoming, USA. Infection rates were simulated using a stretched beta distribution with mean = 0.07, SD = 0.055, min = 0.005, and max = 1.0. Median infection rate from this distribution = 0.055.

Figure 4. An example of the predicted distribution of the annual number of WNv transmission days based on temperature data from Sheridan Field Station, WY (station no. 488160) with (a) degree-day criteria based on a 14.3º temperature threshold for virus amplification within *Culex tarsalis* and 109 degree-day extrinsic incubation period for median virus transmission (Reisen et al. 2006, Zou et al. 2006*b*) and (b) degree-day criteria modified to match observed WNv mortalities in sage-grouse near Decker, MT.

Figure 5. Variance in population growth (i.e., finite rate of increase, λ) based on (a) mean elasticity values, (b) coefficients of determination in life-stage simulation analysis for each vital rate, and (c) for vital rates affected by different management strategies. All analyses are based on vital rates from the Powder River Basin, Montana and Wyoming, USA, 2003-2006. Simulated data included correlations between vital rates. Values in (a) are mean elasticity values standardized to 1. Values in (b) and (c) are coefficients of determination ($r^2$) standardized to 1. YR = yearling, AD = adult. Vital rates with a "1" refer to first nests, "2" refers to renests. See text for vital rate definitions.

Figure 6. Annual population growth (i.e., finite rate of increase, λ) regressed on (a, b) yearling nest success (first nests), (c, d) adult nest success (first nests), (e, f) survival of chicks from yearling females, (g, h) survival of chicks from adult females, (i, j) survival of juveniles from first nests, (k, l) survival of juveniles from second nests, (m, n) annual yearling survival, and (o, p) annual adult survival for female greater sage-grouse in the Powder River Basin, Montana and Wyoming, USA from 2003-2006 and for range-wide values. Relationships are based on 1000 replicates from life-stage simulation analysis. The left panel illustrates relationships based on Powder River Basin data; the right panel illustrates relationships based on range-wide data. All simulations included correlations between vital rates. Range-wide values in (f) and (h) are based on the same mean and variance.

Figure 7. Distribution of simulated annual population growth rates (i.e., finite rate of increase, λ) for female greater sage-grouse based on life-stage simulation analysis using

data on vital rates from the Powder River Basin, Montana and Wyoming, USA, 2003-2006, assuming no WNv impacts. Values are based on 1,000 simulation replicates.

Figure 8. Projected change in resistance to WNv disease of greater sage-grouse females (at the start of the breeding season) over a 20-year period based on simulated vital rates from the Powder River Basin, 2003-2006 using life-stage simulation analysis. Error bars represent 1 SD. All estimates are based on 1000 simulation replicates with an initial value for resistance of 0.04 at year 1 (i.e., 4% of the initial population resistant to WNv disease). Scenarios presented are for: (a) current WNv mortality with (black squares) and without (hollow squares) carryover effects and (b) elevated WNv mortality with (black squares) and without (hollow squares) carryover effects. Values are offset for clarity.

Figure 9. Distribution of WNv-related mortality among female greater sage-grouse (a) in the 1$^{st}$ year of the simulation and (b) in the 20$^{th}$ year of the simulation with increasing resistance over time based on simulated infection rates from the Powder River Basin, 2003-2006, assuming no carryover effects of WNv infection. Values are based on 1,000 simulation replicates.

Figure 10. Projected change in the proportion of WNv-infected resistant sage-grouse in the spring population (i.e., at the start of the breeding season) over a 20-year period based on simulated vital rates from the Powder River Basin, 2003-2006 using life-stage simulation analysis. Error bars represent 1 SD. Estimates are based on 1000 simulation replicates with an initial value for resistance of 0.04 at year 1.

Figure 1.

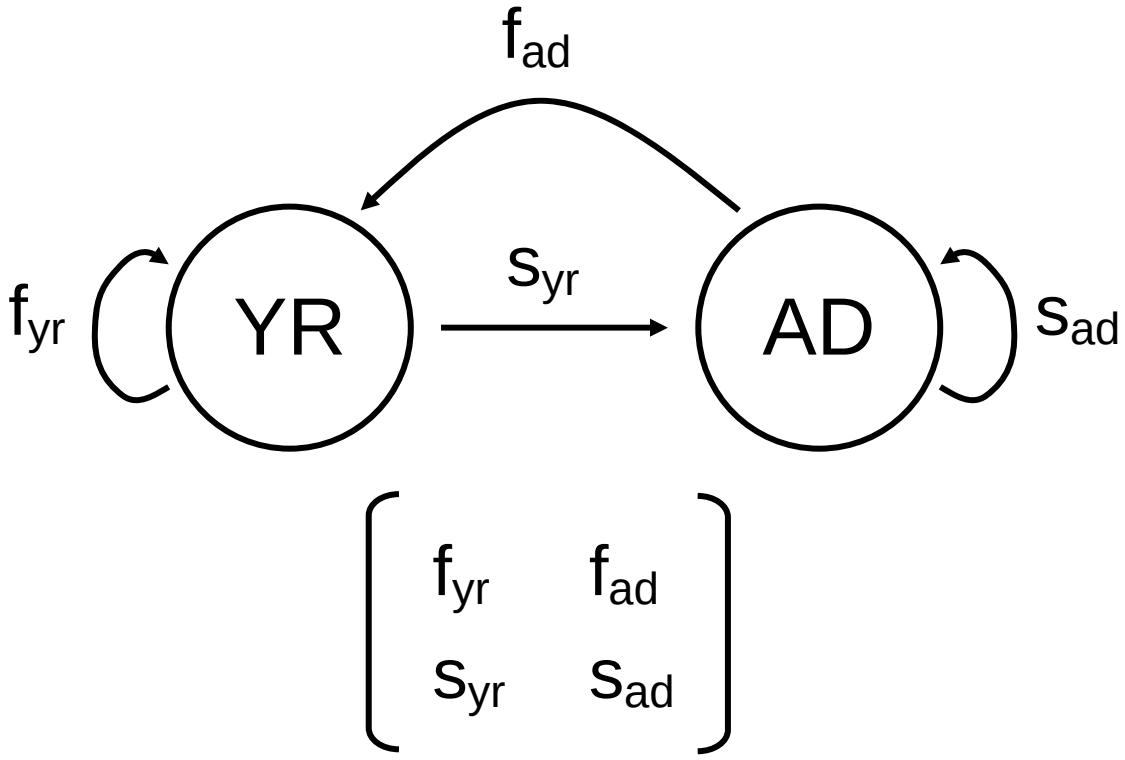
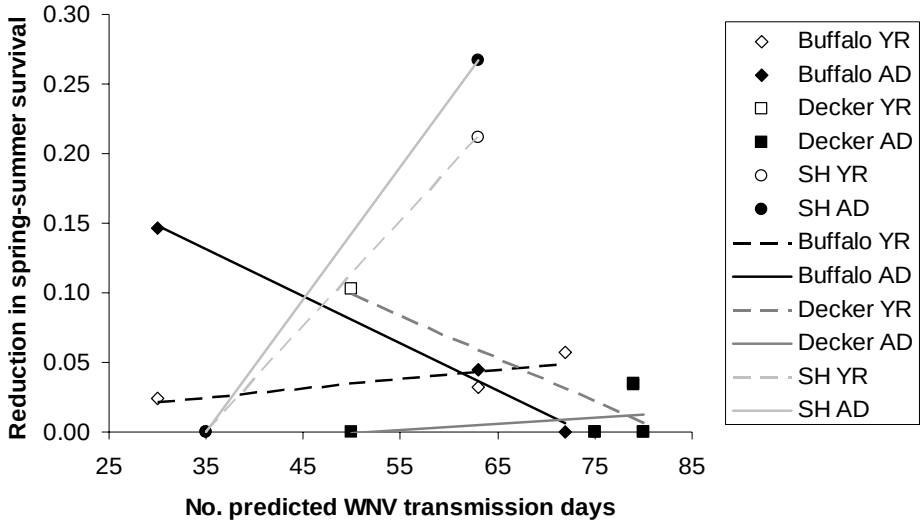


