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

$$w_i = \frac{\exp(-0.5 \times \Delta_i)}{\sum_{i=1}^{R} \exp(-0.5 \times \Delta_i)} \tag{3}$$

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:

$$\hat{K} = -\hat{b}^{-1}(\hat{a} + \hat{c}Year + \hat{d}Period) \tag{4}$$

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

$$N(t+1) = N(t) + e^{\hat{r}(t)} \tag{5}$$

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

$$N(t+1) = N(t) \times e^{\hat{a}+\hat{b}N(t)+\hat{c}Year+\hat{d}Period+E(t)} \tag{6}$$

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 ΔAICc < 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,

$$\hat{\Pr}(Extinction) = \sum_{i=1}^{R} \left\langle \hat{\Pr}(Extinction \left| Model_i \right\rangle \times w_i) \tag{8}$$

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)

$$V\hat{a}r\left[\hat{\Pr}(Extinction)\right] = \sum_{i=1}^{R} w_i^2 \times [\hat{\Pr}(Extinction) - \hat{\Pr}(Extinction \left| Model_i \right.)]^2 \tag{9}$$

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

$$N_{Meta}\left(t+1\right) = \sum_{j=1}^{7} N_j\left(t+1\right) \tag{10}$$

where *Nj* is the abundance of SMZj. Abundance of each SMZ was projected using

$$N_j\left(t+1\right) = N_j\left(t\right) \times e^{r_j(t)} + \sum_{i=1 \neq j}^{7} N_i\left(t\right) \times D_{ij} - \sum_{i=1 \neq j}^{7} N_j\left(t\right) \times D_{ji} \tag{11}$$

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 (σ^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 α=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.

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List of Tables

Appendices

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

	Estimated Minimum				
Sage-Grouse Management Zone	No. Males	SE	No. Males	SE	Change
	2007		2013		
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.

	Estimated Males		Estimated Carrying Capacity of Minimum No. of Males					
Sage-Grouse Population	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.

	Time	Probability (as %) for each SMZ individually (SE)				Probability Under Metapopulation	
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.

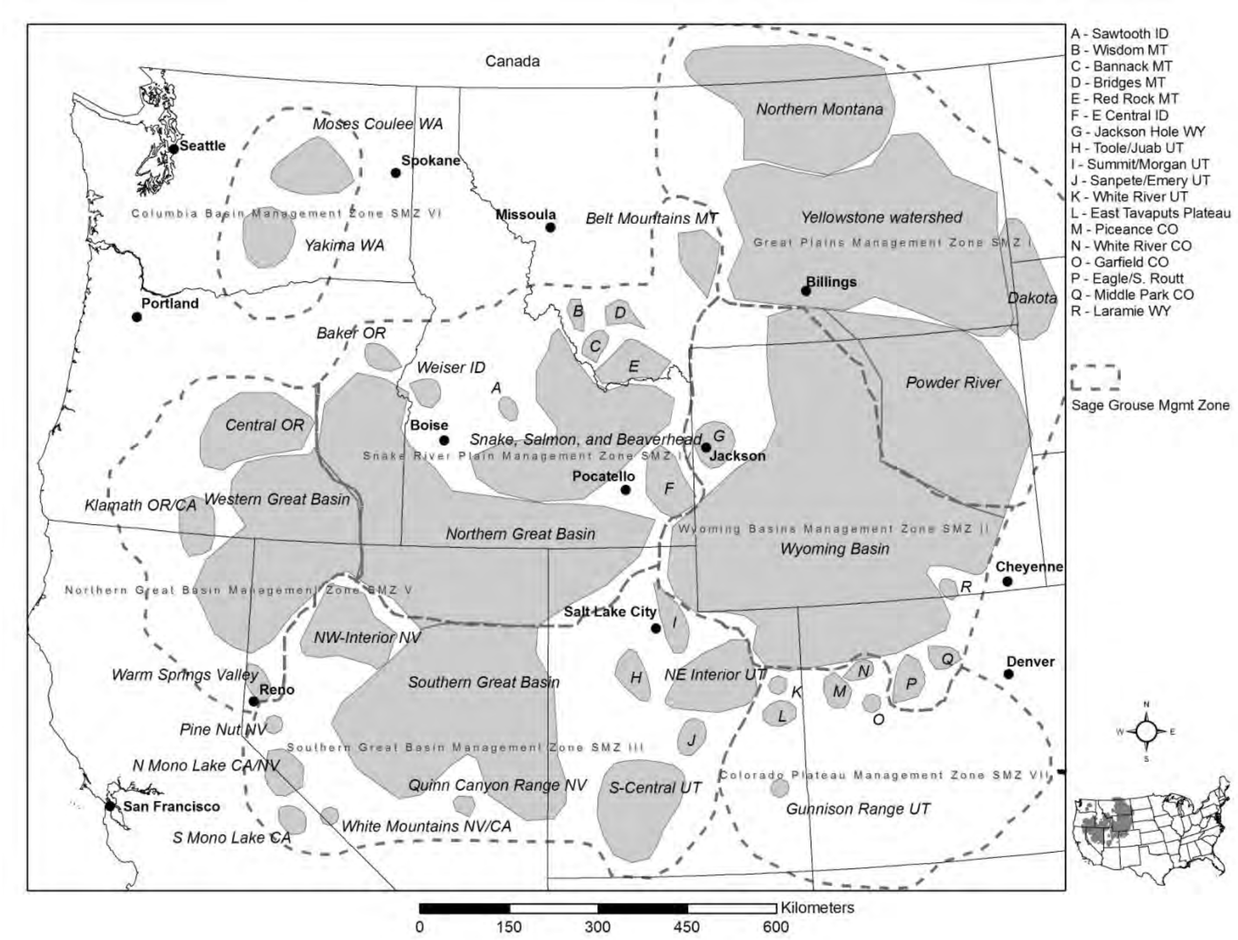
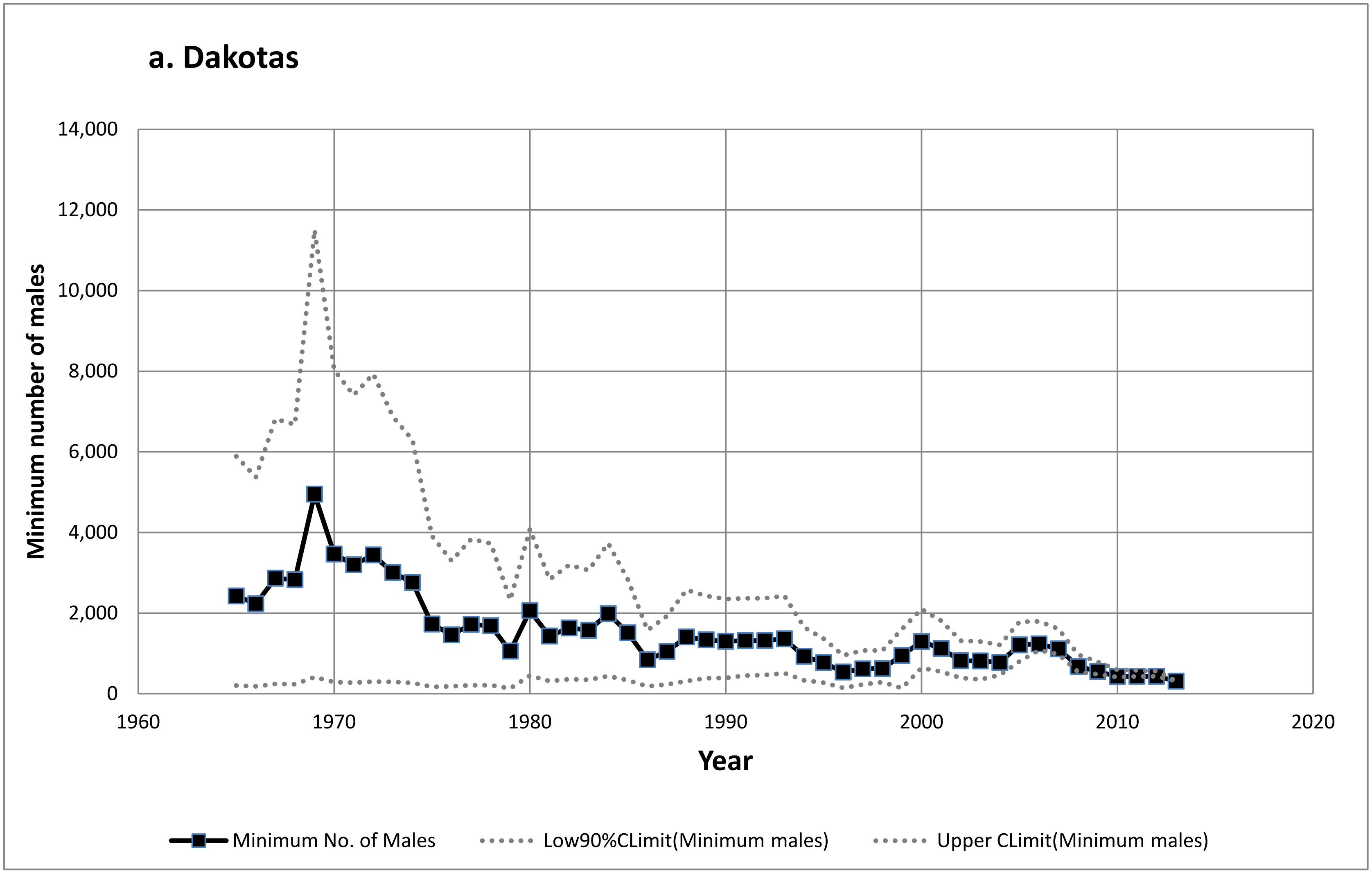
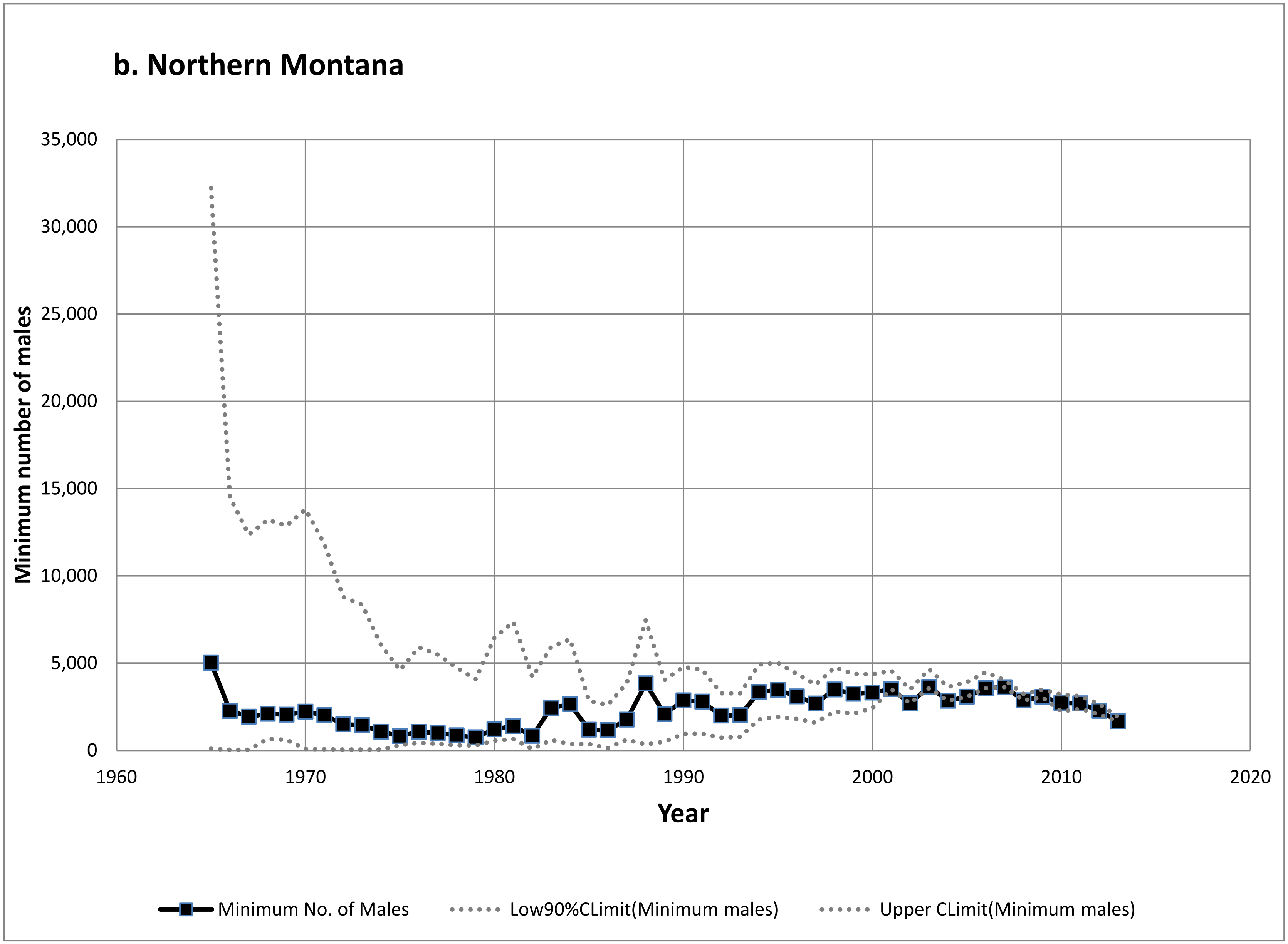
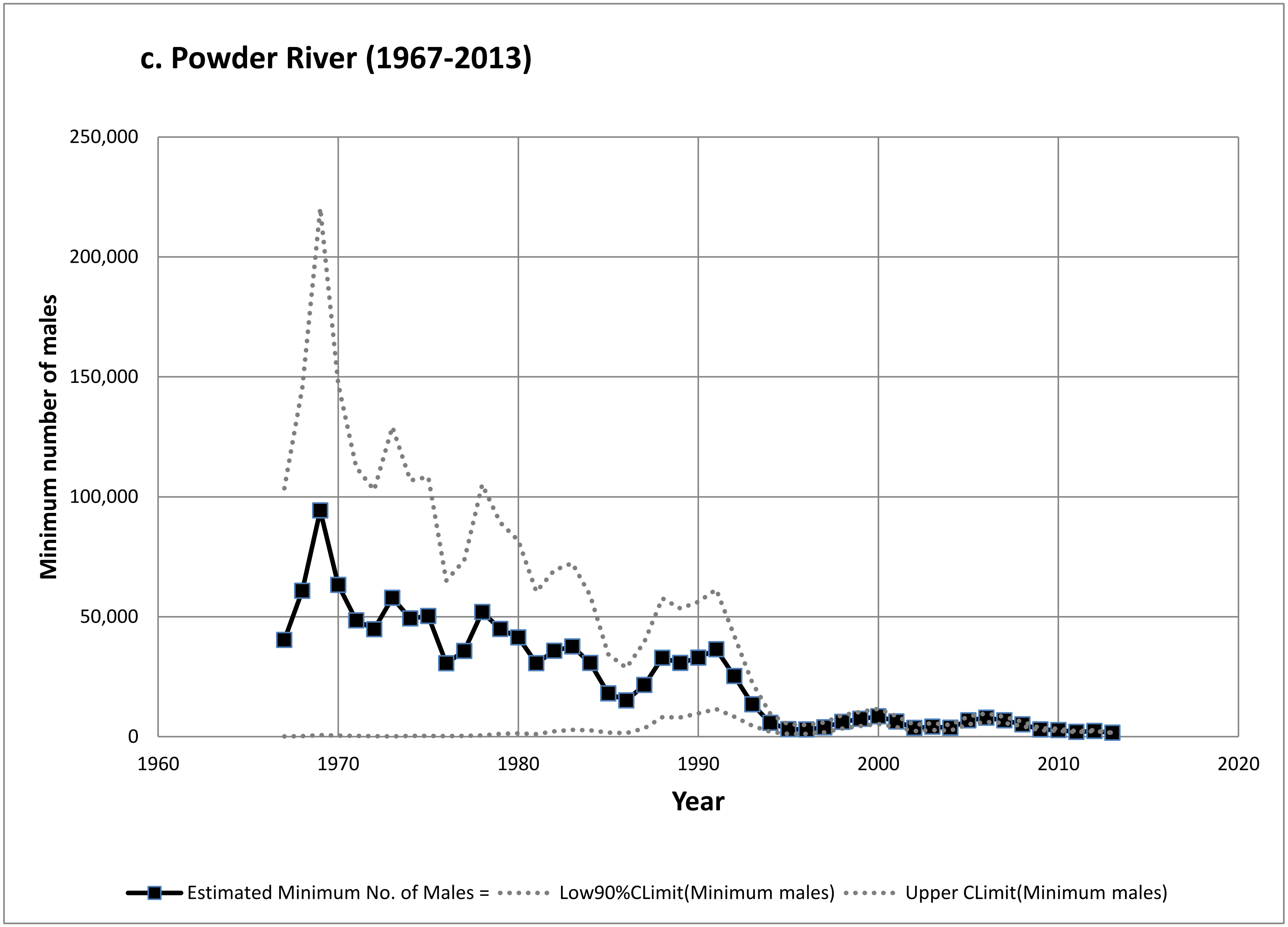
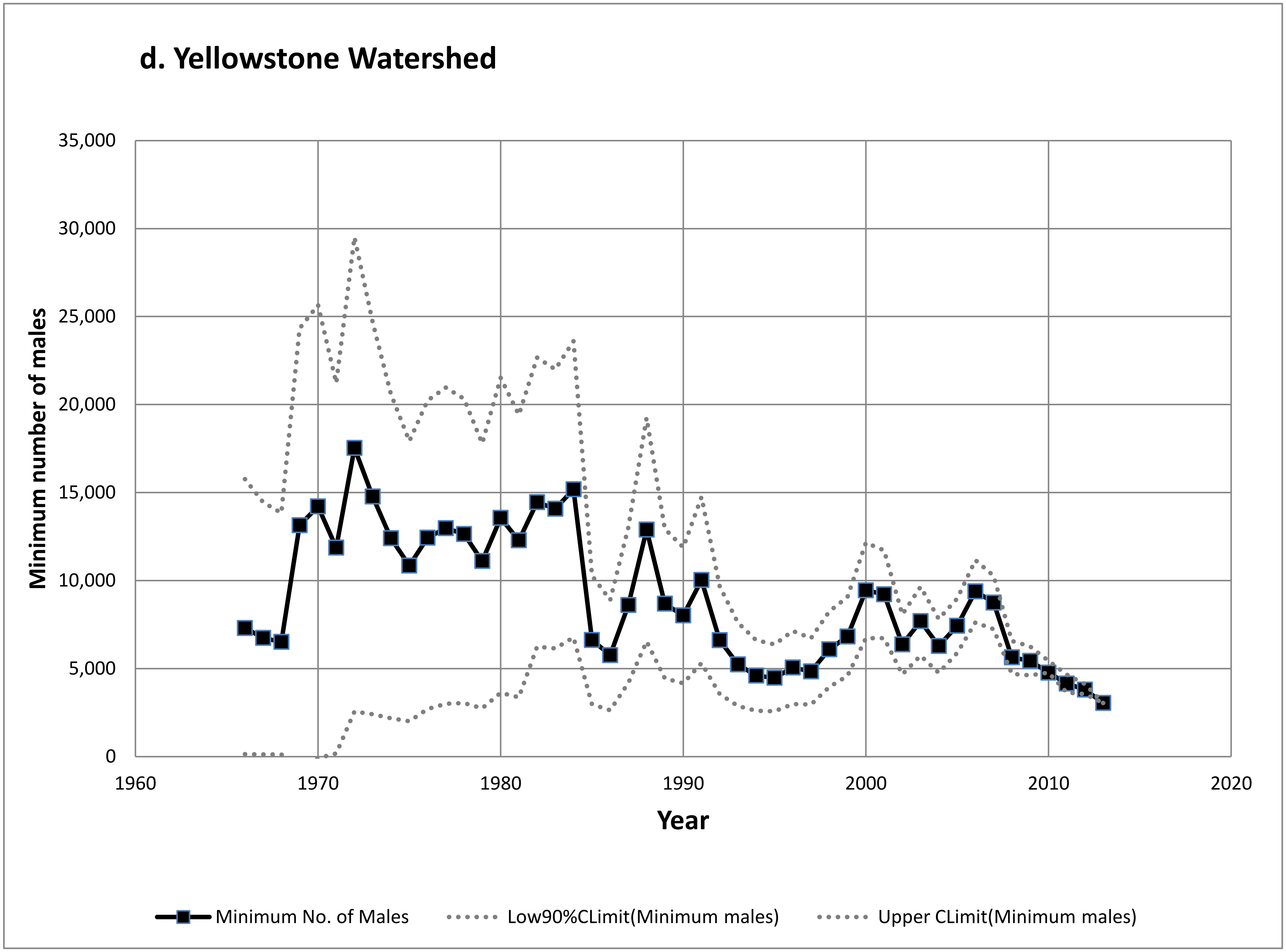


Figure 2. Population reconstructions for Great Plains populations and Management Zone I: a. Dakotas b. Northern Montana c. Powder River Basin d. Yellowstone Watershed e. Great Plains Management Zone I.