Figure 2.

a.


Reduction in spring-summer survival
0.30
0.25
0.20
0.15
0.10
0.05
0.00
25
35
45
55
65
75
85
No. predicted WNV transmission days
Buffalo YR
Buffalo AD
Decker YR
Decker AD
SH YR
SH AD
Buffalo YR
Buffalo AD
Decker YR
Decker AD
SH YR
SH AD

b

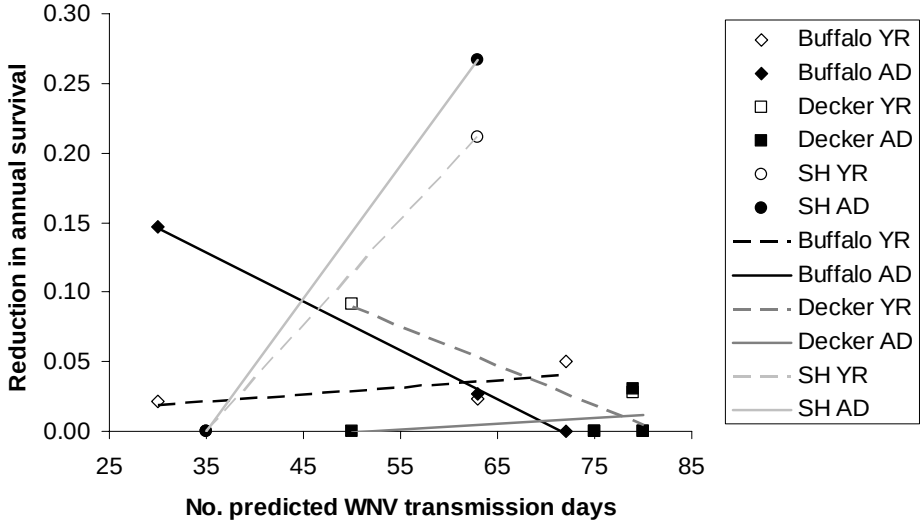

Reduction in annual survival
0.30
0.25
0.20
0.15
0.10
0.05
0.00
25
35
45
55
65
75
85
No. predicted WNV transmission days
Buffalo YR
Buffalo AD
Decker YR
Decker AD
SH YR
SH AD
Buffalo YR
Buffalo AD
Decker YR
Decker AD
SH YR
SH AD

Figure 3.

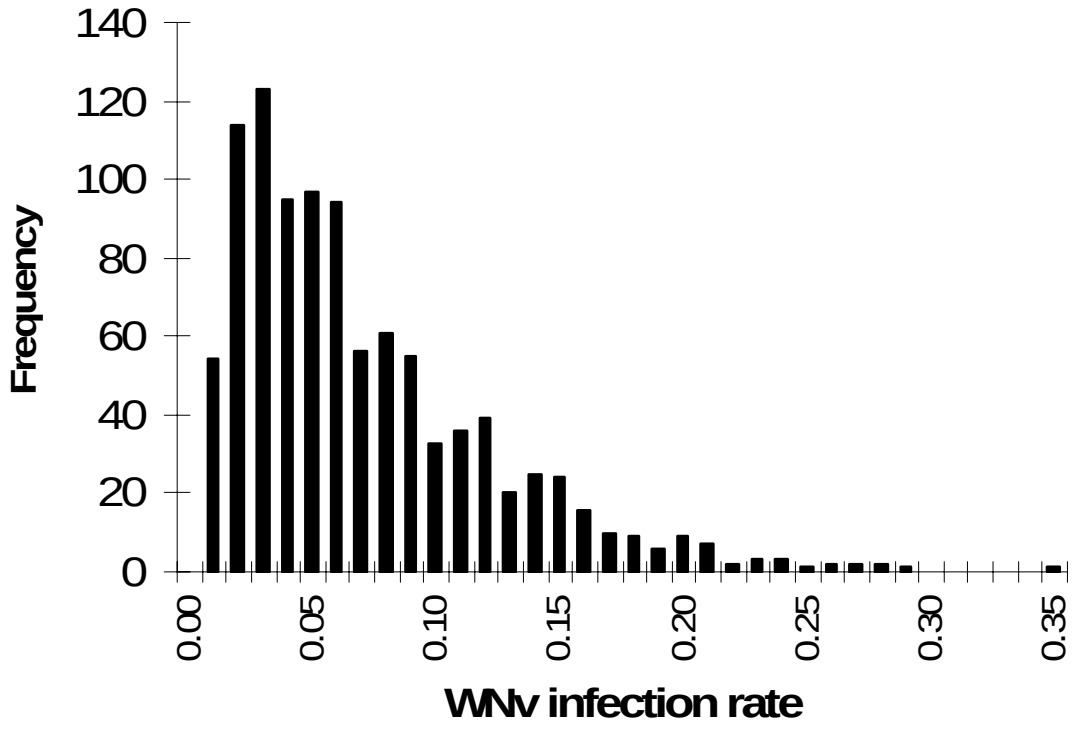
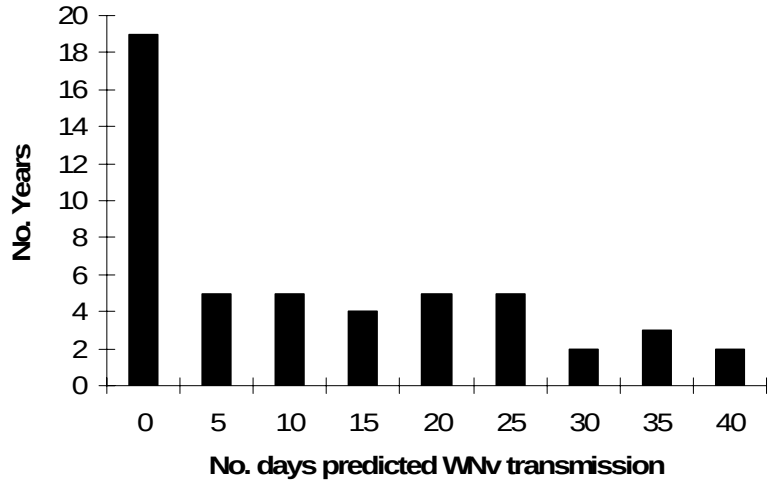

140
120
100
80
60
40
20
0
Frequency
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
WNv infection rate

Figure 4.

a.


20
18
16
14
12
10
8
6
4
2
0
No. Years
0
5
10
15
20
25
30
35
40
No. days predicted WNv transmission

b

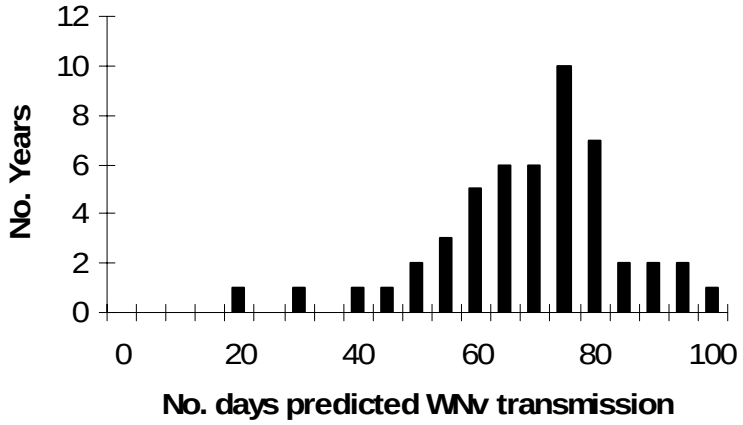
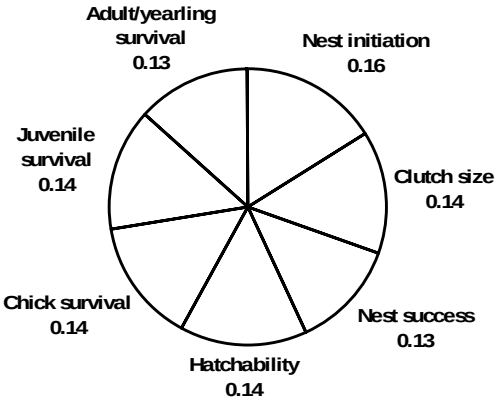
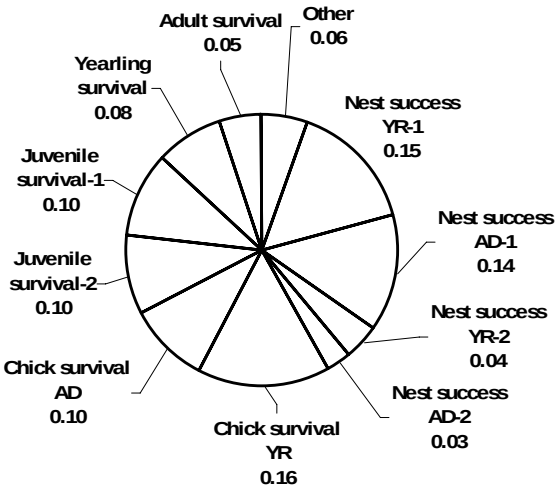

12
10
8
6
4
2
0
No. Years
0
20
40
60
80
100
No. days predicted WNv transmission

Figure 5.

a Mean elasticity




b $r^2$




c $r^2$

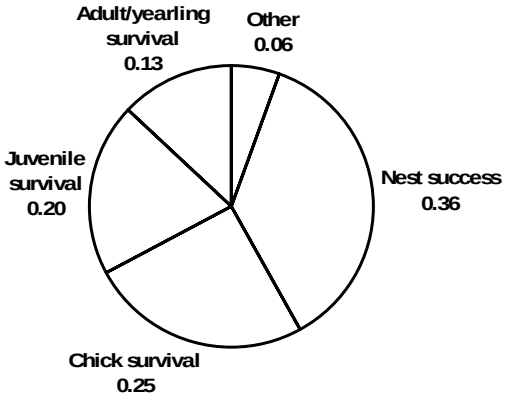
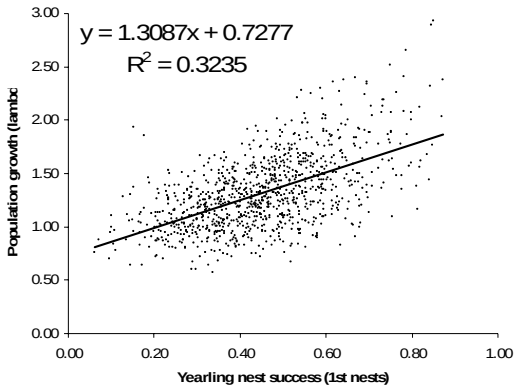
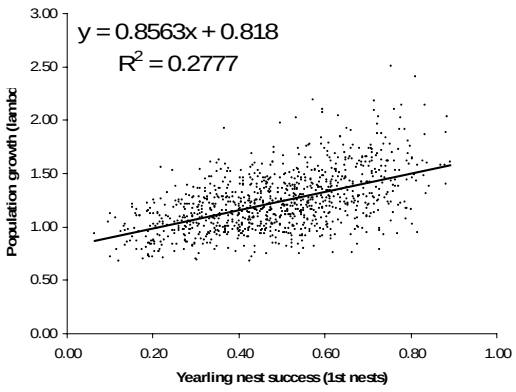


Figure 6.