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)

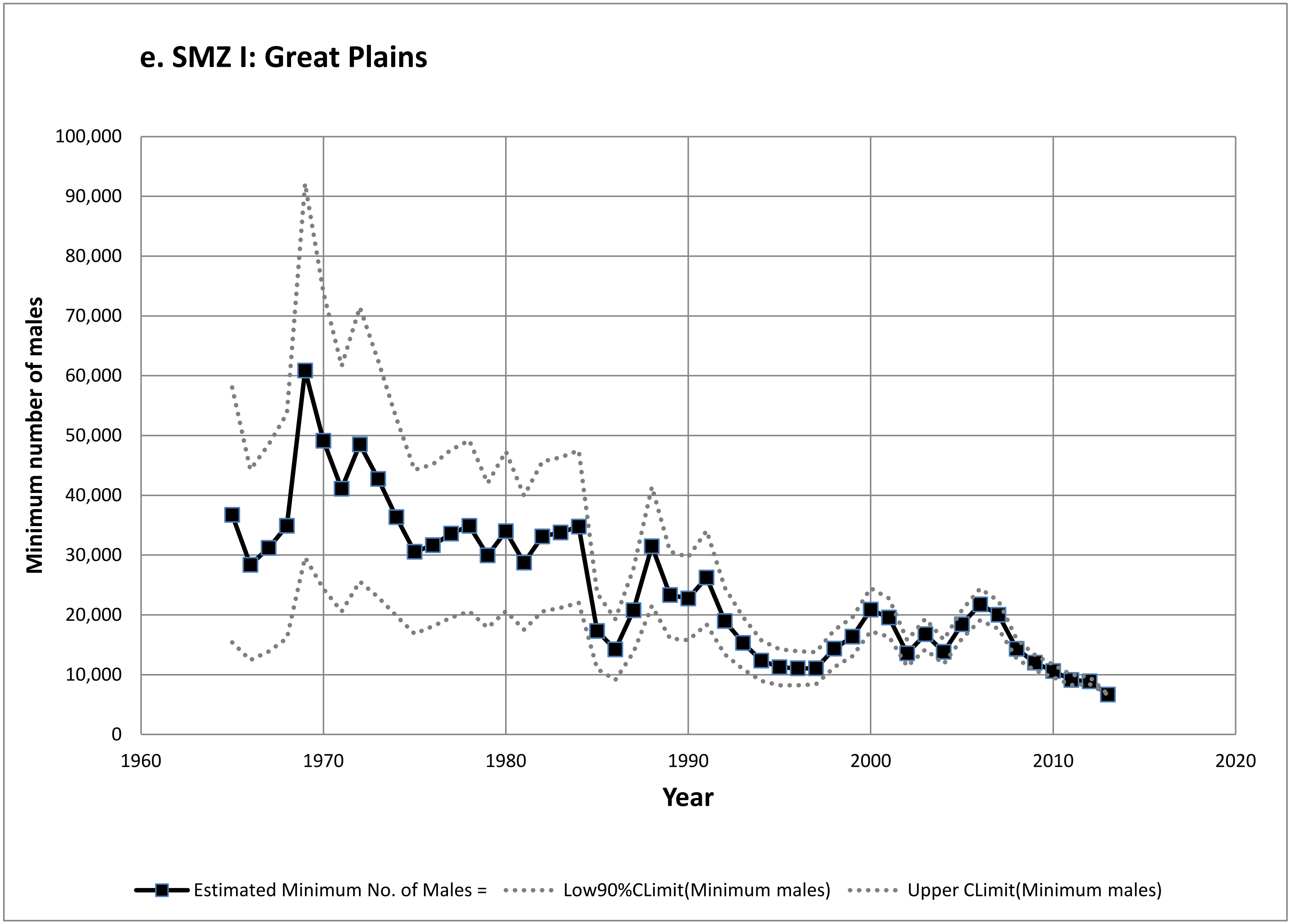
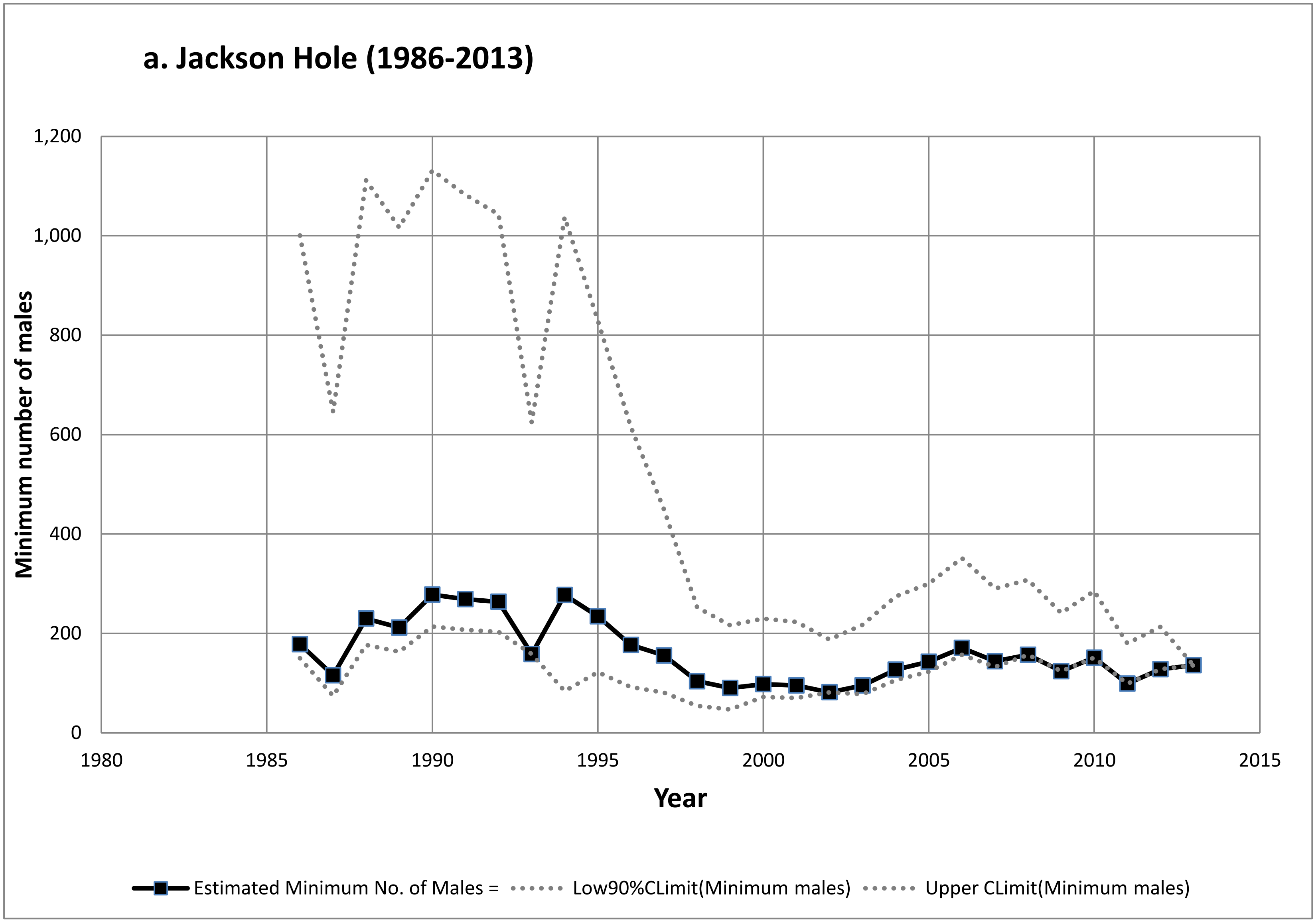
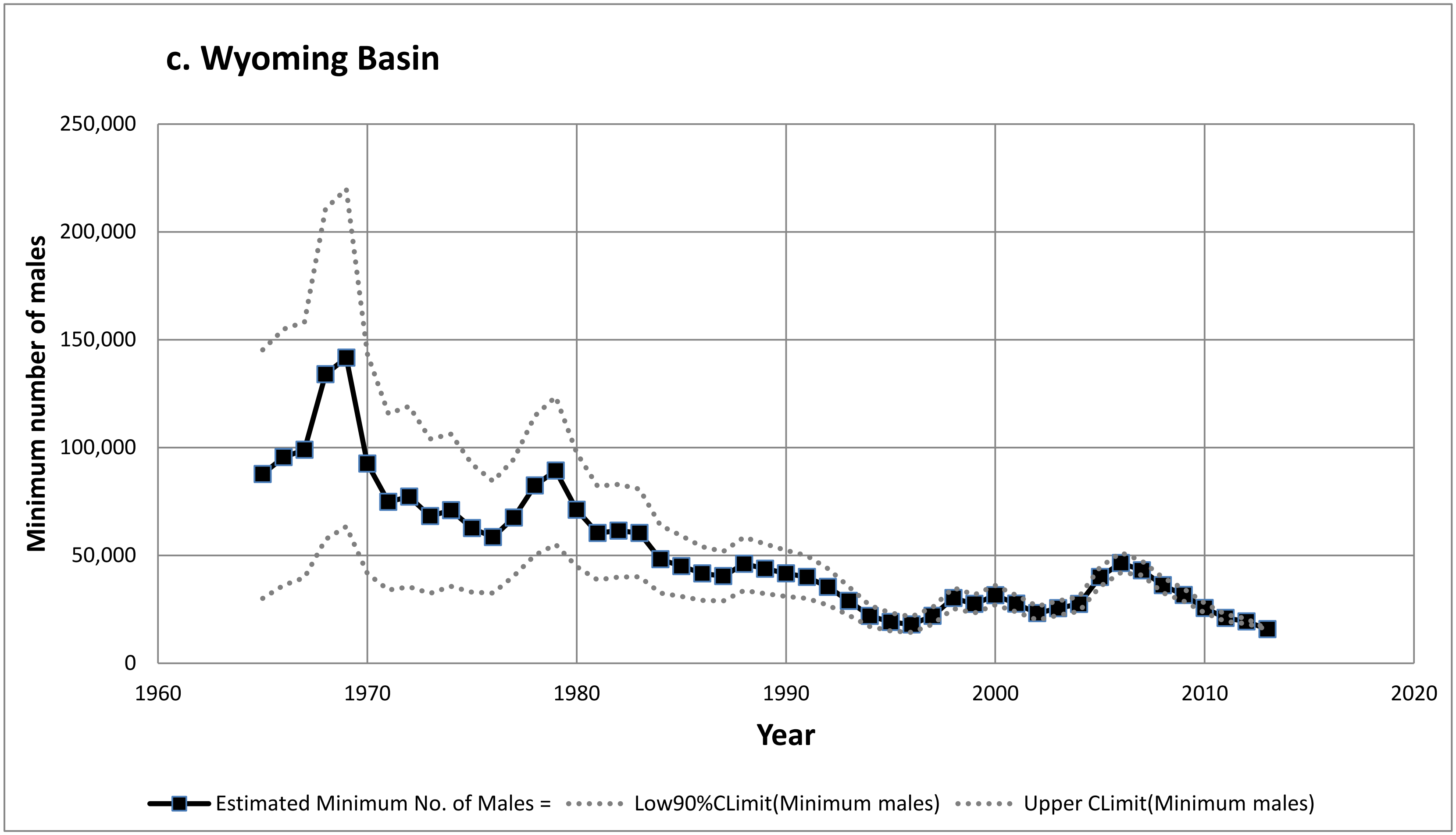

e. SMZ I: Great Plains
Minimum number of males
100,000
90,000
80,000
70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

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)