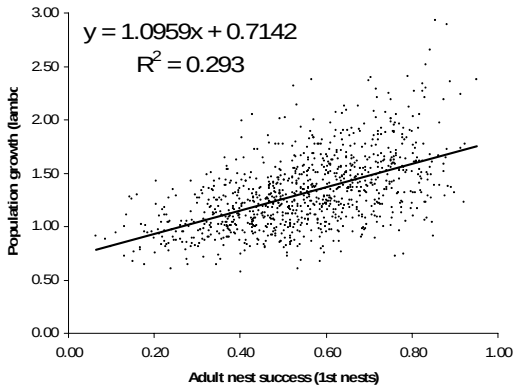
a Powder River Basin



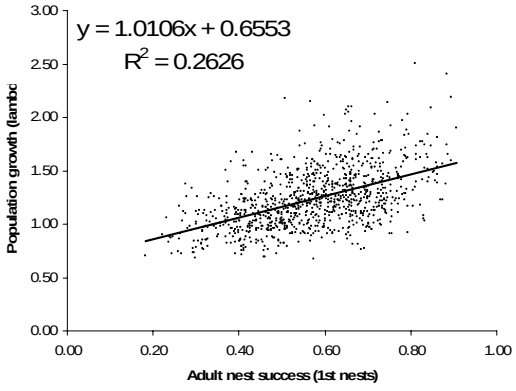

b Range-wide



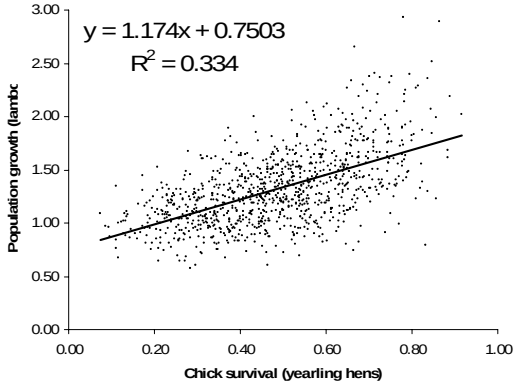

c




d




e




f

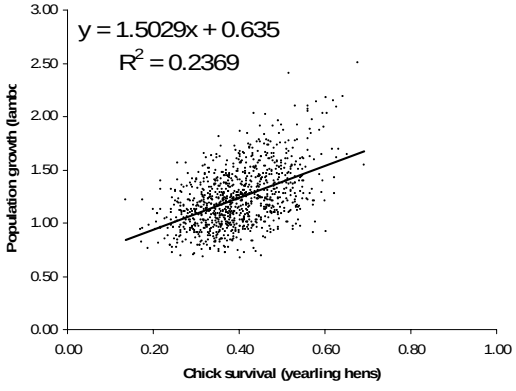
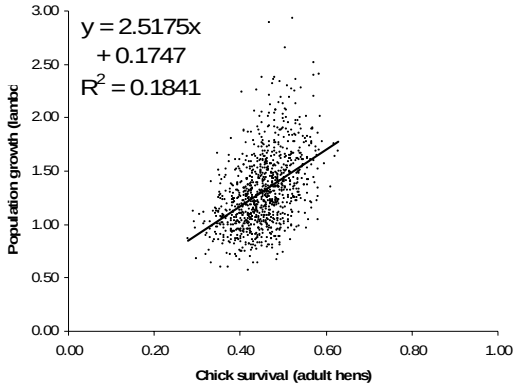
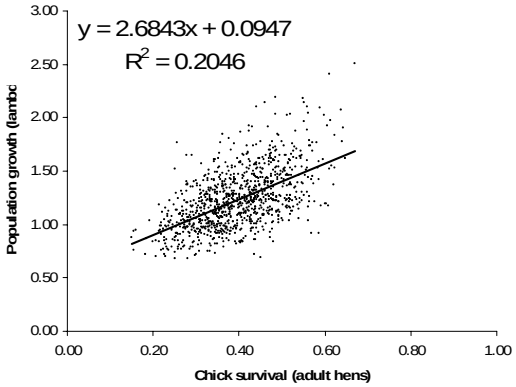


Figure 6 (cont.).

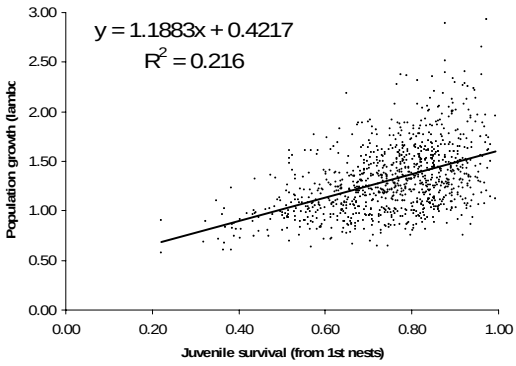
g Powder River Basin



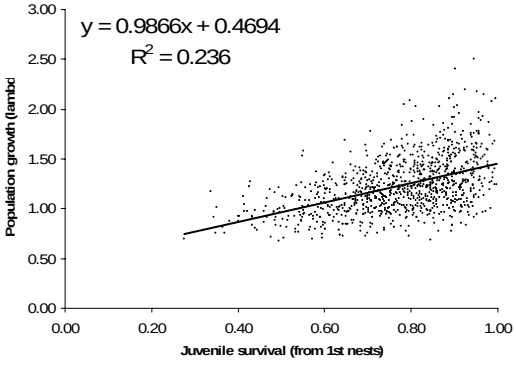

h Range-wide



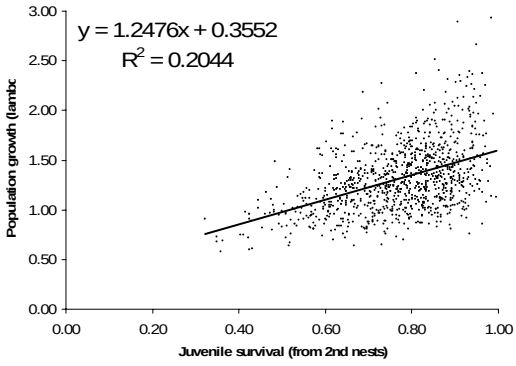

i




j




k




l

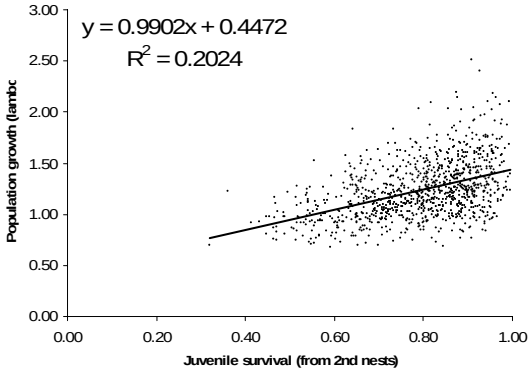
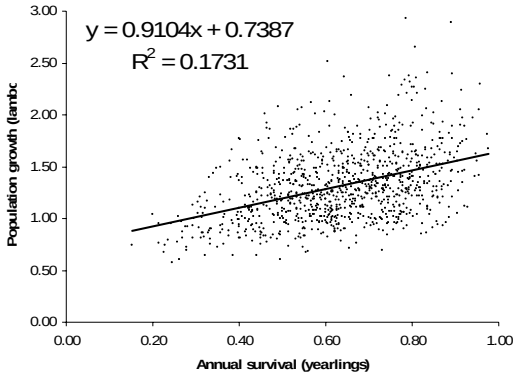
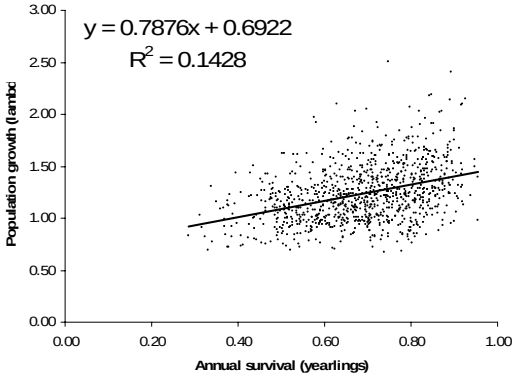


Figure 6 (cont.).

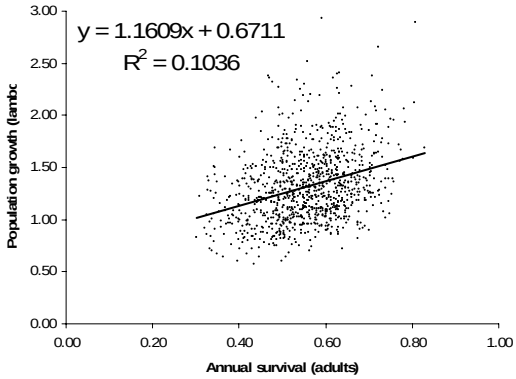
m Powder River Basin



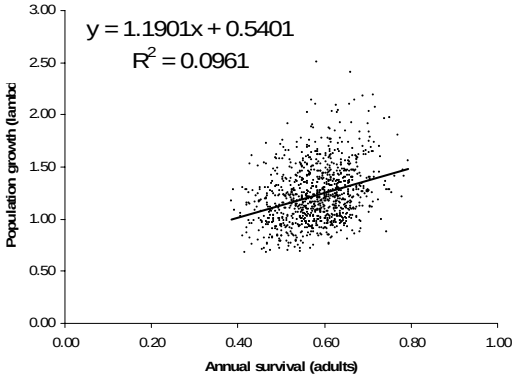

n Range-wide



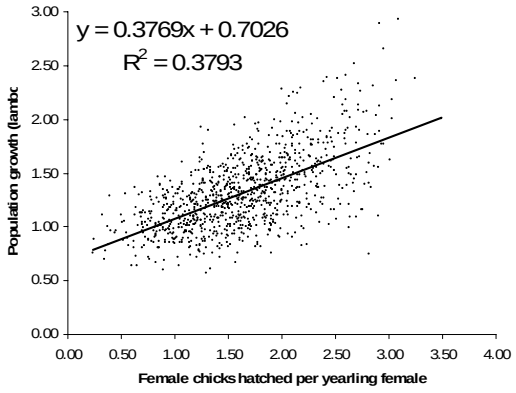

o




p




q




r

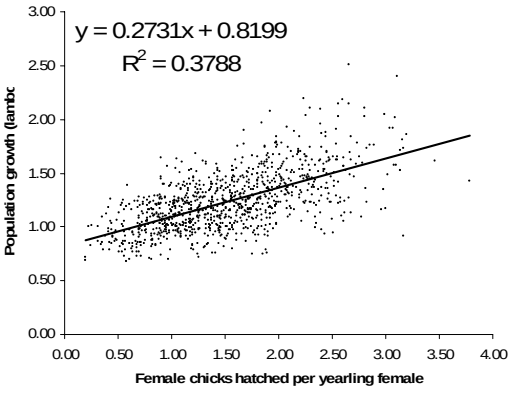


Figure 6 (cont.).

s Powder River Basin t Range-wide

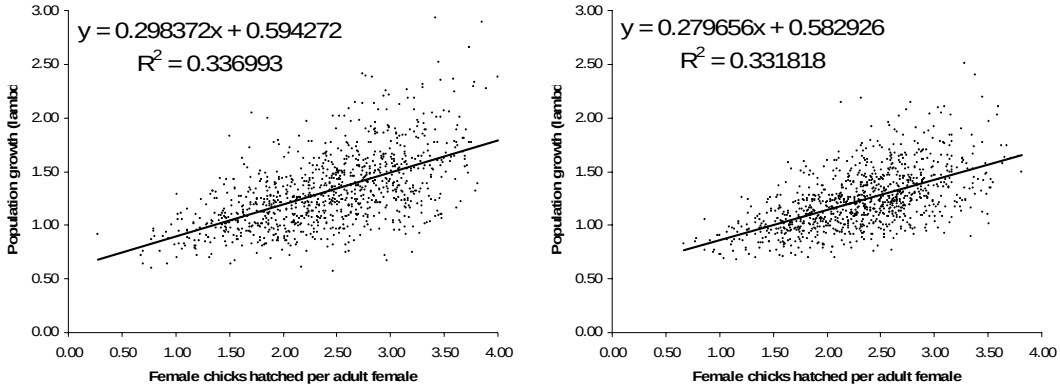


Figure 7.

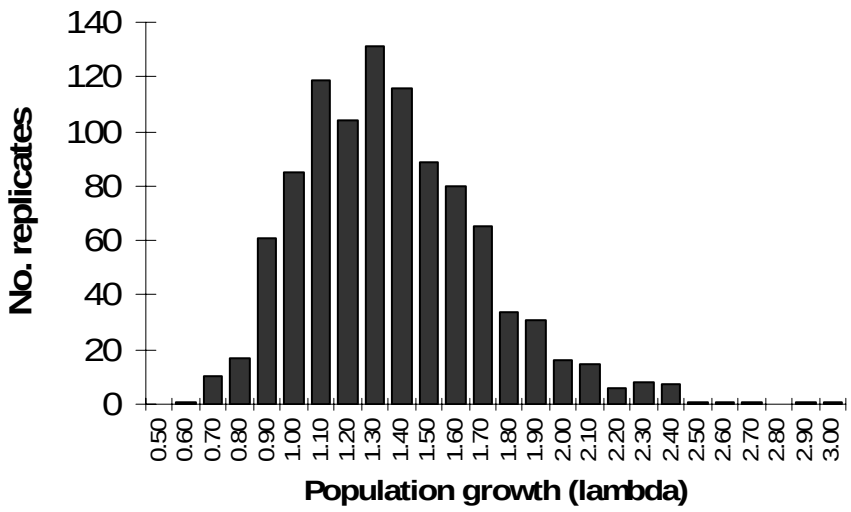
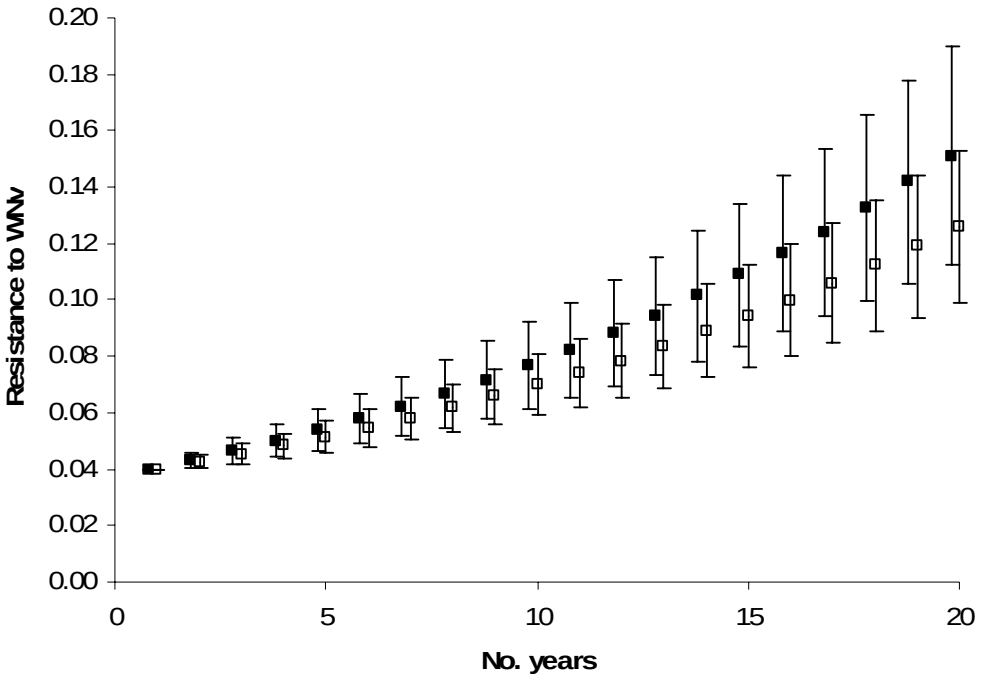