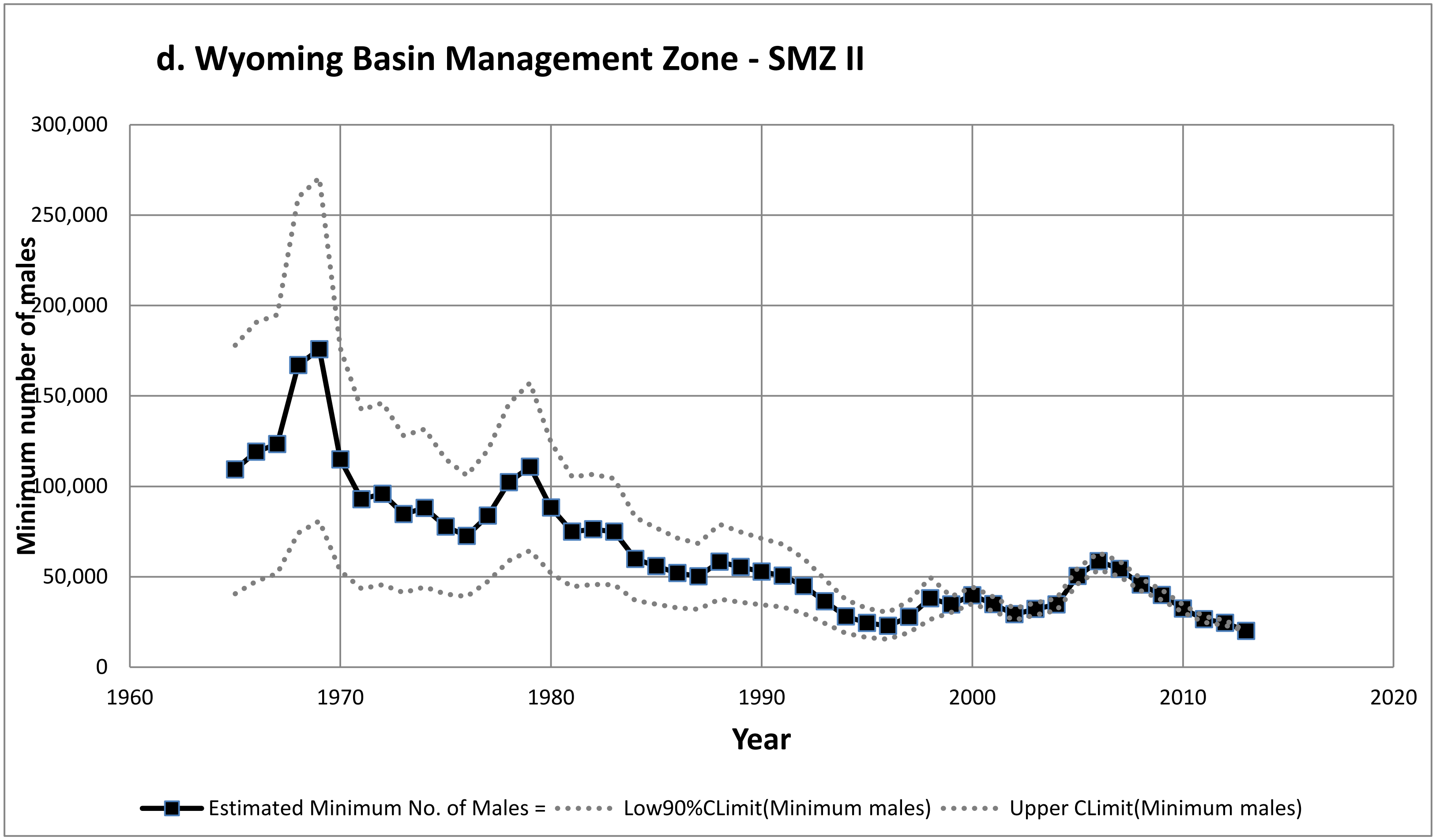
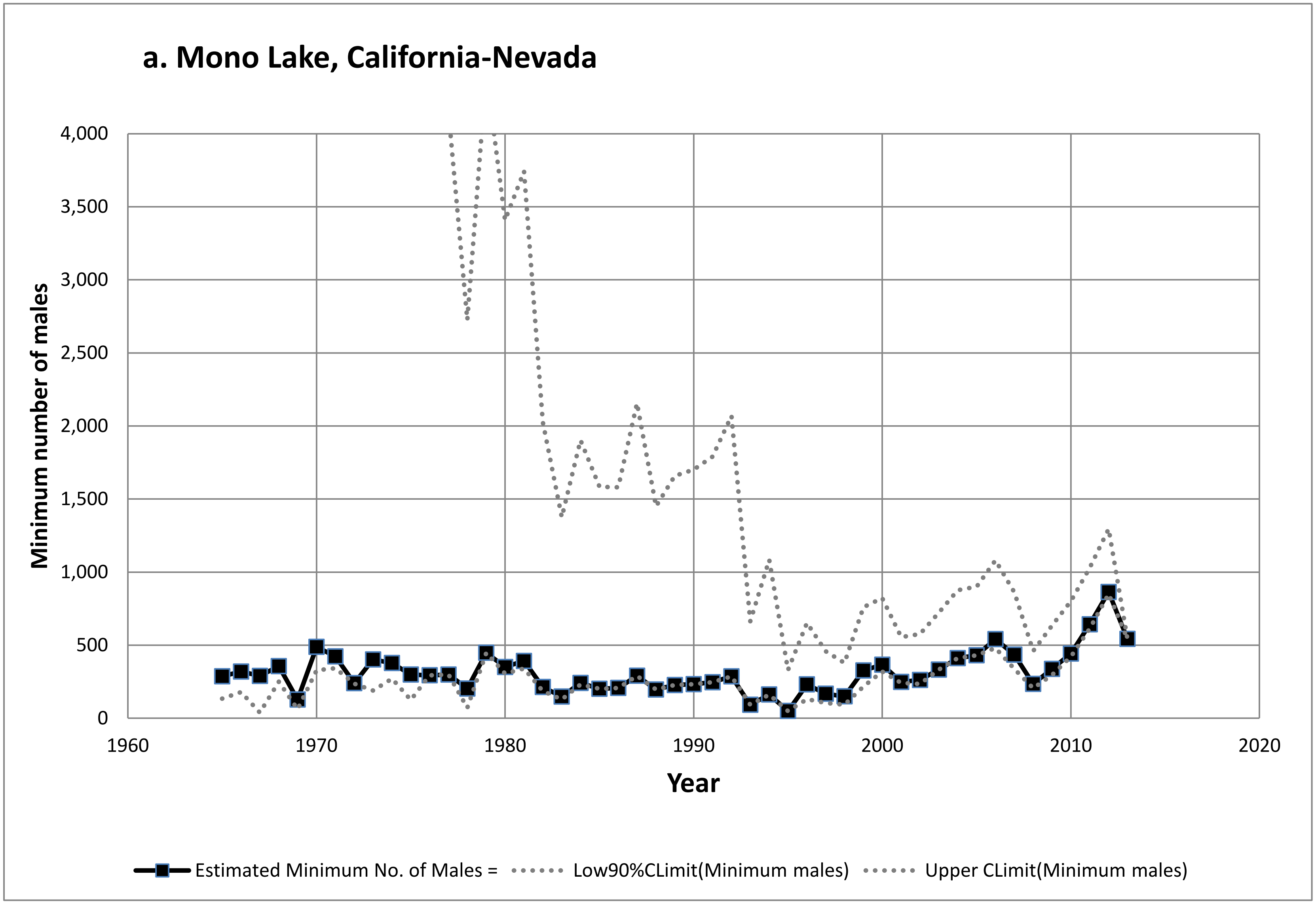
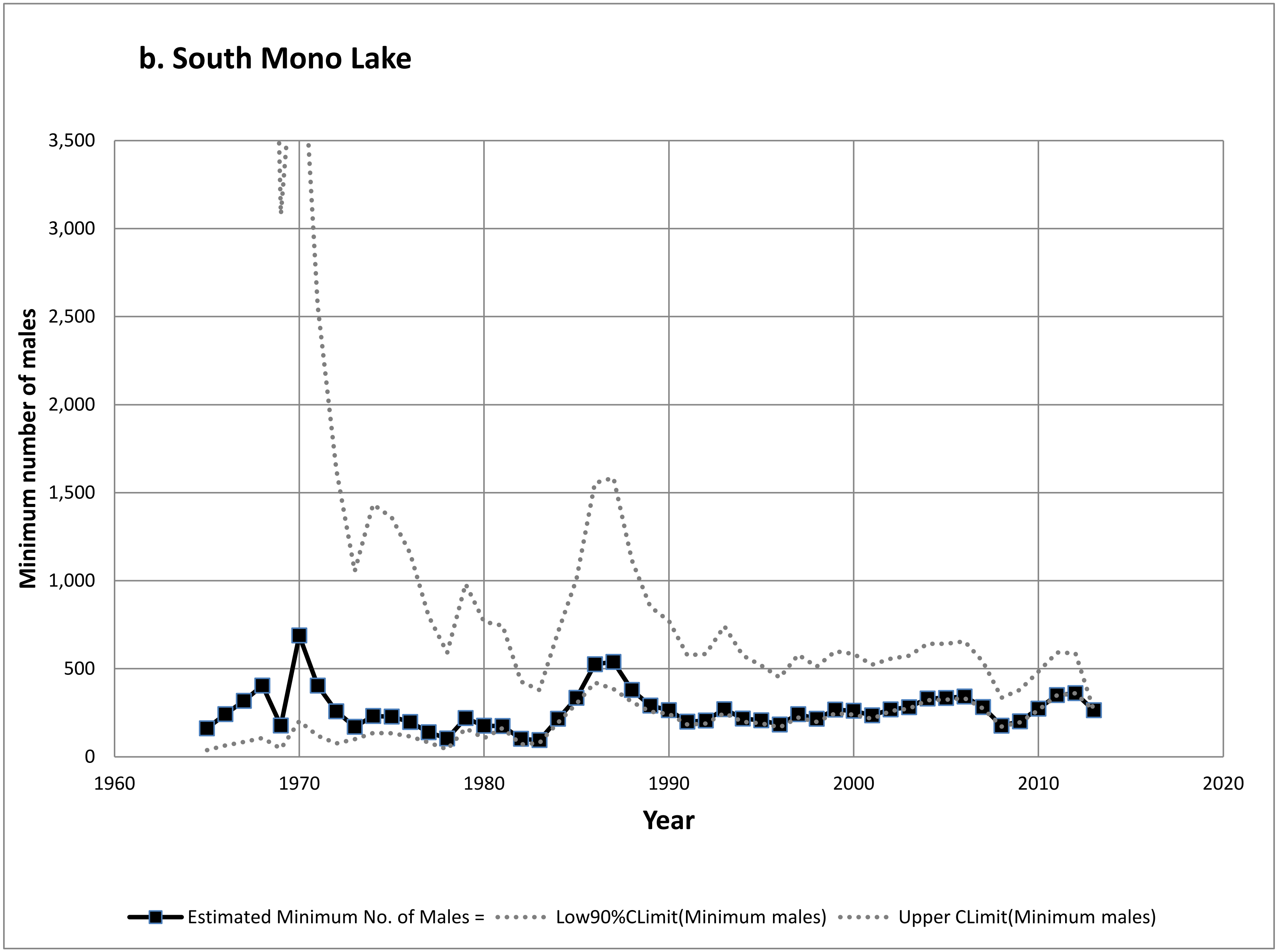
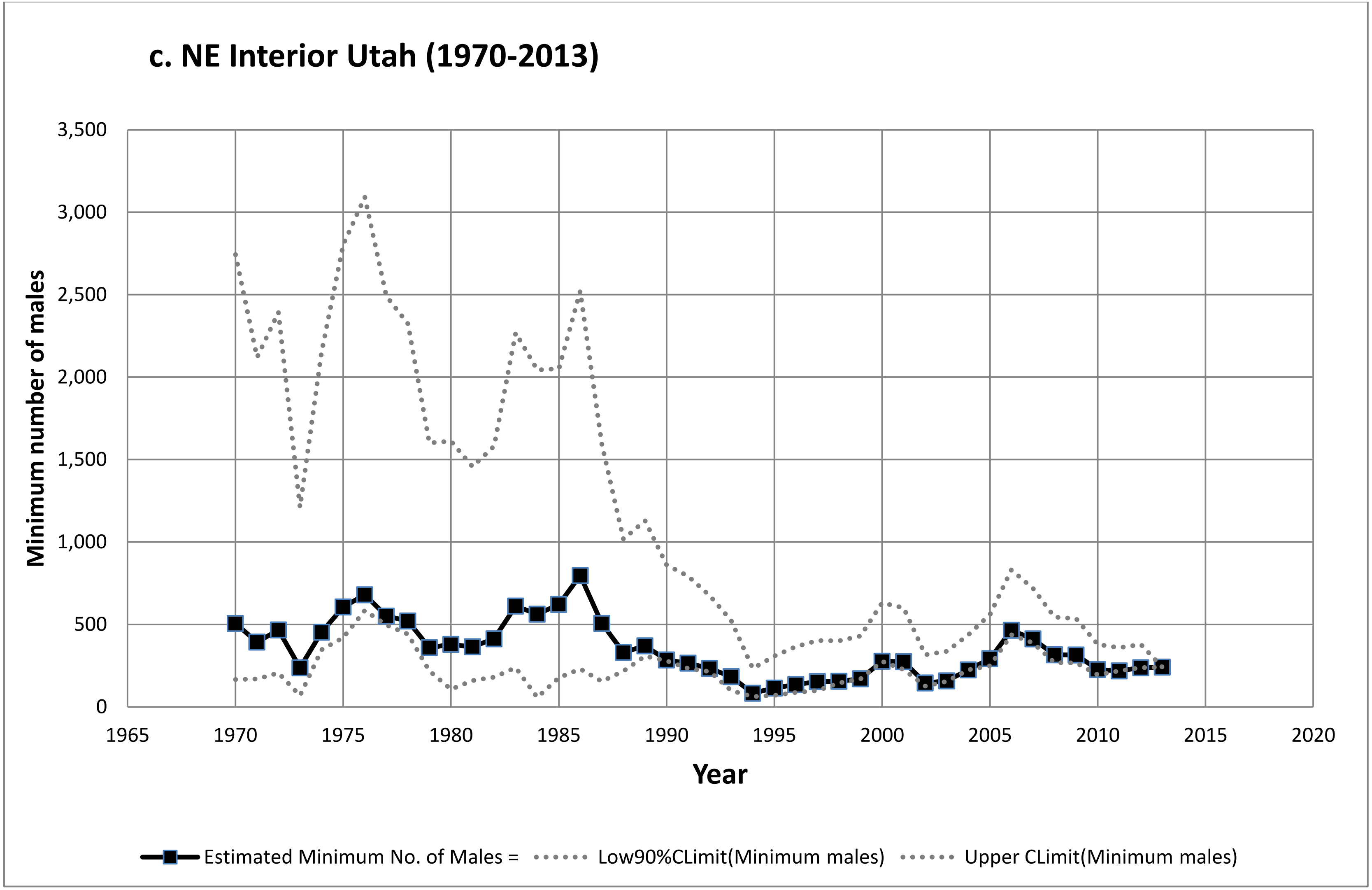
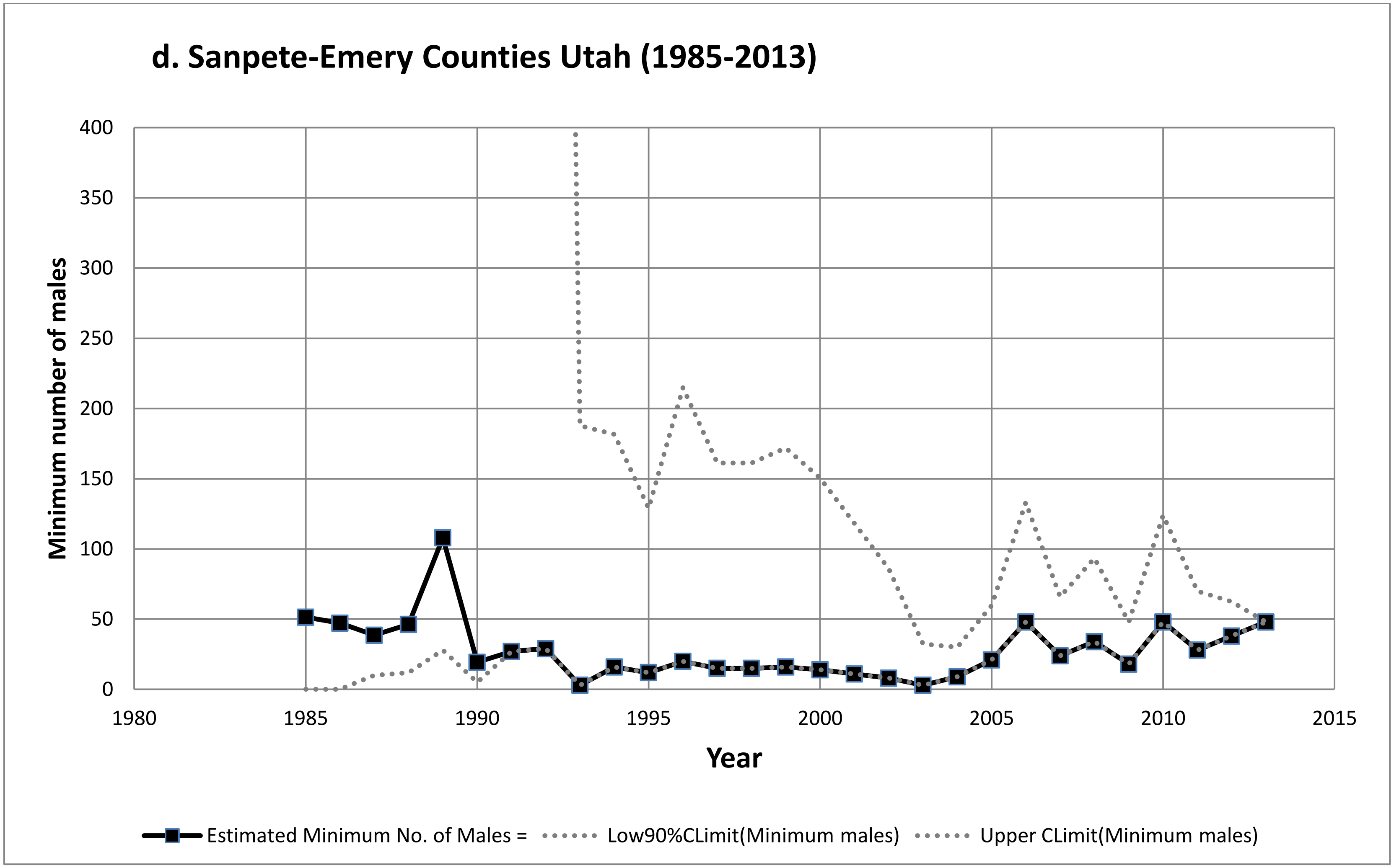

d. Wyoming Basin Management Zone - SMZ II
Minimum number of males
300,000
250,000
200,000
150,000
100,000
50,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

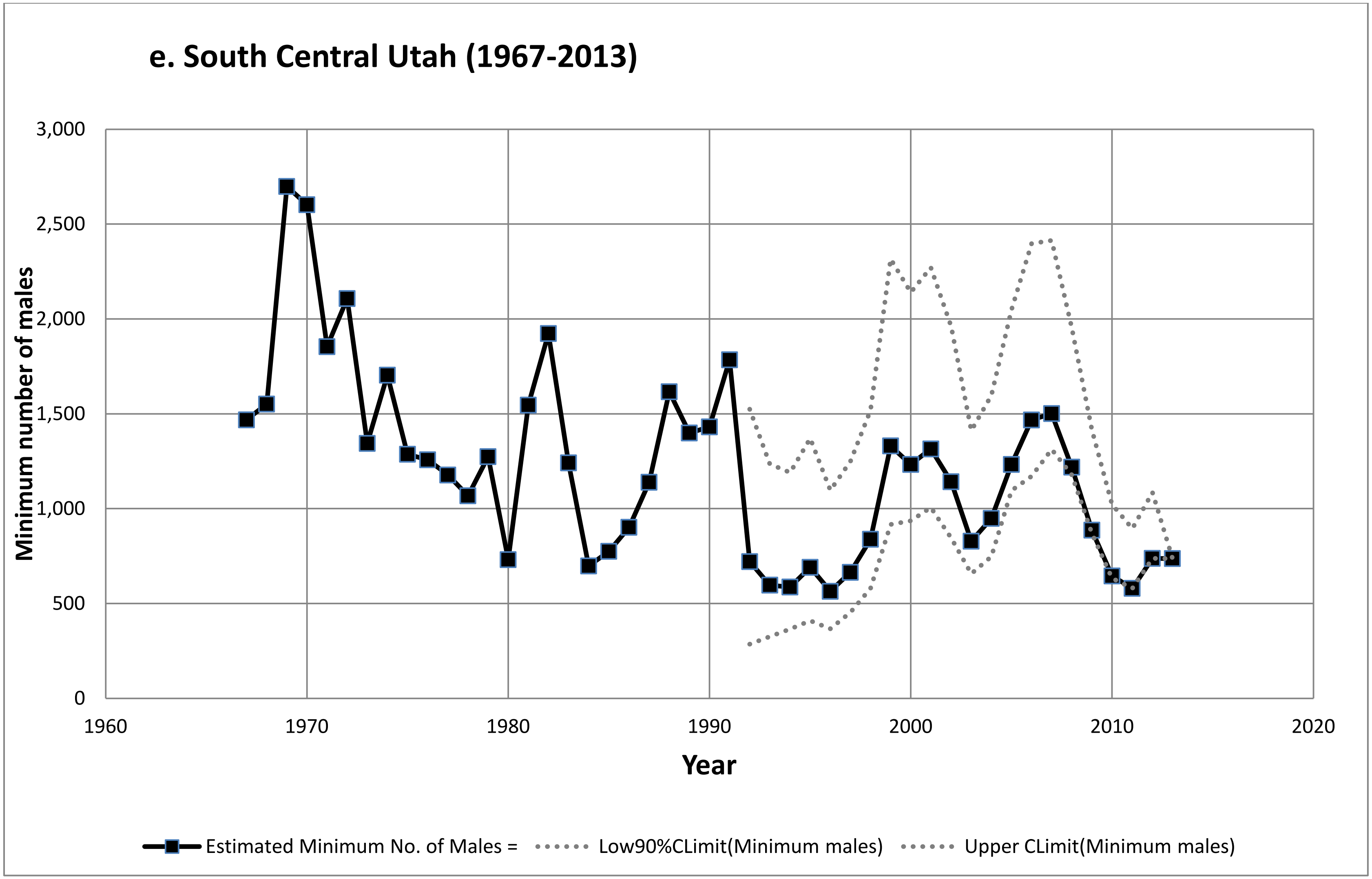
Figure 4. Population reconstructions for Southern Great Basin populations and Management Zone III: a. Mono Lake, California-Nevada; b. South Mono Lake; c. Northeast Interior, Utah; d. Sanpete-Emery; e. South-central Utah; f. Summit-Morgan, g. Toole-Juab Utah; h. Southern Great Basin; i. Management Zone III.