No. replicates
140
120
100
80
60
40
20
0
0.50
0.60
0.70
0.80
0.90
1.00
1.10
1.20
1.30
1.40
1.50
1.60
1.70
1.80
1.90
2.00
2.10
2.20
2.30
2.40
2.50
2.60
2.70
2.80
2.90
3.00
Population growth (lambda)

Figure 8.

a Current WNv infection rates




b Elevated WNv infection rates

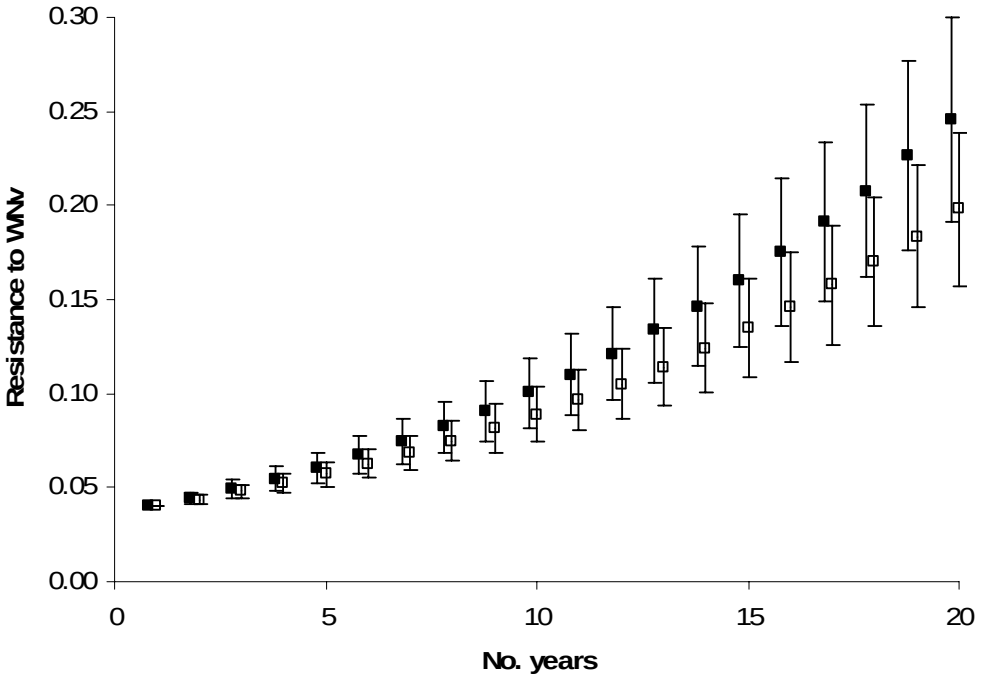


Figure 9.

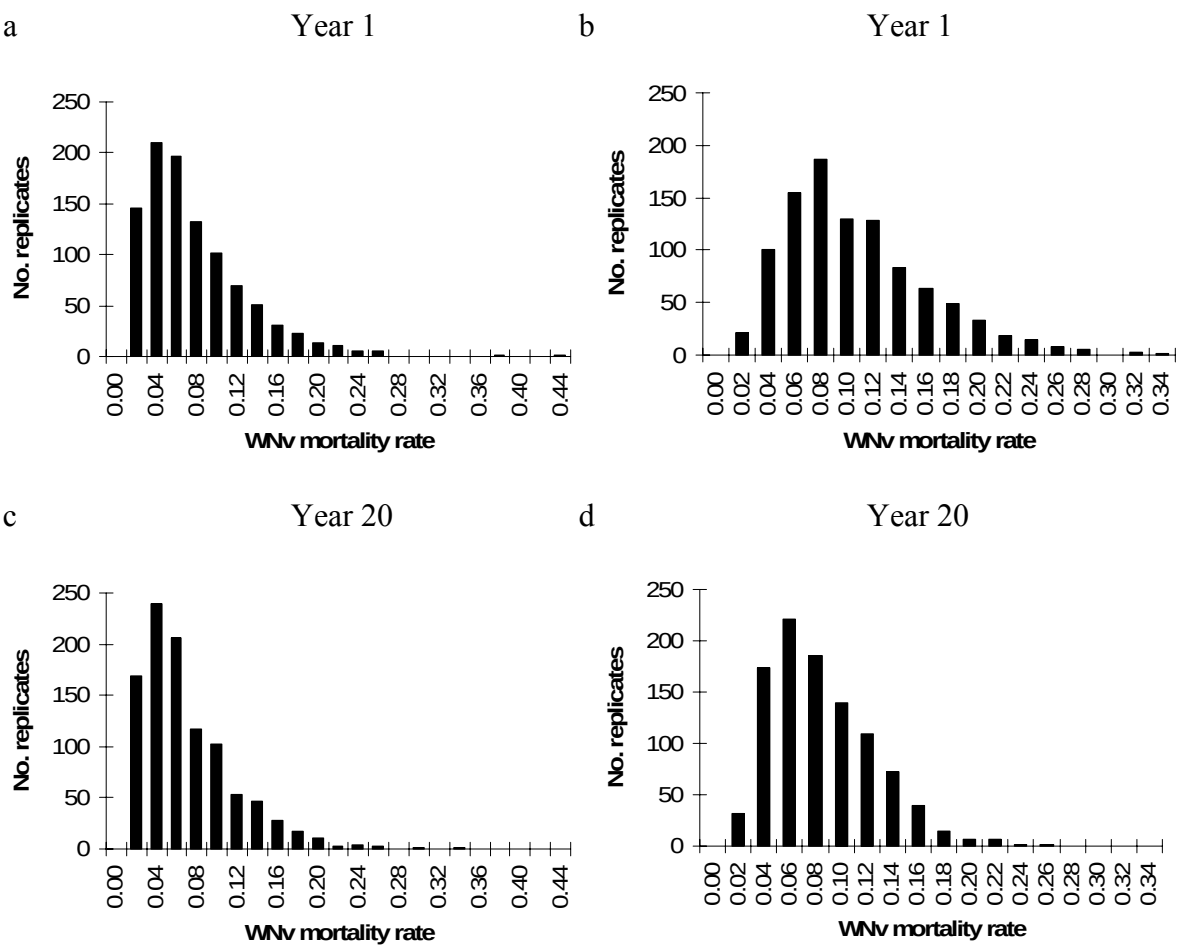
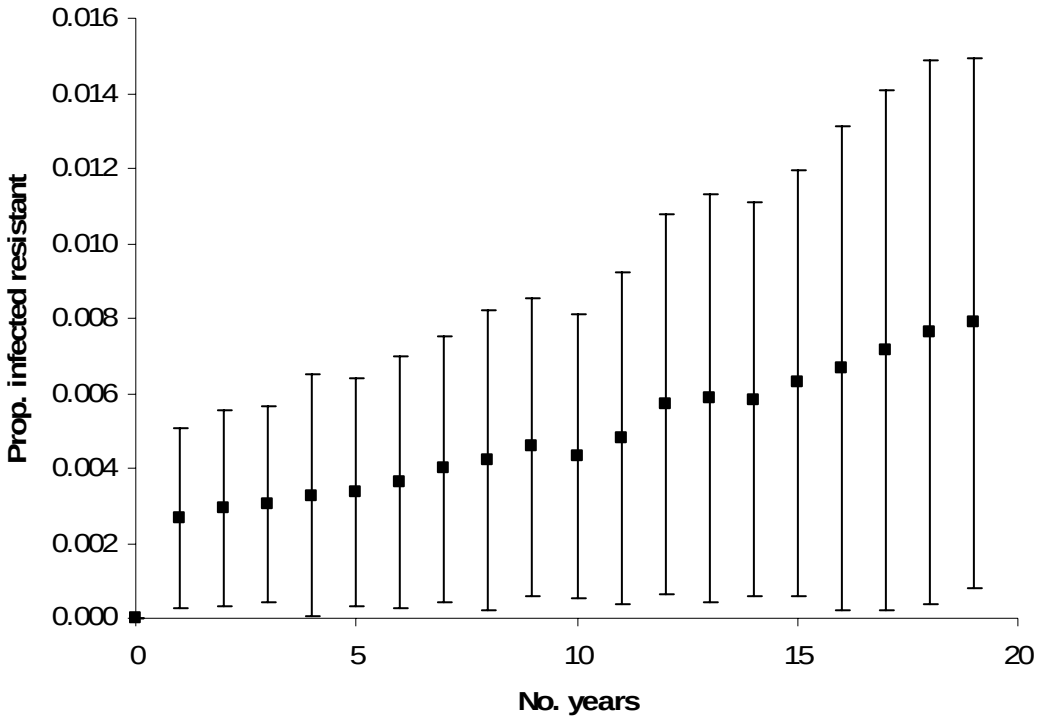

a
Year 1
b
Year 1
c
Year 20
d
Year 20
No. replicates
WNv mortality rate
0
50
100
150
200
250
0.00
0.04
0.08
0.12
0.16
0.20
0.24
0.28
0.32
0.36
0.40
0.44
0.02
0.06
0.10
0.14
0.18
0.22
0.26
0.30
0.34

Figure 10.


0.016
0.014
0.012
0.010
0.008
0.006
0.004
0.002
0.000
Prop. infected resistant
0
5
10
15
20
No. years

## Appendix A. Correlation structure

Incorporating correlation structure is important for generating realistic combinations of vital rates for simulations that are representative of typical values for the population of interest (Mills and Lindberg 1999, Wisdom et al. 2000, Morris and Doak 2002). We assigned pairs of vital rates a correlation coefficient of none (0.00), low (0.25), moderate (0.50), or high (0.75) based on whether published data indicated that both vital rates were regulated by the same biological mechanism(s). We also examined correlation coefficients between vital rates in the Powder River Basin and range-wide vital-rate data to check for evidence for or against hypothesized correlations. Below are the biological justifications for each correlation.

Reproductive effort should be influenced by female nutritional condition during the pre-laying period. Yearling and adults occur in mixed flocks during the winter and early spring, so nutritional condition should be similar between stages, and initiation rates of yearlings and adults should be moderately correlated. Females may also adjust their reproductive effort if environmental cues such as residual grass height, winter and spring precipitation, or early spring forb abundance are reliable indicators of nest success or chick survival. Years in which reproductive effort is high suggests that rates of nest initiation and renesting should be at least weakly positively correlated as well. Renesting rates of yearlings and adults were moderately, positively correlated both in the Powder River Basin and range-wide. Clutch size is also a form of reproductive effort, and should show moderate, positive correlations among stages. The correlation should be weakly positive across nesting attempts because clutch sizes of renests vary more than those of

first nests. We also estimated weak positive correlations between clutch size and nest initiation and renesting rates within each stage and nesting attempt (i.e., renesting rates of yearlings weakly positively correlated with renest clutch sizes of yearlings).

Both yearling and adult nest success are strongly influenced by predator abundance (Schroeder et al. 1999), and yearlings and adults use the same habitats for nesting and initiate both first nests and renests at about the same time (Chapter 4). Yearling and adult nest success were moderately correlated ($r$ = 0.654) both in the range-wide data and in the Powder River Basin data (0.704), so these were estimated to have at least a moderate correlation (0.50). The same logic applies to success of renesting attempts. We estimated a weak positive correlation between first nest success and chick survival because both may benefit from increased understory growth and cover (Hagen et al. 2007). In the Powder River Basin, years with higher nest success tracked years with higher brood success (Chapter 4).

Survival of chicks is regulated by availability of forbs and insects and understory cover, so chick survival of yearling and adult chicks should show at least a moderate positive correlation. Survival of juveniles from first nests and renests is, in essence, the same vital rate, so we assigned it a correlation of 0.9. Juvenile survival, yearling survival, and adult survival are all influenced by the same environmental conditions (e.g., snowstorms), parasite communities, and predator communities and should show at least a weak positive correlation. No negative correlations were identified that had a clear biological basis.

The estimated correlation matrix among variables used in all analyses along with variable definitions are shown below.

Variables[a]

| | $I_{Y1}$ | $I_{A1}$ | $I_{Y2}$ | $I_{A2}$ | $I_{A3}$ | $C_{Y1}$ | $C_{Y2}$ | $C_{A1}$ | $C_{A2}$ | $C_{A3}$ | $N_{Y1}$ | $N_{A1}$ | $N_{Y2}$ | $N_{A2}$ | H | $S_{CY}$ | $S_{CA}$ | $S_{J83}$ | $S_{J91}$ | $S_Y$ | $S_A$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $I_{Y1}$ | 1 | 0.50 | 0.25 | 0.25 | 0 | 0.25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $I_{A1}$ | 0.50 | 1 | 0.25 | 0.25 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $I_{Y2}$ | 0.25 | 0.25 | 1 | 0.50 | 0.25 | 0 | 0.25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $I_{A2}$ | 0.25 | 0.25 | 0.50 | 1 | 0.50 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $I_{A3}$ | 0 | 0 | 0.25 | 0.50 | 1 | 0 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $C_{Y1}$ | 0.25 | 0 | 0 | 0 | 0 | 1 | 0.25 | 0.50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $C_{Y2}$ | 0 | 0 | 0.25 | 0 | 0 | 0.25 | 1 | 0.25 | 0.25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $C_{A1}$ | 0 | 0.25 | 0 | 0 | 0 | 0.50 | 0.25 | 1 | 0.25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $C_{A2}$ | 0 | 0 | 0 | 0.25 | 0 | 0 | 0.25 | 0.25 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $C_{A3}$ | 0 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $N_{Y1}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0.50 | 0.25 | 0.25 | 0 | 0.25 | 0.25 | 0 | 0 | 0 | 0 |
| $N_{A1}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.50 | 1 | 0.25 | 0.25 | 0 | 0.25 | 0.25 | 0 | 0 | 0 | 0 |
| $N_{Y2}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.25 | 0.25 | 1 | 0.50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $N_{A2}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.25 | 0.25 | 0.50 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | $I_{Y1}$ | $I_{A1}$ | $I_{Y2}$ | $I_{A2}$ | $I_{A3}$ | $C_{Y1}$ | $C_{Y2}$ | $C_{A1}$ | $C_{A2}$ | $C_{A3}$ | $N_{Y1}$ | $N_{A1}$ | $N_{Y2}$ | $N_{A2}$ | H | $S_{CY}$ | $S_{CA}$ | $S_{J83}$ | $S_{J91}$ | $S_Y$ | $S_A$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| H | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| $S_{CY}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.25 | 0.25 | 0 | 0 | 0 | 1 | 0.50 | 0 | 0 | 0 | 0 |
| $S_{CA}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.25 | 0.25 | 0 | 0 | 0 | 0.50 | 1 | 0 | 0 | 0 | 0 |
| $S_{J83}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0.9 | 0.25 | 0.25 |
| $S_{J91}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.9 | 1 | 0.25 | 0.25 |
| $S_Y$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.25 | 0.25 | 1 | 0.25 |
| $S_A$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.25 | 0.25 | 0.25 | 1 |