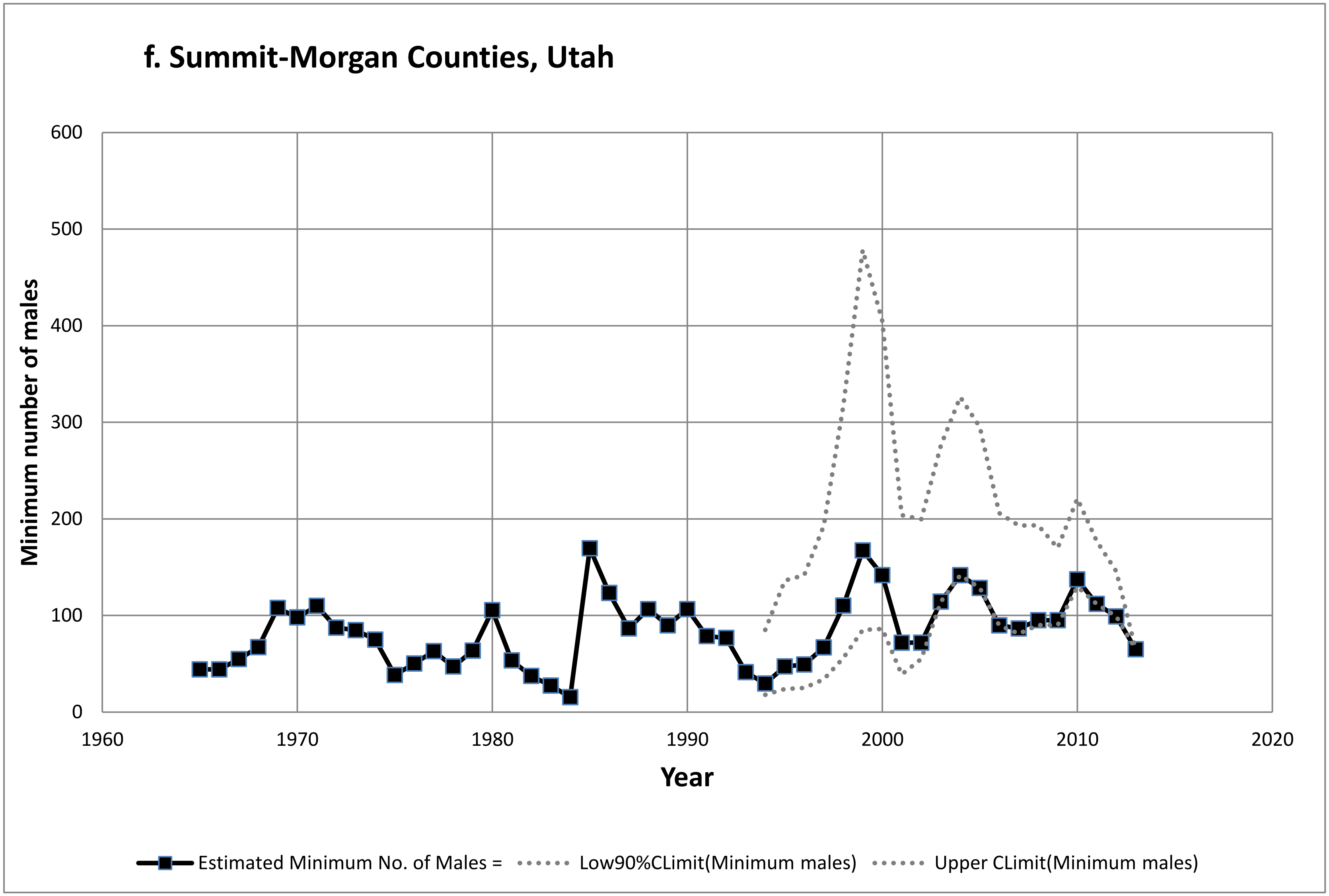

a. Mono Lake, California-Nevada
4,000
3,500
3,000
2,500
2,000
1,500
1,000
500
0
Minimum number of males
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

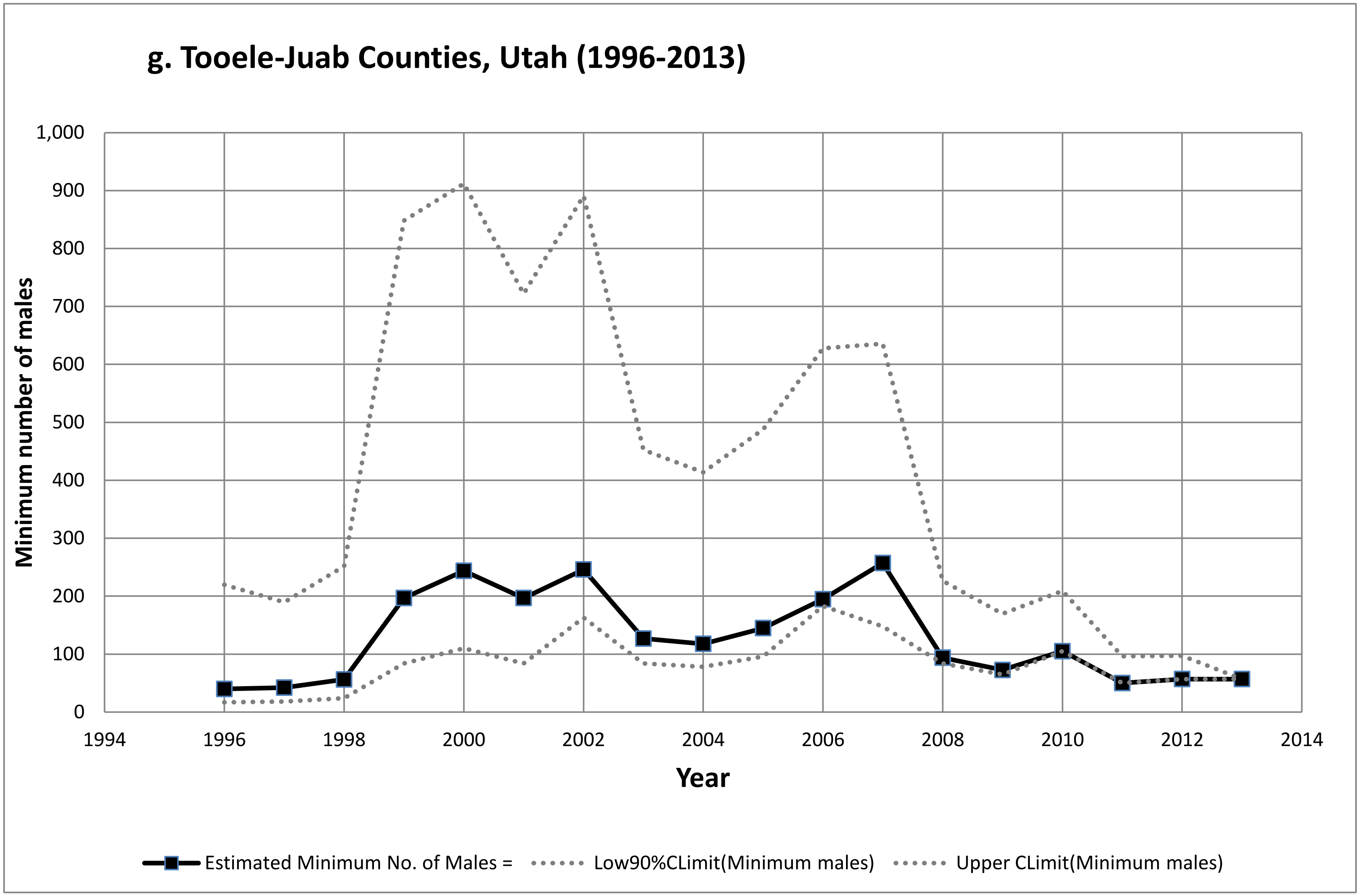

b. South Mono Lake
Minimum number of males
3,500
3,000
2,500
2,000
1,500
1,000
500
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

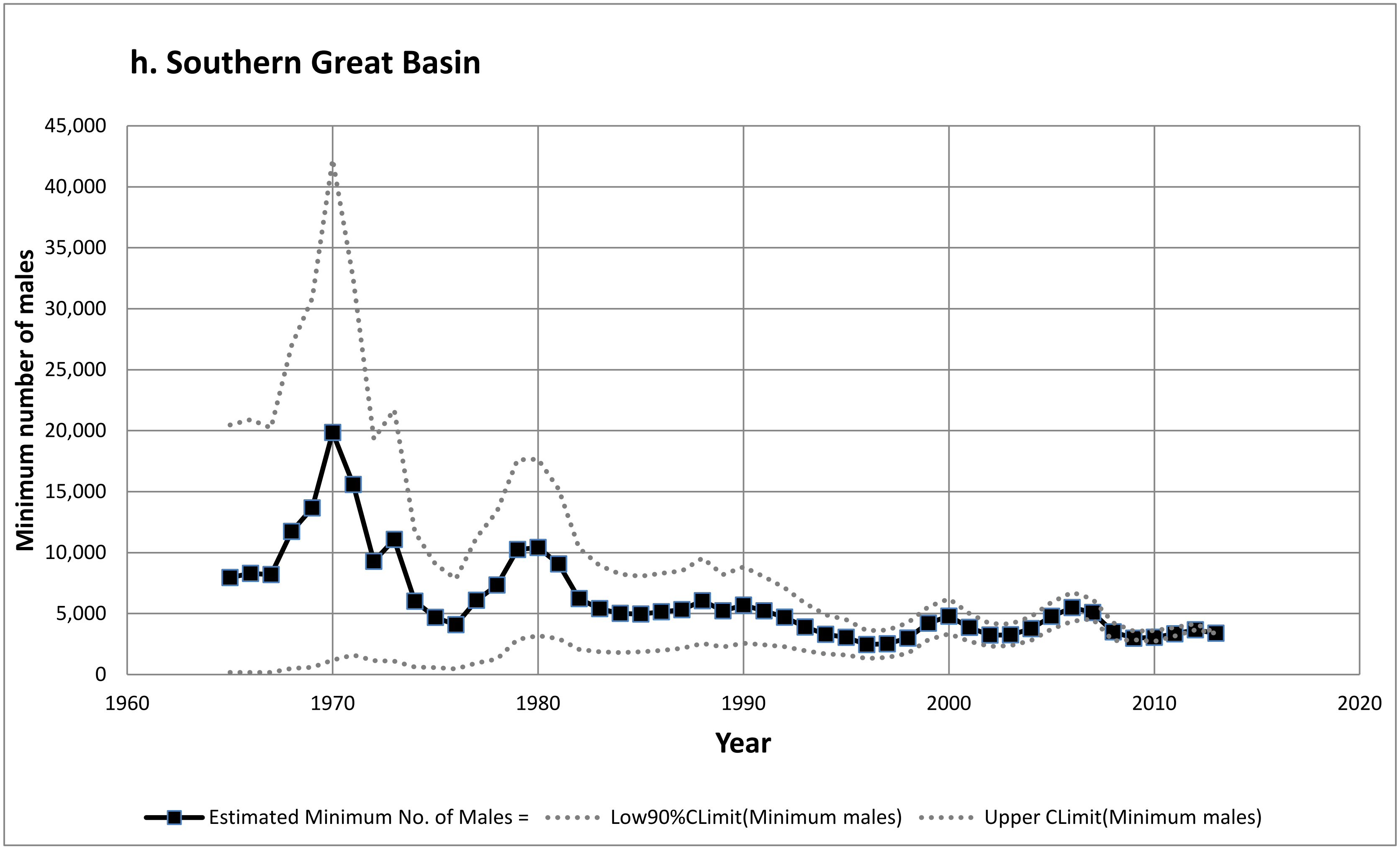

c. NE Interior Utah (1970-2013)
3,500
3,000
2,500
2,000
1,500
1,000
500
0
Minimum number of males
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
2015
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


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)

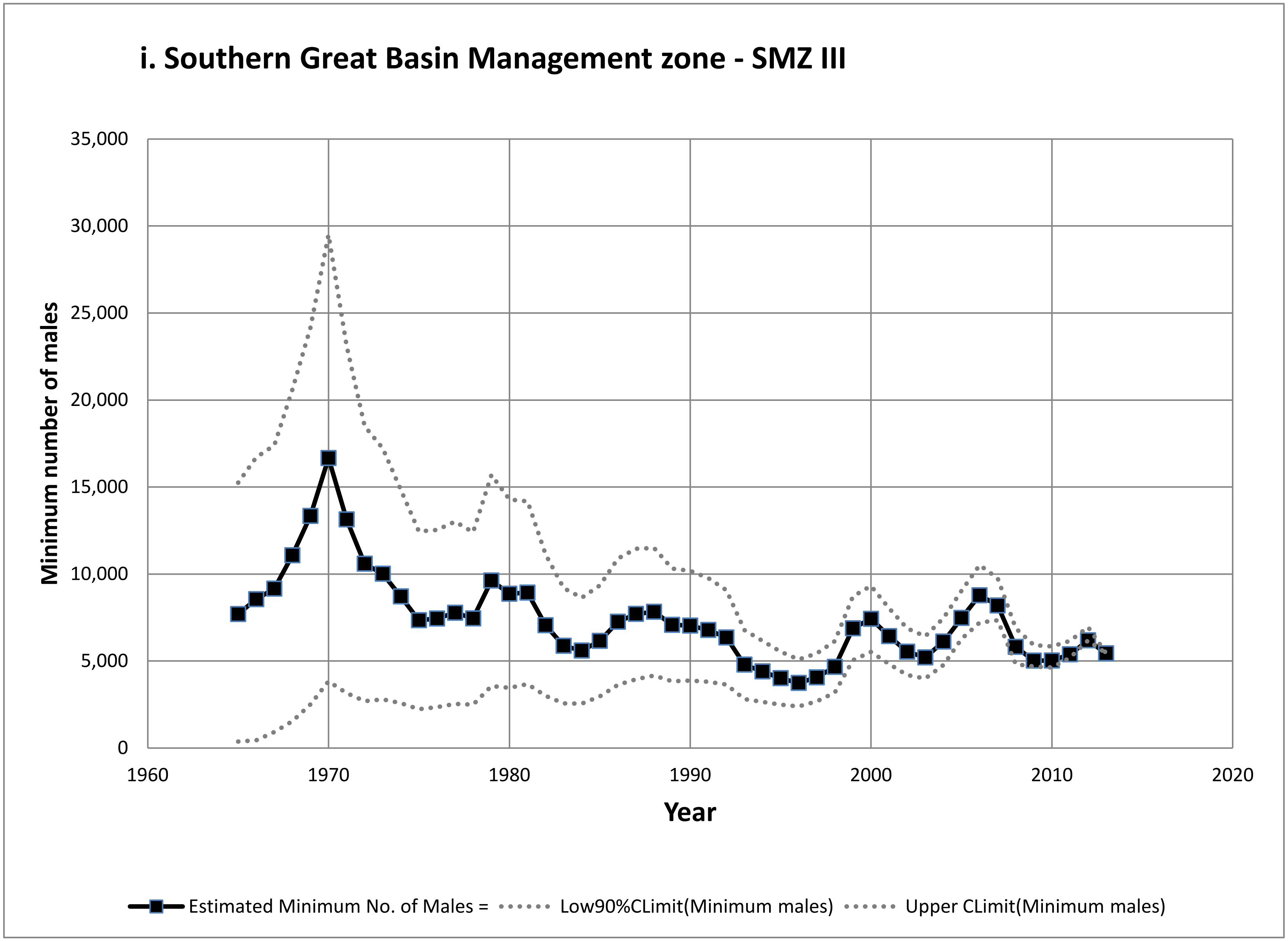
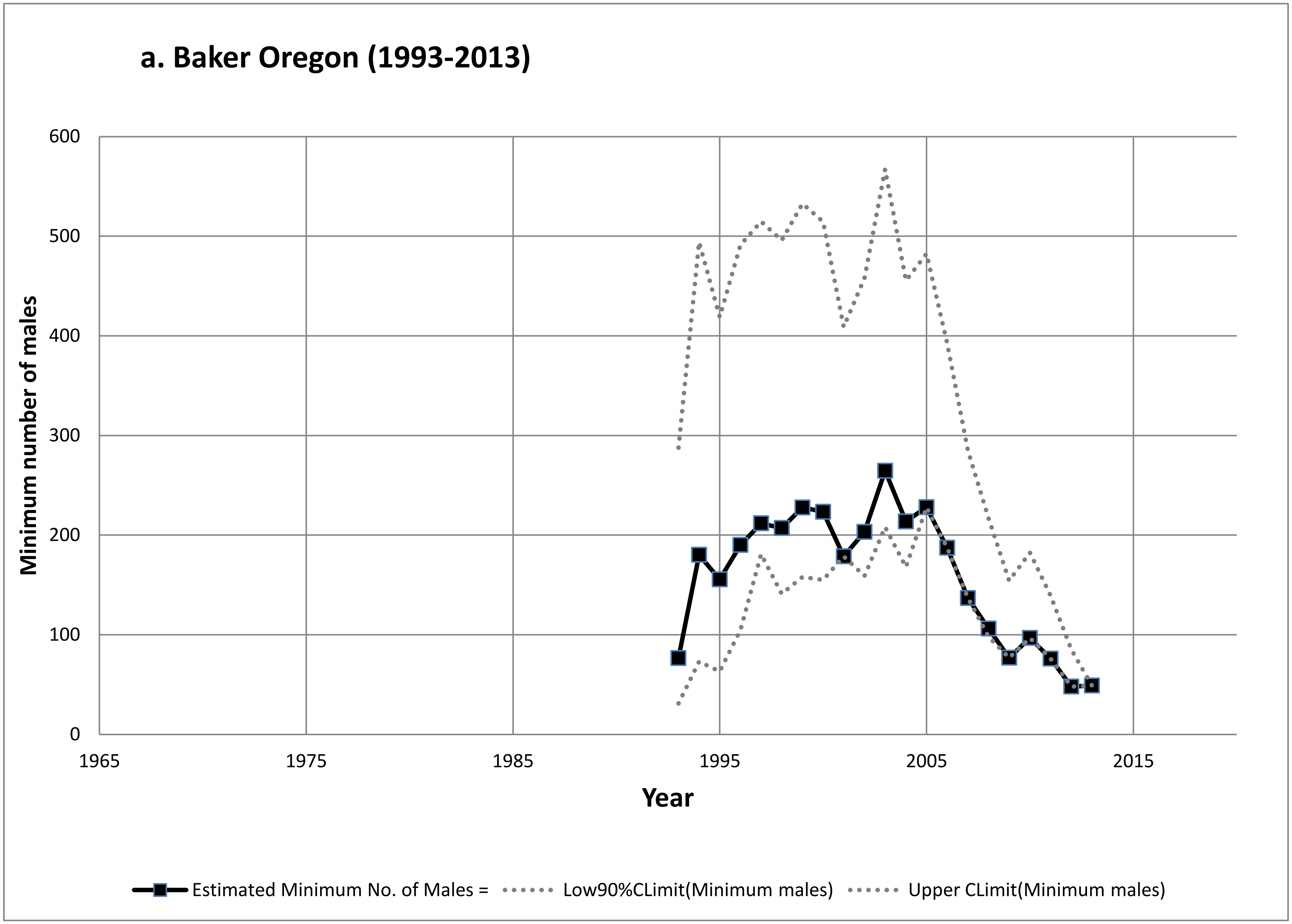
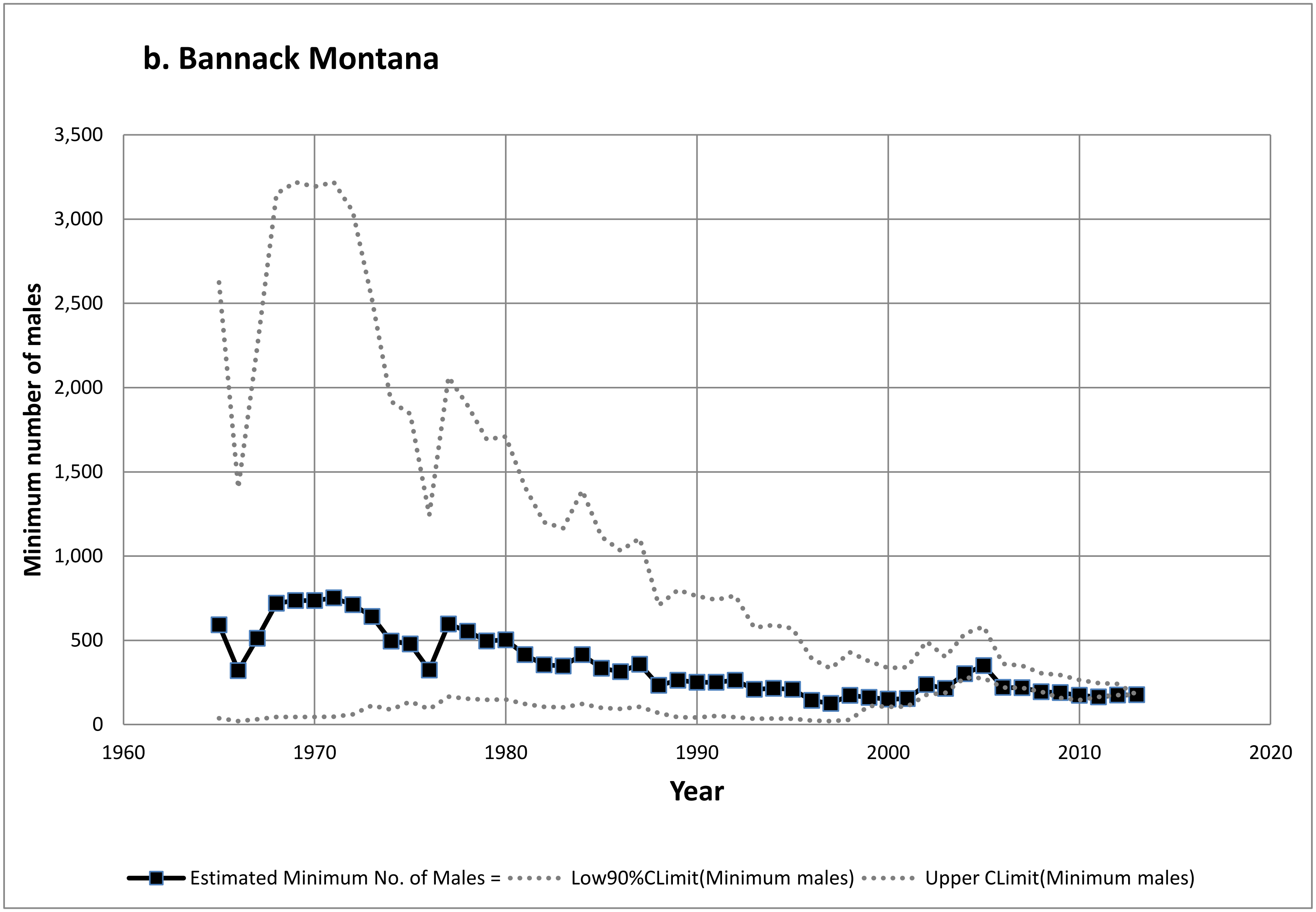
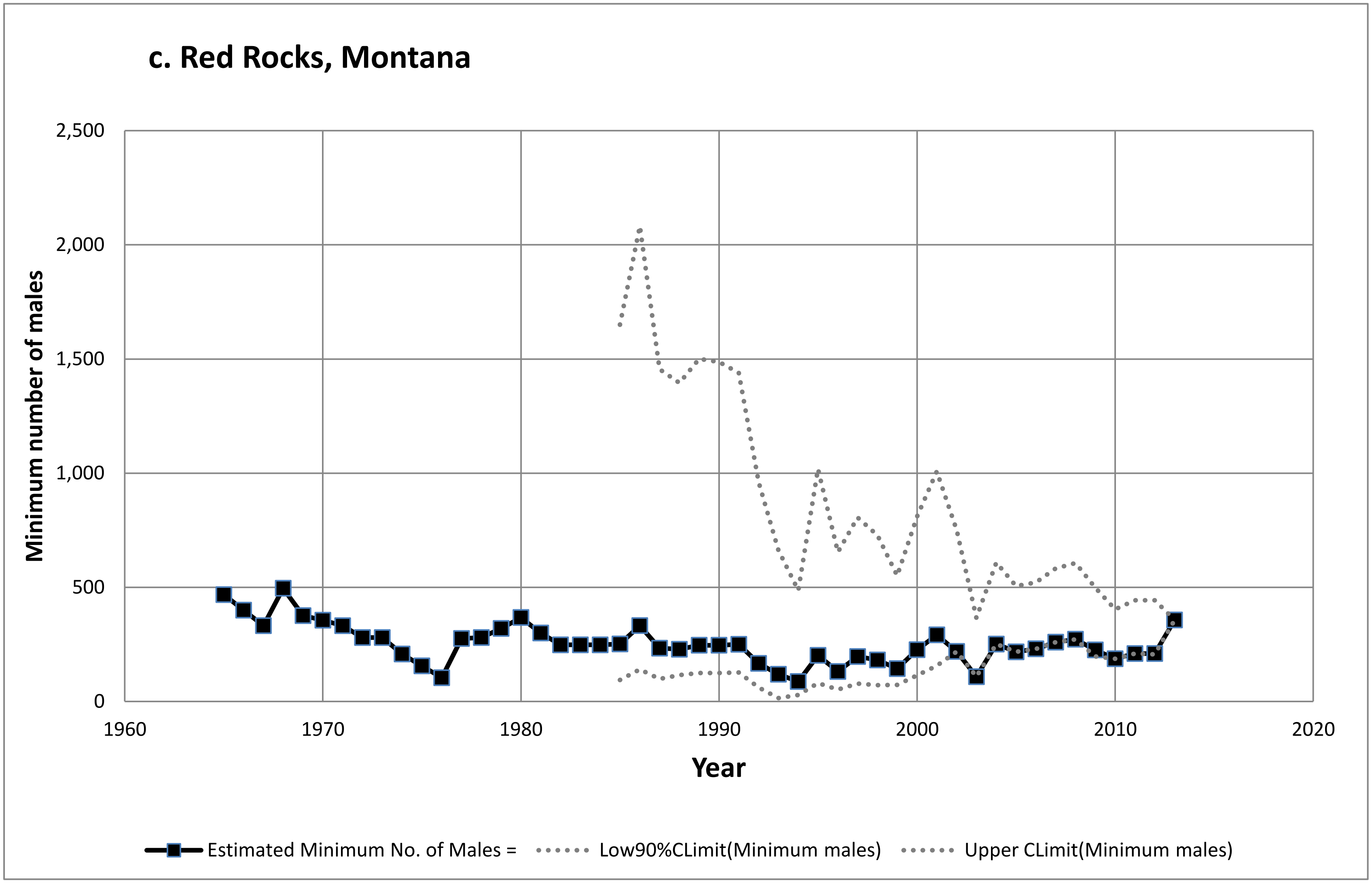
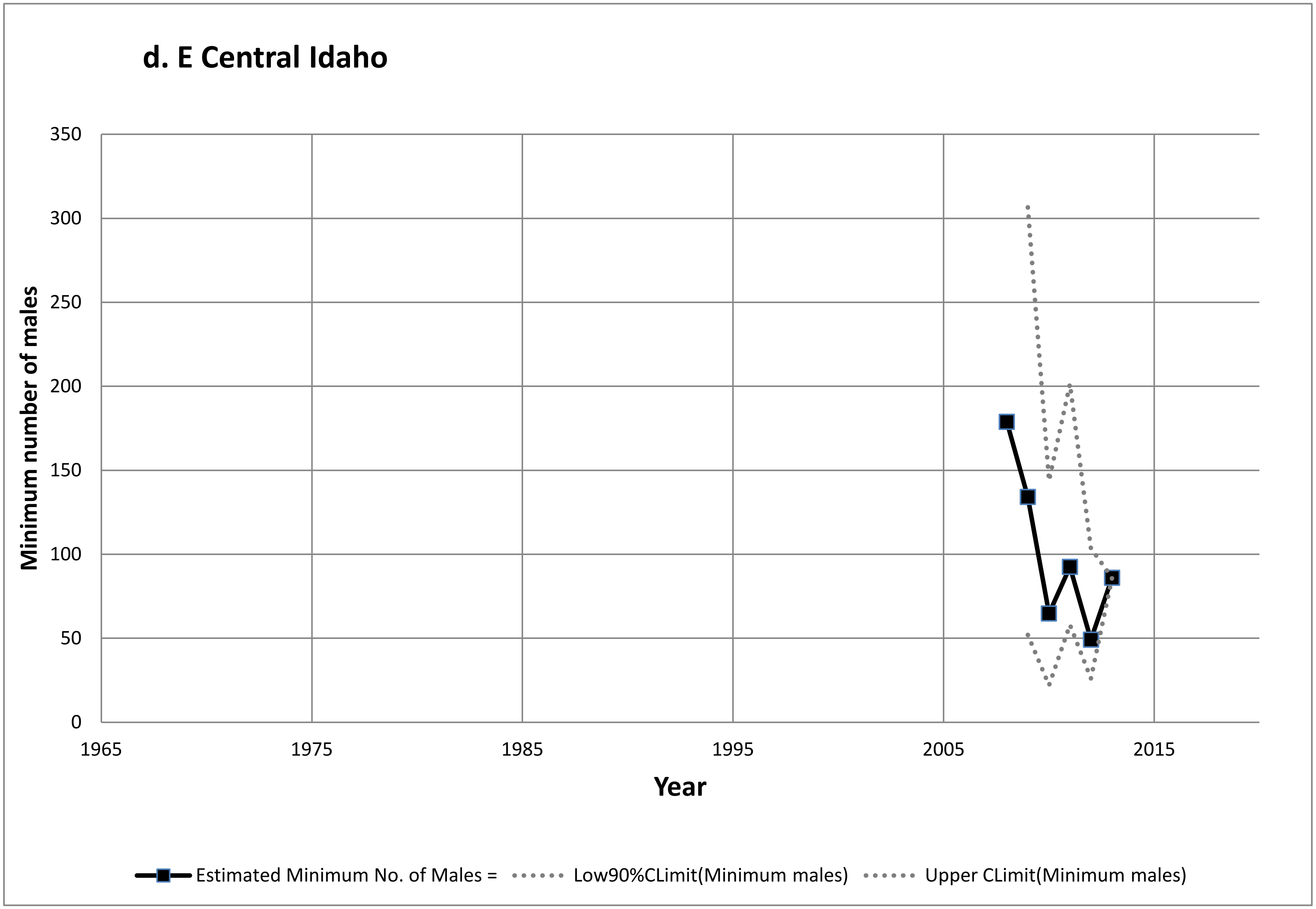

i. Southern Great Basin Management zone - SMZ III
Minimum number of males
35,000
30,000
25,000
20,000
15,000
10,000
5,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

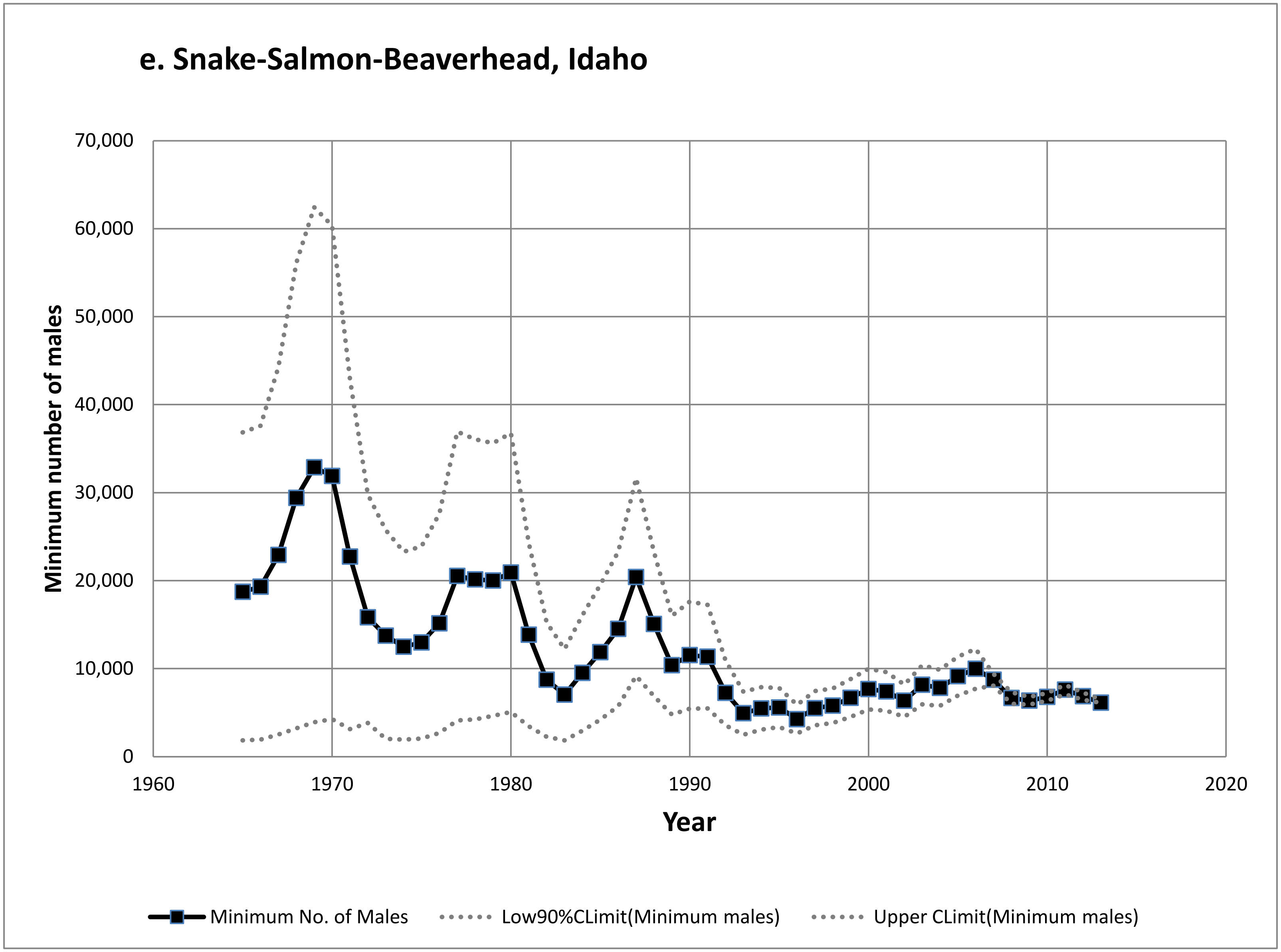
Figure 5. Population reconstructions for Snake River Plain populations and Management Zone IV: a. Baker, Oregon; b. Bannack, Montana; c. Red Rocks, Montana; d. East-central Idaho; e. Snake-Salmon-Beaverhead; f. Northern Great Basin; g. Weiser Idaho; h. Management Zone IV.

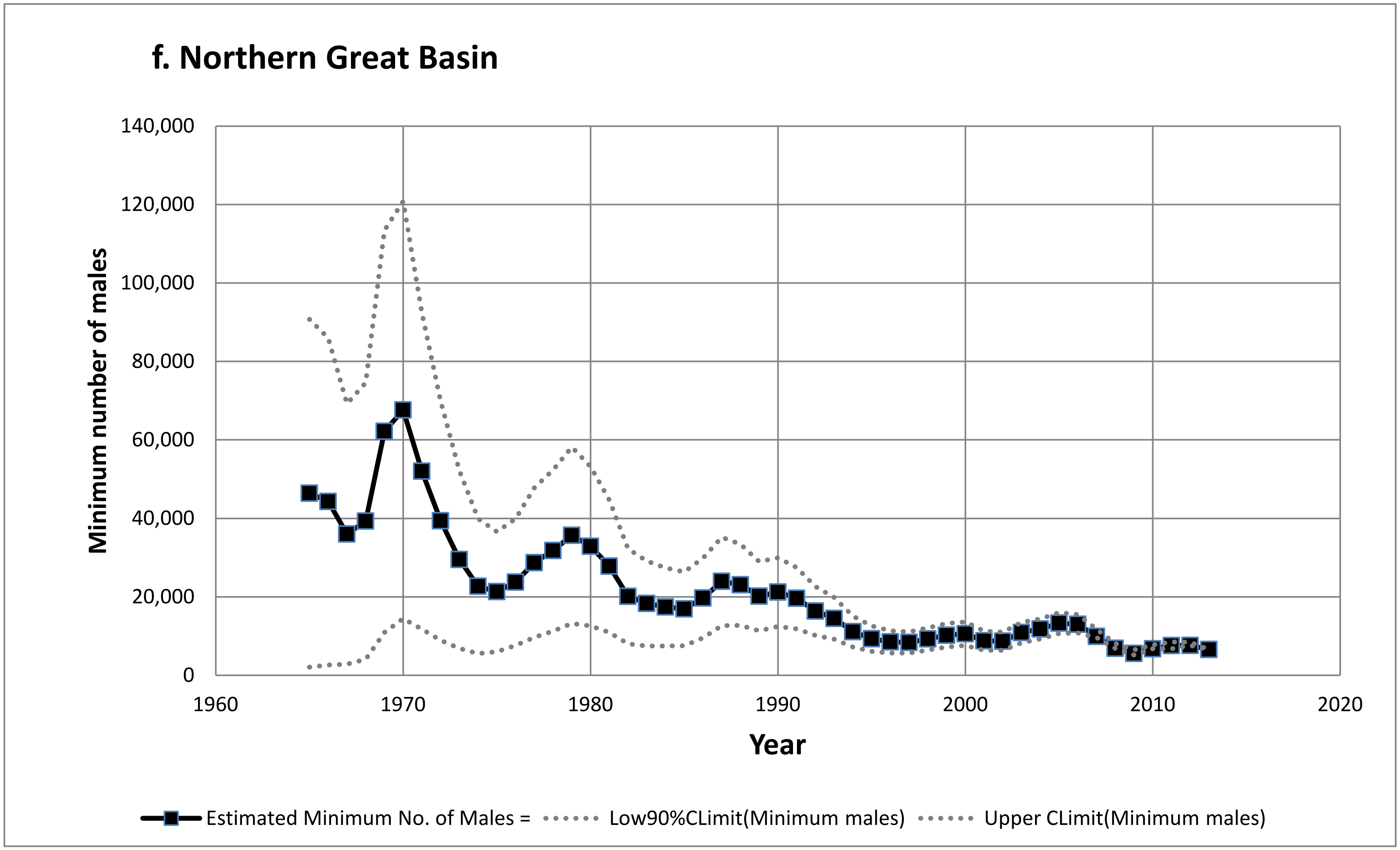

a. Baker Oregon (1993-2013)
Minimum number of males
600
500
400
300
200
100
0
1965
1975
1985
1995
2005
2015
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