[a] Variables include. $I_{Y1}$ = nest initiation rate of yearlings; $I_{A1}$ = nest initiation rate of adults; $I_{Y2}$ = renesting rate of yearlings; $I_{A2}$ = renesting rate of adults; $I_{A3}$ = second renesting rate of adults; $C_{Y1}$ = clutch size (female eggs) of yearling first nests; $C_{Y2}$ = clutch size (female eggs) of yearling renests; $C_{A1}$ = clutch size (female eggs) of adult first nests; $C_{A2}$ = clutch size (female eggs) of adult renests; $C_{A3}$ = clutch size (female eggs) of adult second renests; $N_{Y1}$ = nest success of yearling first nests; $N_{A1}$ = nest success of adult first nests; $N_{Y2}$ = nest success of yearling renests; $N_{A2}$ = nest success of adult renests (and second nests); H = hatching success; $S_{CY}$ = survival of chicks from yearling females from hatch to 35 d; $S_{CA}$ = survival of chicks from adult females from hatch to 35 d; $S_{J83}$ = survival of juveniles from 35 d of age to 10 September for renests; $S_{J91}$ = survival of juveniles from 35 d of age to 10 September for first nests; $S_Y$ = annual survival of yearlings; $S_A$ = annual survival of adults.

## Appendix B. Vital rate summary

| Vital Rate[a] | Powder River Basin | | Range-wide | |
|---|---|---|---|---|
| | Mean | Variance[b] | Mean | Variance[b] |
| $INIT_{YR1}$ | 0.982 | 0.0003 | 0.829 | 0.0166 |
| $INIT_{AD1}$ | 0.990 | 0.0001 | 0.930 | 0.0038 |
| $INIT_{YR2}$ | 0.151 | 0.0284 | 0.148 | 0.0368 |
| $INIT_{AD2}$ | 0.460 | 0.0681 | 0.395 | 0.0599 |
| $INIT_{AD3}$ | 0.042 | 0.0021 | 0.074 | 0.0051 |
| $FCLUTCH_{YR1}$ | 3.74 | 0.0880 | 3.81 | 0.118 |
| $FCLUTCH_{YR2}$ | 2.98 | 0.1460 | 3.29 | 0.316 |
| $FCLUTCH_{AD1}$ | 4.10 | 0.0860 | 4.16 | 0.040 |
| $FCLUTCH_{AD2}$ | 3.19 | 0.1930 | 3.52 | 0.200 |
| $FCLUTCH_{AD3}$ | 2.69 | 0.1500 | 3.02 | 0.200[c] |
| $SUCC_{YR1}$ | 0.453 | 0.0226 | 0.481 | 0.0268 |
| $SUCC_{AD1}$ | 0.555 | 0.0284 | 0.569 | 0.0183 |
| $SUCC_{YR2}$ | 0.521 | 0.1739 | 0.540 | 0.1309 |
| $SUCC_{AD2}$ | 0.618 | 0.0958 | 0.553 | 0.0623 |
| HATCH | 0.923 | 0.0005 | 0.921 | 0.0018 |
| $CHSURV_{YR}$ | 0.488 | 0.0274 | 0.391[d] | 0.0084[d] |
| $CHSURV_{AD}$ | 0.456 | 0.0033 | 0.391[d] | 0.0084[d] |
| $JUVSURV_{83}$ | 0.776 | 0.0154[e] | 0.799 | 0.0154 |
| $JUVSURV_{91}$ | 0.757 | 0.0177[e] | 0.782 | 0.0177 |
| $SURV_{YR}$ | 0.639 | 0.0239 | 0.684 | 0.0182 |

| | | | | |
|---|---|---|---|---|
| $SURV_{AD}$ | 0.556 | 0.0082 | 0.582 | 0.0050 |

[a] Variables defined as: $INIT_{YR1}$ = nest initiation rate of yearlings; $INIT_{AD1}$ = nest initiation rate of adults; $INIT_{YR2}$ = renesting rate of yearlings; $INIT_{AD2}$ = renesting rate of adults; $INIT_{AD3}$ = second renesting rate of adults; $FCLUTCH_{YR1}$ = clutch size (female eggs) of yearling first nests; $FCLUTCH_{YR2}$ = clutch size (female eggs) of yearling renests; $FCLUTCH_{AD1}$ = clutch size (female eggs) of adult first nests; $FCLUTCH_{AD2}$ = clutch size (female eggs) of adult renests; $FCLUTCH_{AD3}$ = clutch size (female eggs) of adult second renests; $SUCC_{YR1}$ = nest success of yearling first nests; $SUCC_{AD1}$ = nest success of adult first nests; $SUCC_{YR2}$ = nest success of yearling renests; $SUCC_{AD2}$ = nest success of adult renests (and second nests); HATCH = hatching success; $CHSURV_{YR}$ = survival of chicks from yearling females from hatch to 35 d; $CHSURV_{AD}$ = survival of chicks from adult females from hatch to 35 d; $JUVSURV_{83}$ = survival of juveniles from 35 d of age to 10 September for renests; $JUVSURV_{91}$ = survival of juveniles from 35 d of age to 10 September for first nests; $SURV_{YR}$ = annual survival of yearlings; $SURV_{AD}$ = annual survival of adults.

[b] Process variance estimated using the method of White (2000).

[c] Process variance for clutch size of second renests could not be estimated from range-wide data, so the value for clutch size of renests was used instead.

[d] Mean and process variance for chick survival of yearling and adult females were the same in range-wide data because most previous publications did not present chick survival estimates separately for each stage.

[e] Process variance for juvenile survival could not be estimated from Powder River Basin data, so values represent raw variance estimates from range-wide data.