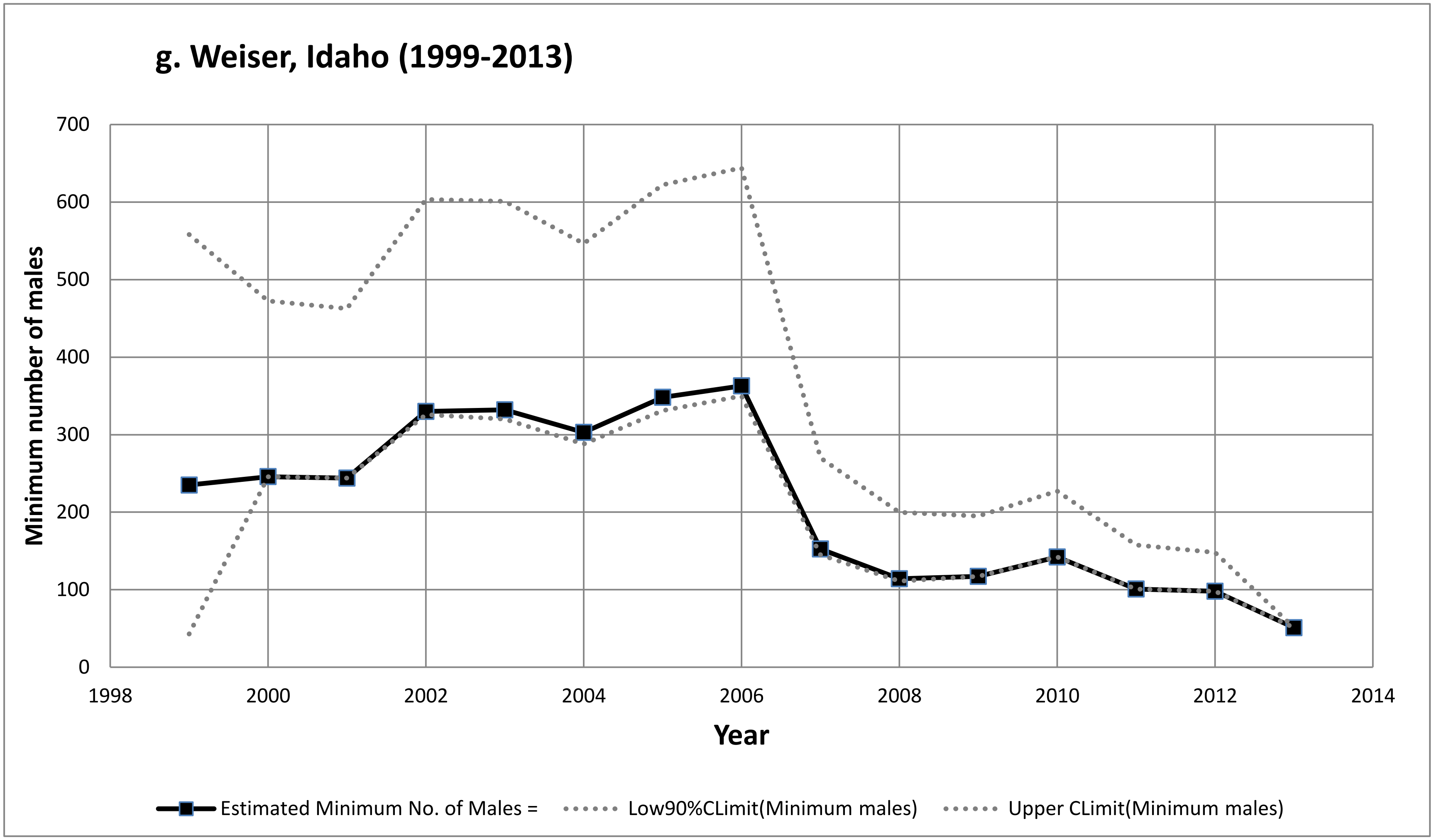

b. Bannack Montana
Minimum number of males
3,500
3,000
2,500
2,000
1,500
1,000
500
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


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
Minimum number of males
70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Minimum No. of Males
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


f. Northern Great Basin
140,000
120,000
100,000
80,000
60,000
40,000
20,000
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)


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)

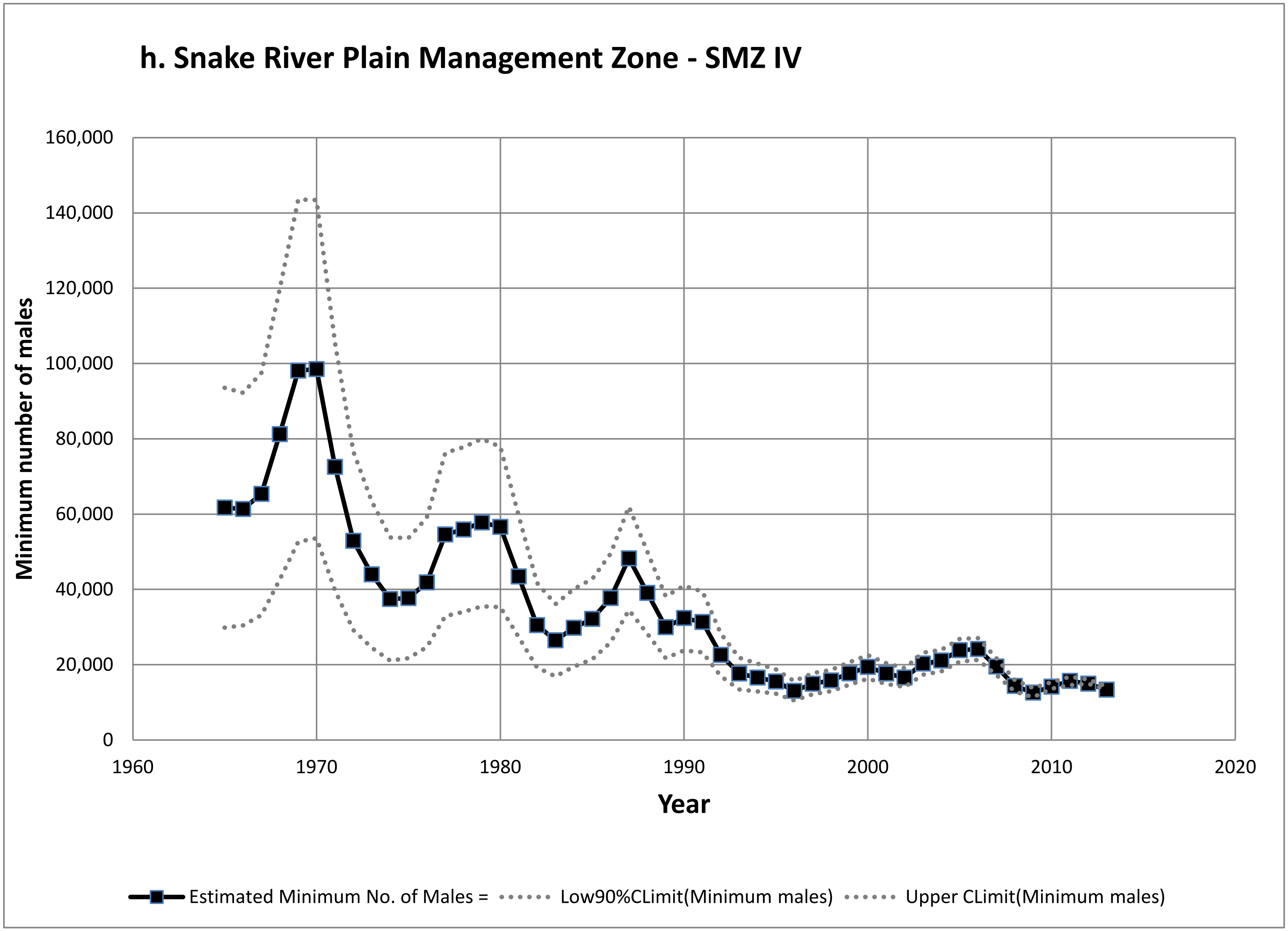
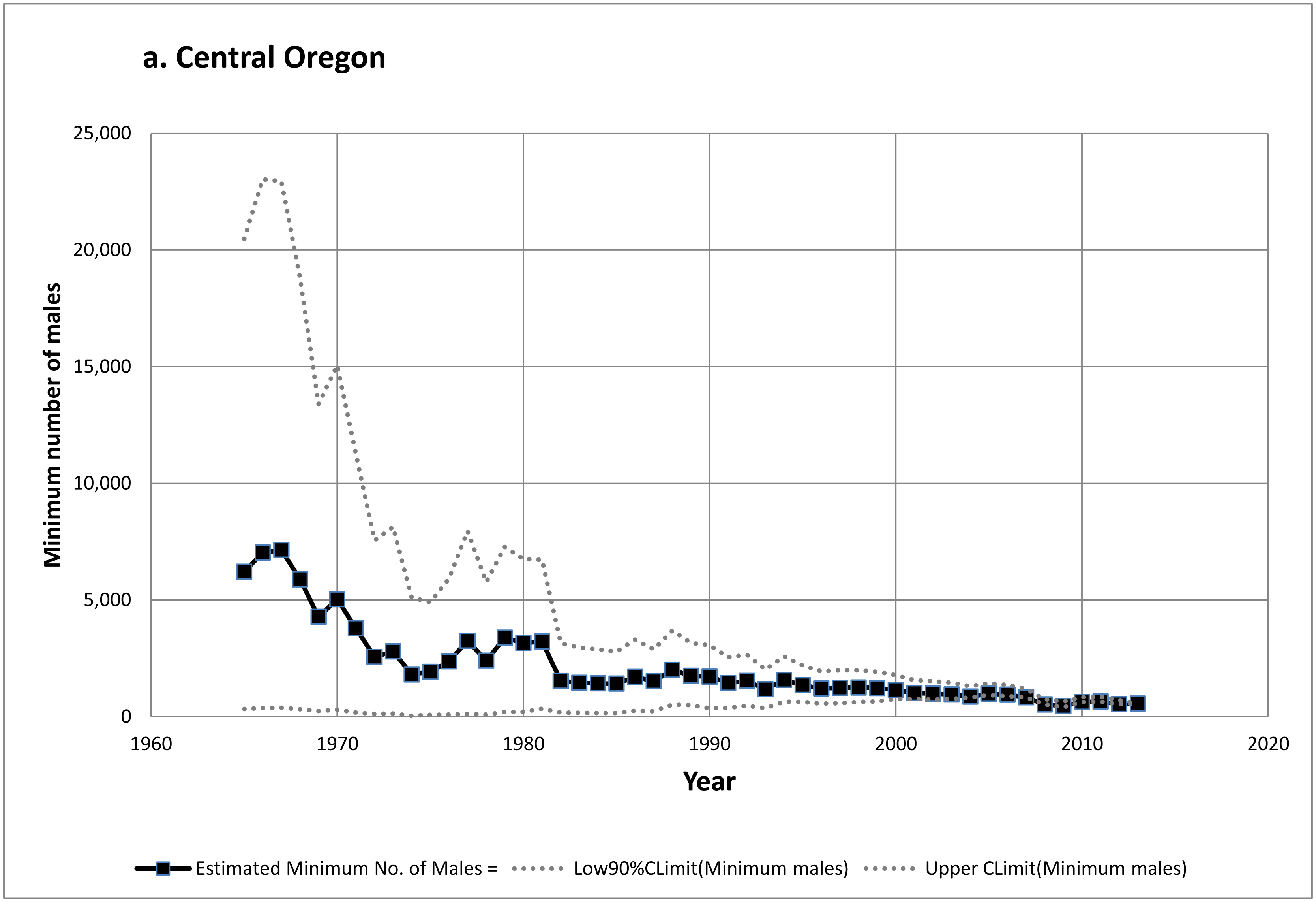
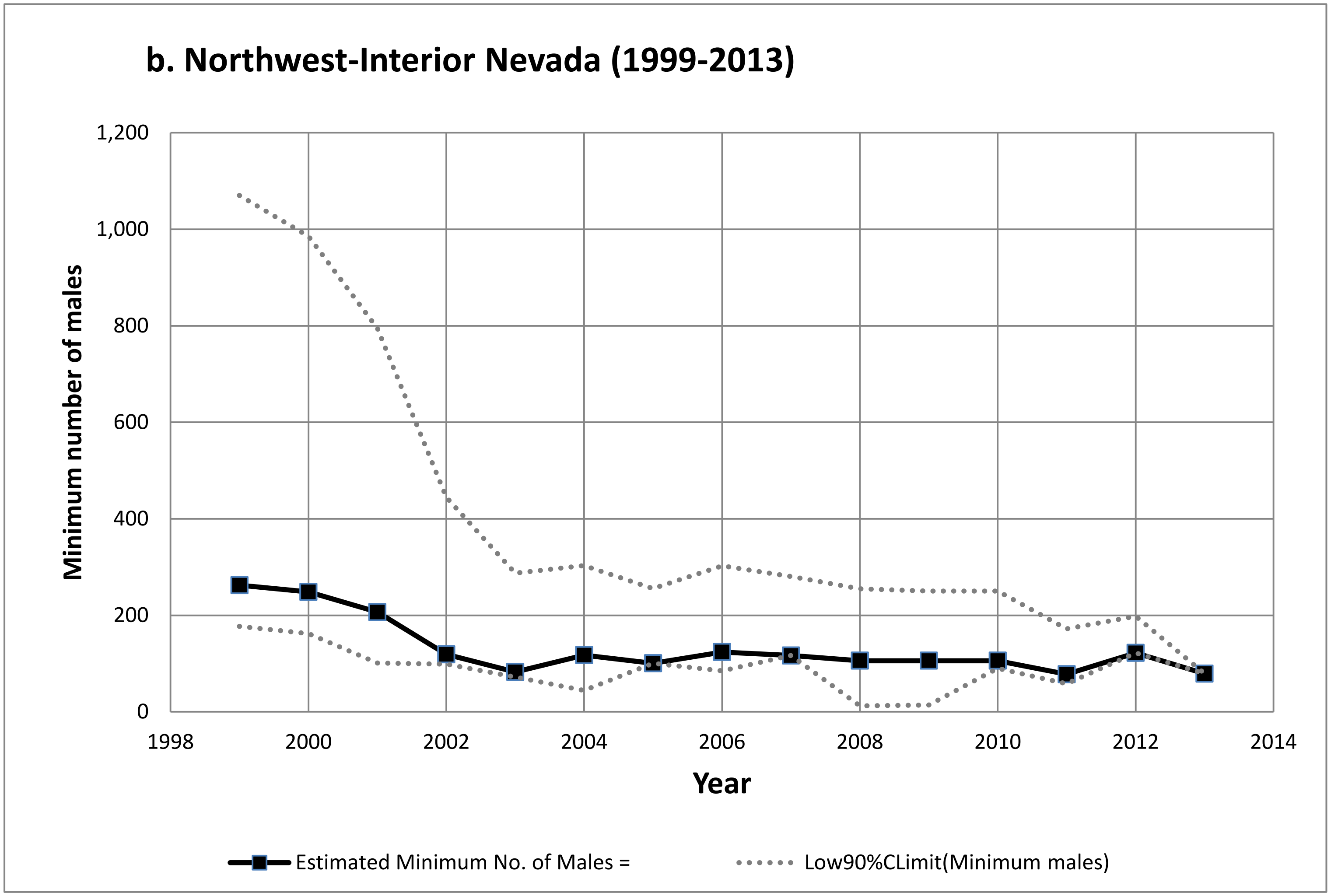
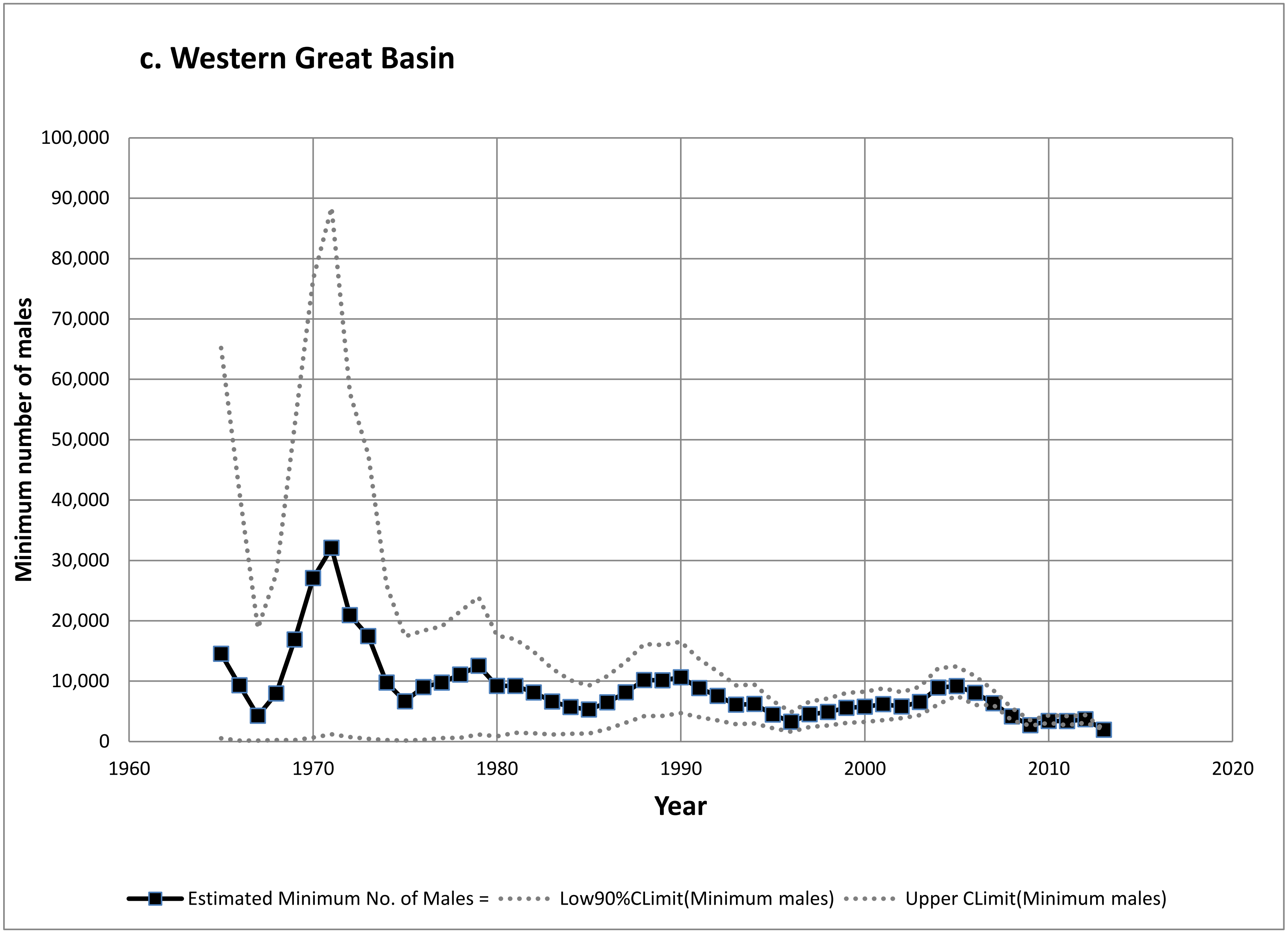

h. Snake River Plain Management Zone - SMZ IV
Minimum number of males
160,000
140,000
120,000
100,000
80,000
60,000
40,000
20,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

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
Minimum number of males
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)


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)

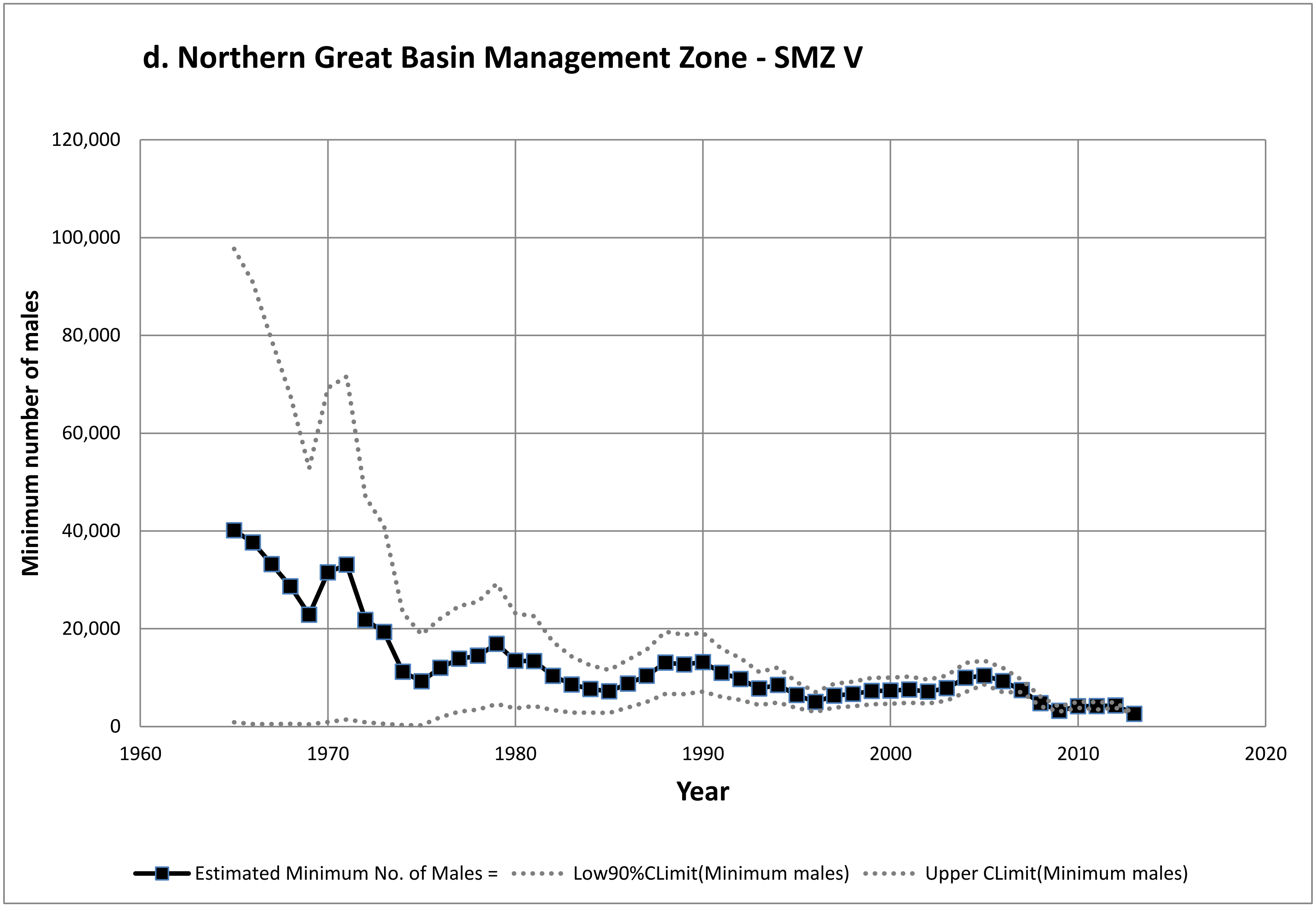
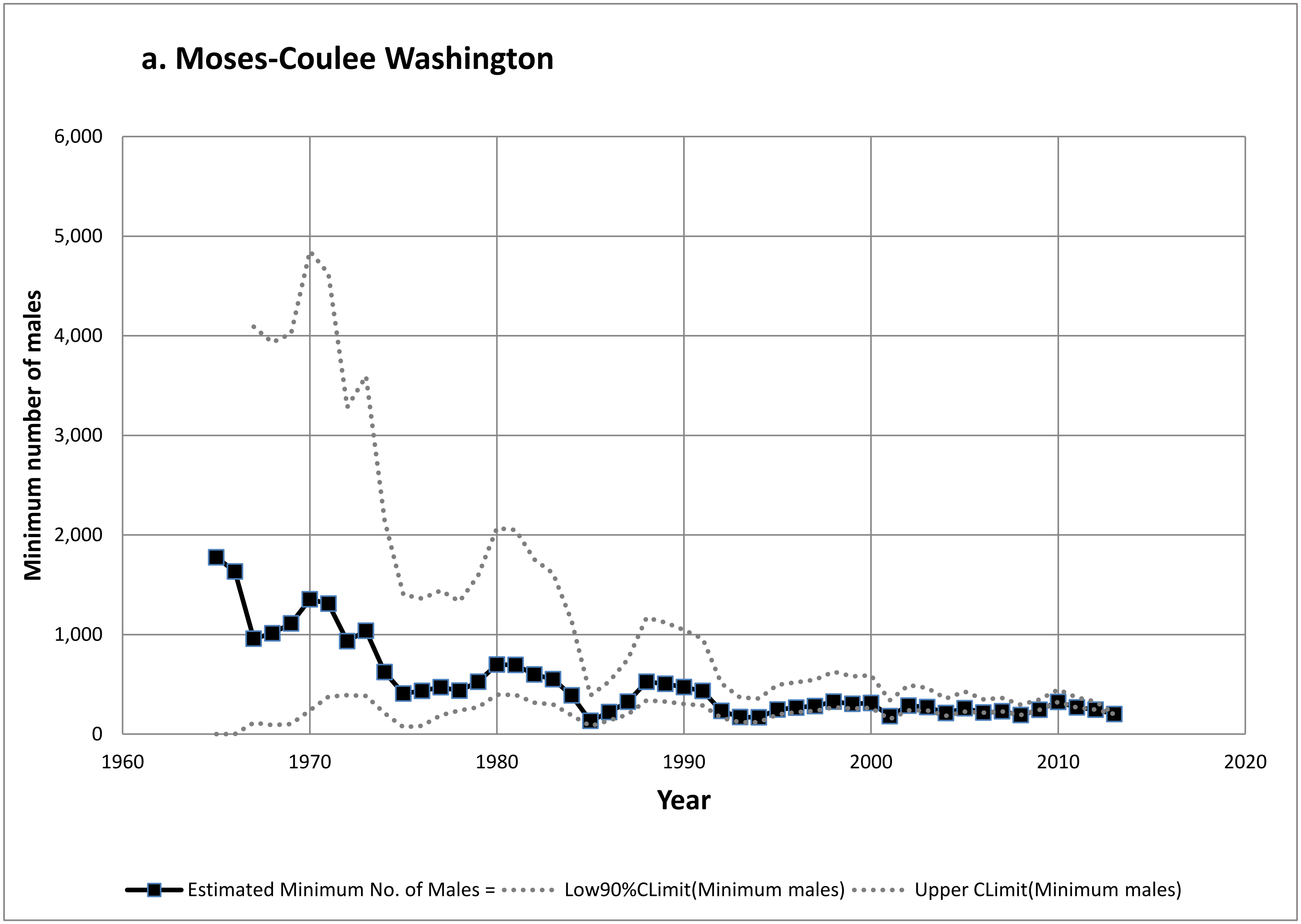
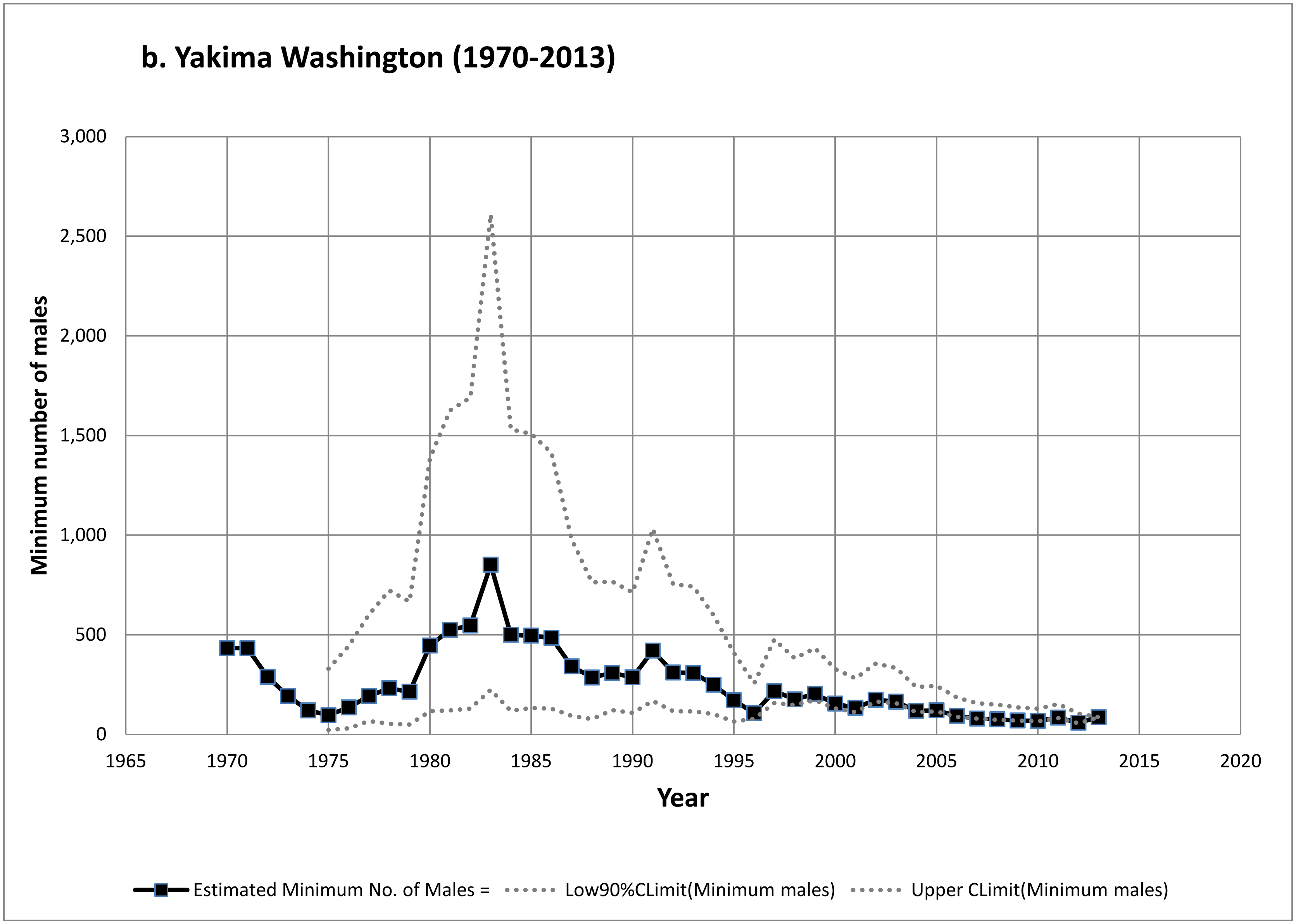

d. Northern Great Basin Management Zone - SMZ V
Minimum number of males
120,000
100,000
80,000
60,000
40,000
20,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

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)

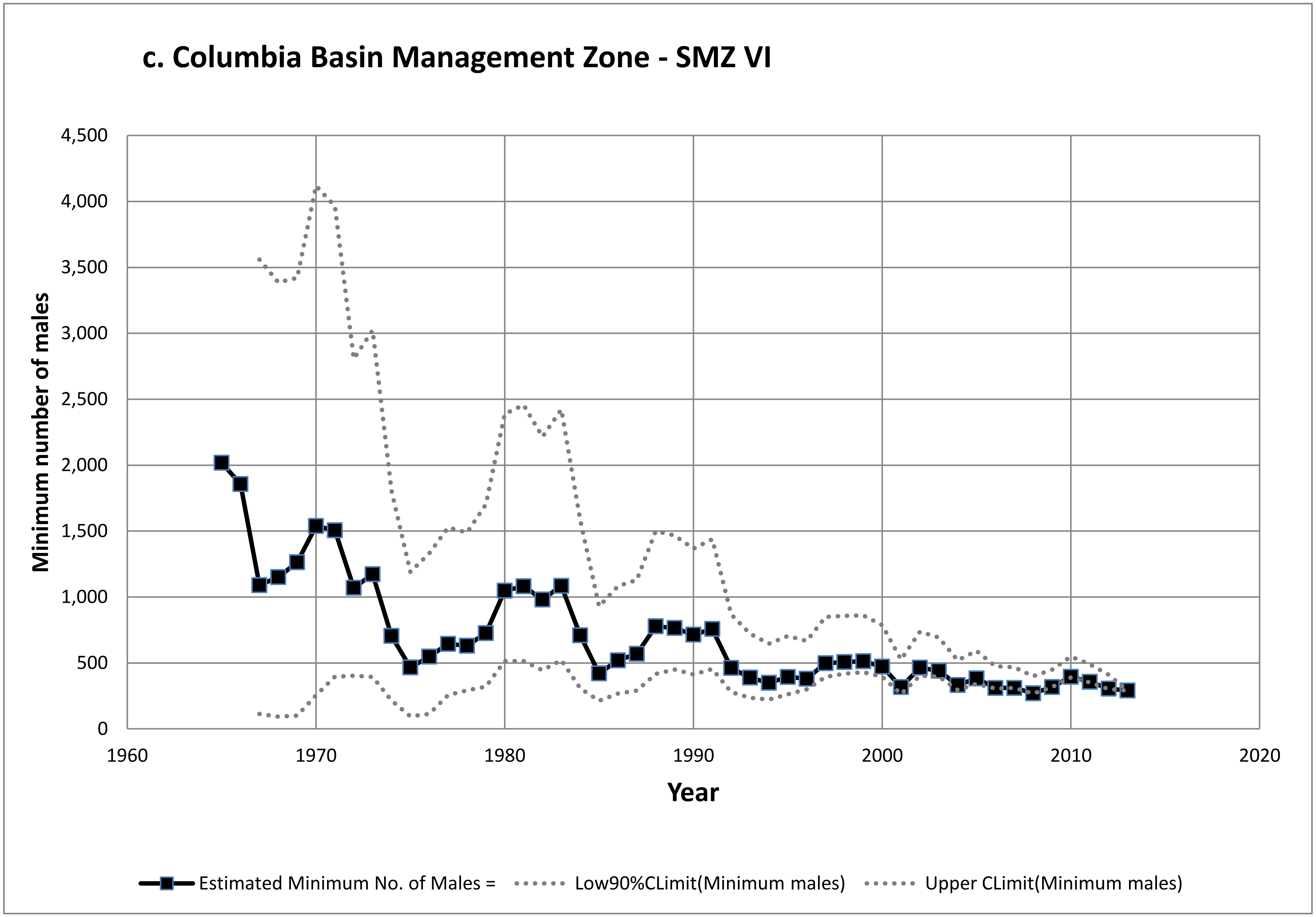

c. Columbia Basin Management Zone - SMZ VI
4,500
4,000
3,500
3,000
2,500
2,000
1,500
1,000
500
0
Minimum number of males
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

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.

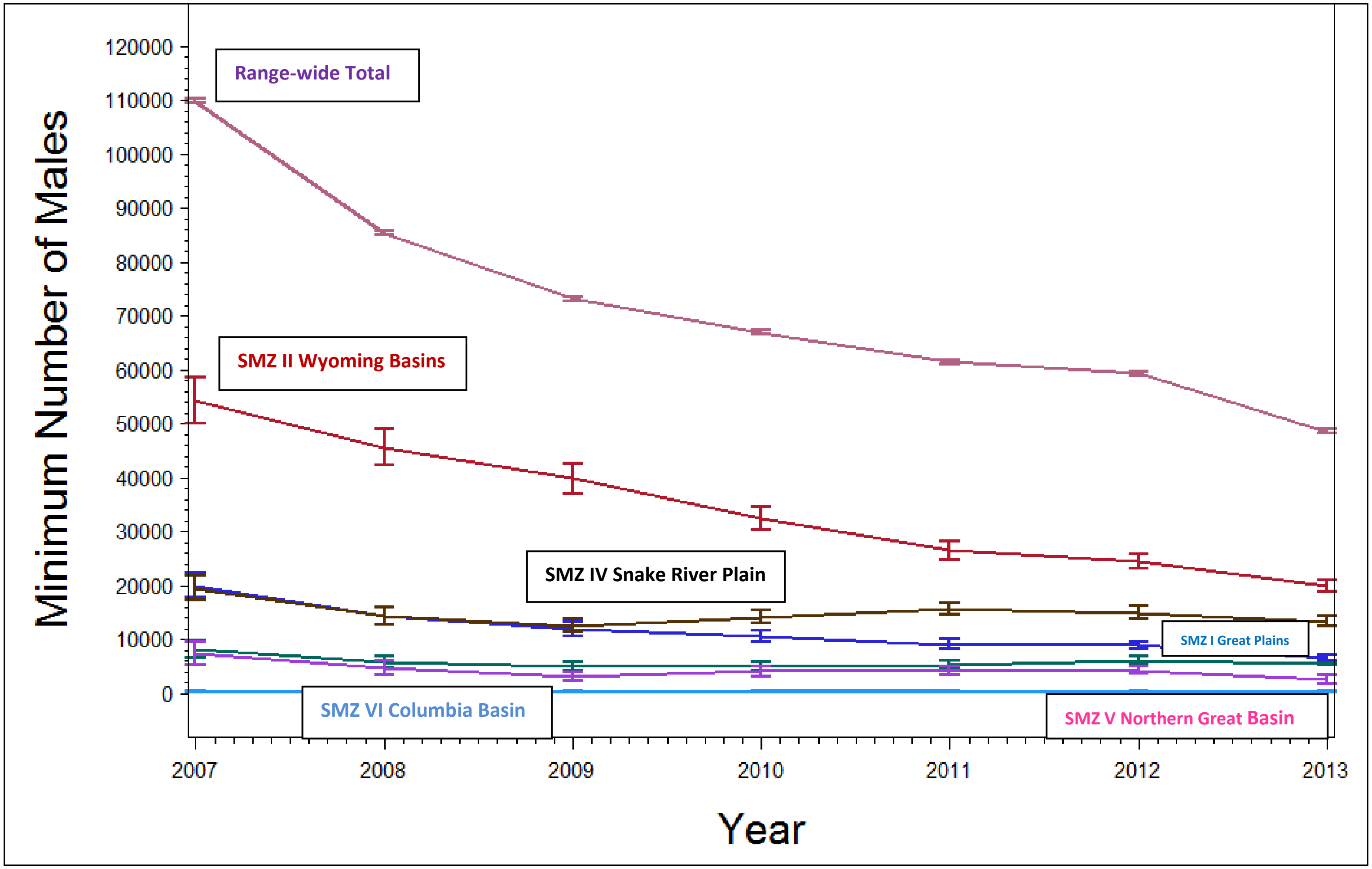


Figure 9. Population reconstruction for range-wide population of Greater Sage-Grouse from combining total estimates across all Sage-Grouse Management Zones I-VI.

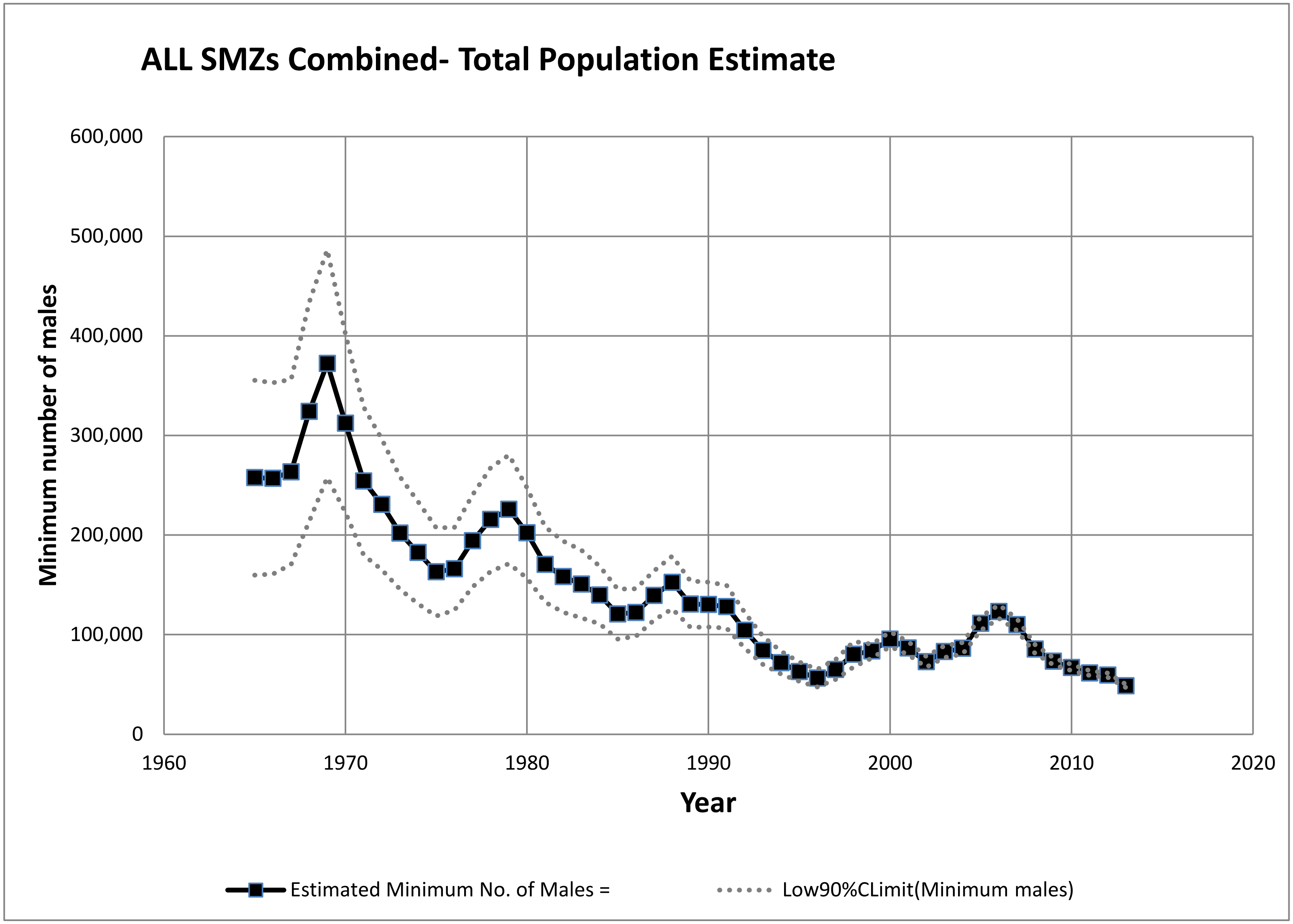
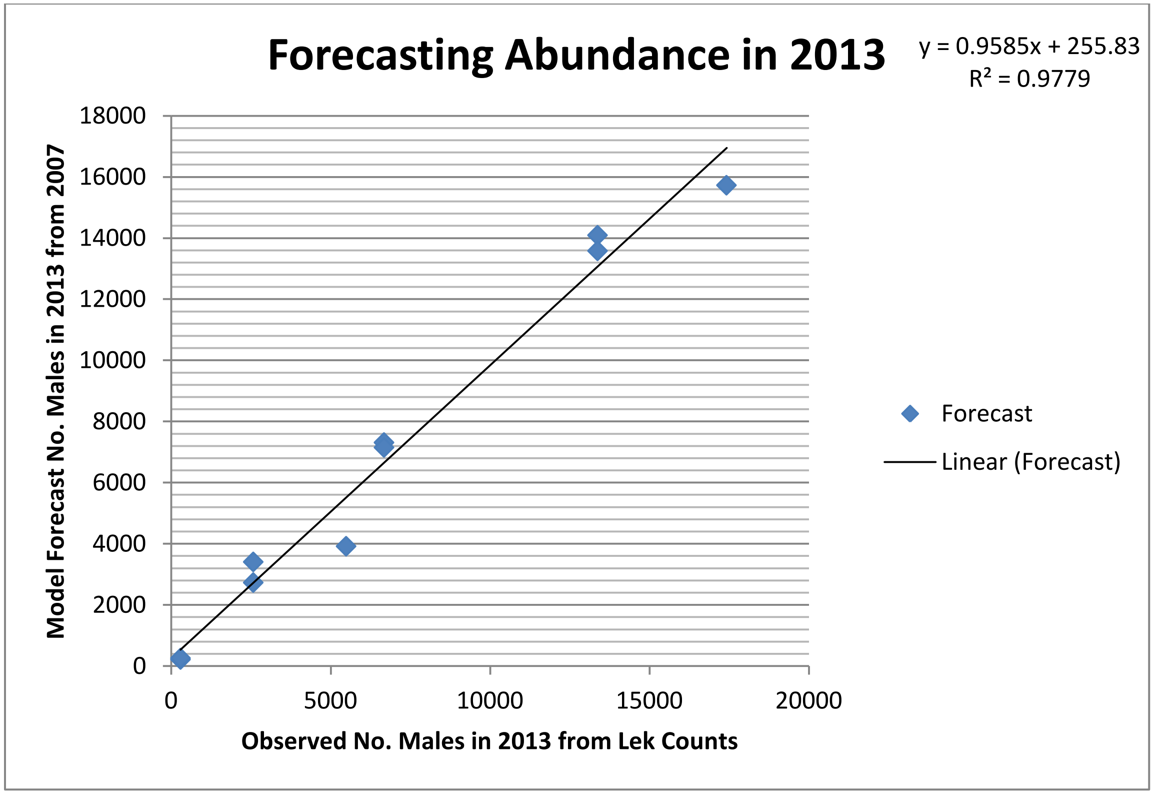


Figure 10. Validation of model predictions by comparing observed abundance in 2013 to forecasts of best models for 2013 estimated from mean rates of change forecast from 2007 to 2013. Note that predictions were tested from the 10 best models in Appendix 2 for all management zones except Colorado Plateau.



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VEGETATIONAL COVER AND PREDATION OF SAGE GROUSE NESTS IN OREGON

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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.

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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.

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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 ≥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 temporal 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.

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A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats

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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

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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 considered 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:

$$d = \frac{\overline{X}^E - \overline{X}^c}{S} J$$

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 (χ^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

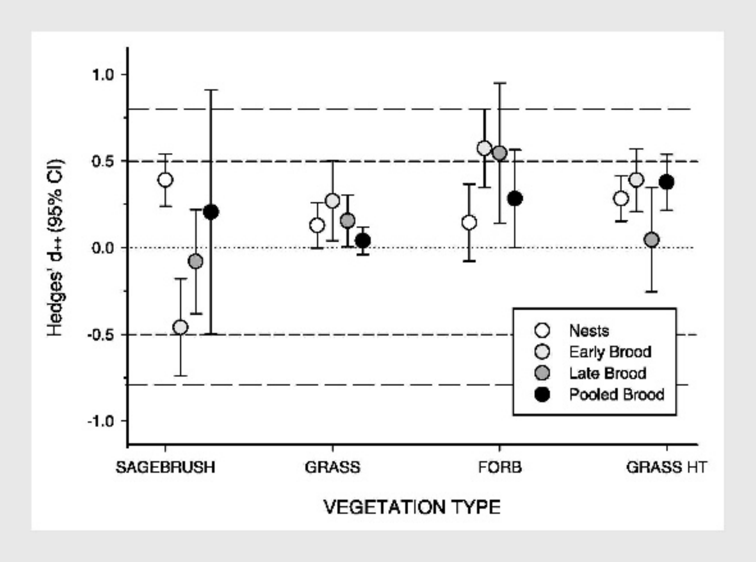

Figure 1. Cumulative effect sizes (d_{++}) by vegetation types and across nesting and brood-rearing habitats. Long-dashed lines indicate large ($d > 0.8$), small-dashed lines indicate medium ($0.8 \geq d > 0.5$), and dotted line indicates small ($0 < d < 0.5$) effects. Significant positive and negative 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 ($d = 0.37\text{-}0.74$) of selection for vegetation characteristics, with greater sagebrush cover for nest concealment and forb cover for females with broods. There were smaller effects ($d \sim 0.2$) 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 ≥ 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.

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GREATER SAGE-GROUSE (*Centrocercus urophasianus*) POPULATION RESPONSE TO NATURAL GAS FIELD DEVELOPMENT IN WESTERN WYOMING

by
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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.

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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.

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CHAPTER 1

Greater Sage-grouse Population Response to Natural Gas Development in Western Wyoming: Are Regional Populations Affected by Relatively Localized Disturbance?

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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:

$$\lambda = [(Initiate \times Success \times Brood) \times ♂Chick] + (♂\ Annual\ Survival)$$

Where λ 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).

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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 (χ^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$_{\mathrm{df}}$, 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 [1st 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 λ 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 [$\text{Overall\_Change} = -0.73+0.66(e^{-0.47(\text{Well\_Density3})})$; $R^2 = 61.1\%$]. 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 1st 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 λ 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.

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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
$P_1(1\text{-}B_2)$	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
$P_{2Y}(1\text{-}B_A)$	Survival (2nd year)[b]	0.024	0.024	0.005	0.027	0.017	0.027	0.017	0.012
$P_{2N}(1\text{-}B_A)$	Survival (2nd year)[c]	0.007	0.059	0.001	0.073	0.063	0.073	0.006	0.002
$P_{AY}(1\text{-}B_A)$	Survival (adult)[b]	0.076	0.118	0.015	0.086	0.118	0.085	0.061	0.026
$P_{AN}(1\text{-}B_A)$	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

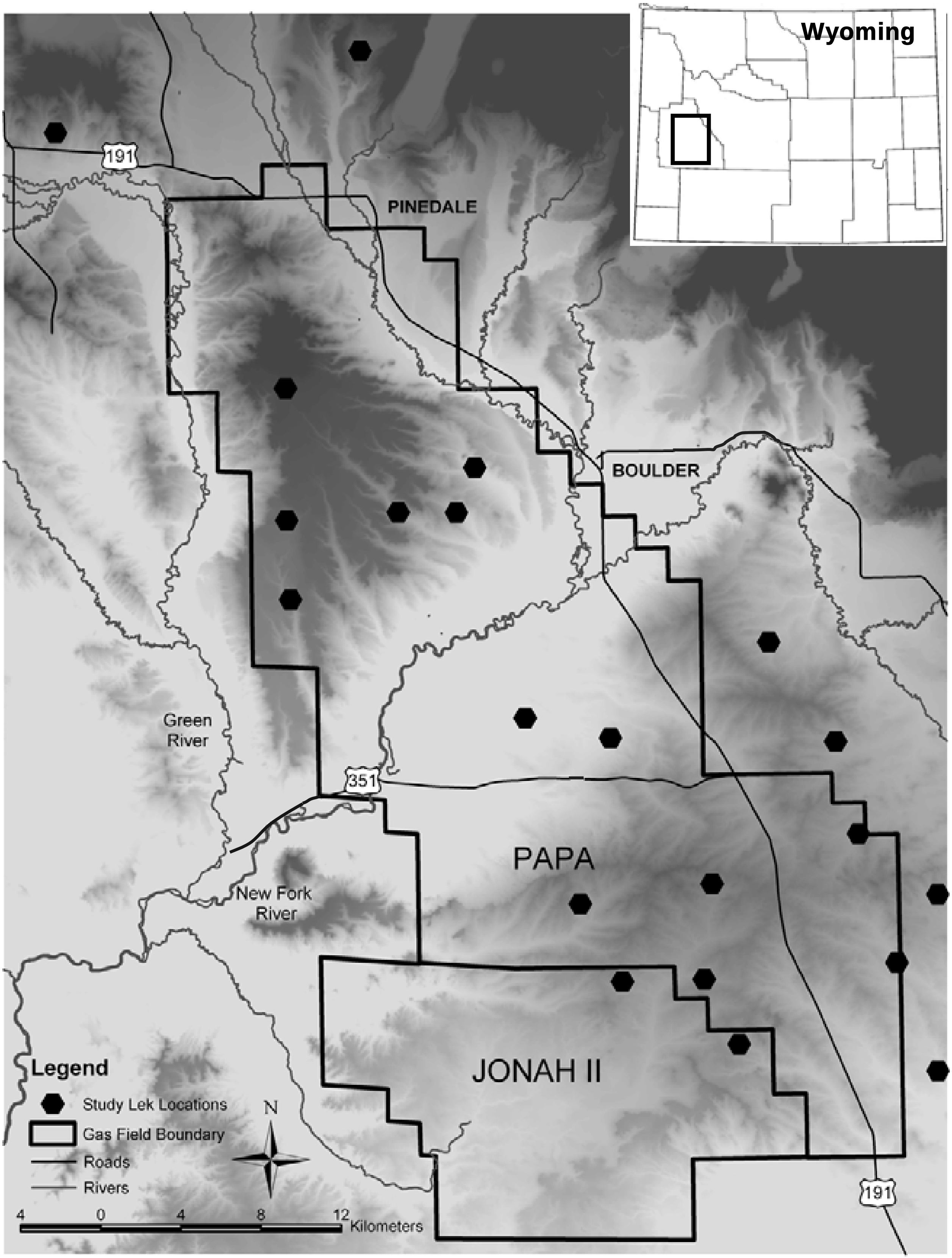

Wyoming
191
PINEDALE
BOULDER
Green River
351
PAPA
New Fork River
JONAH II
191
Legend
Study Lek Locations
Gas Field Boundary
Roads
Rivers
N
4 0 4 8 12 Kilometers

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

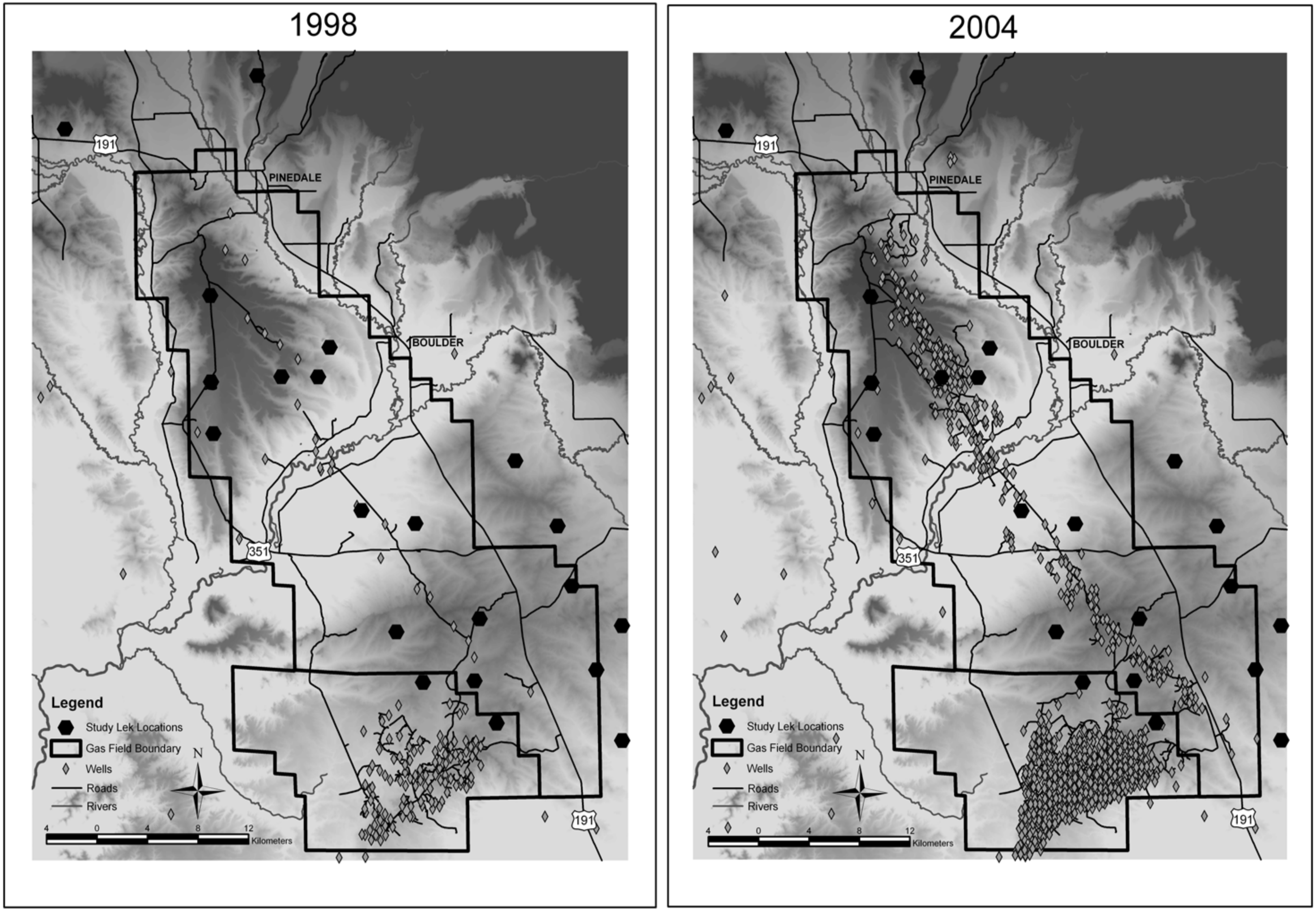
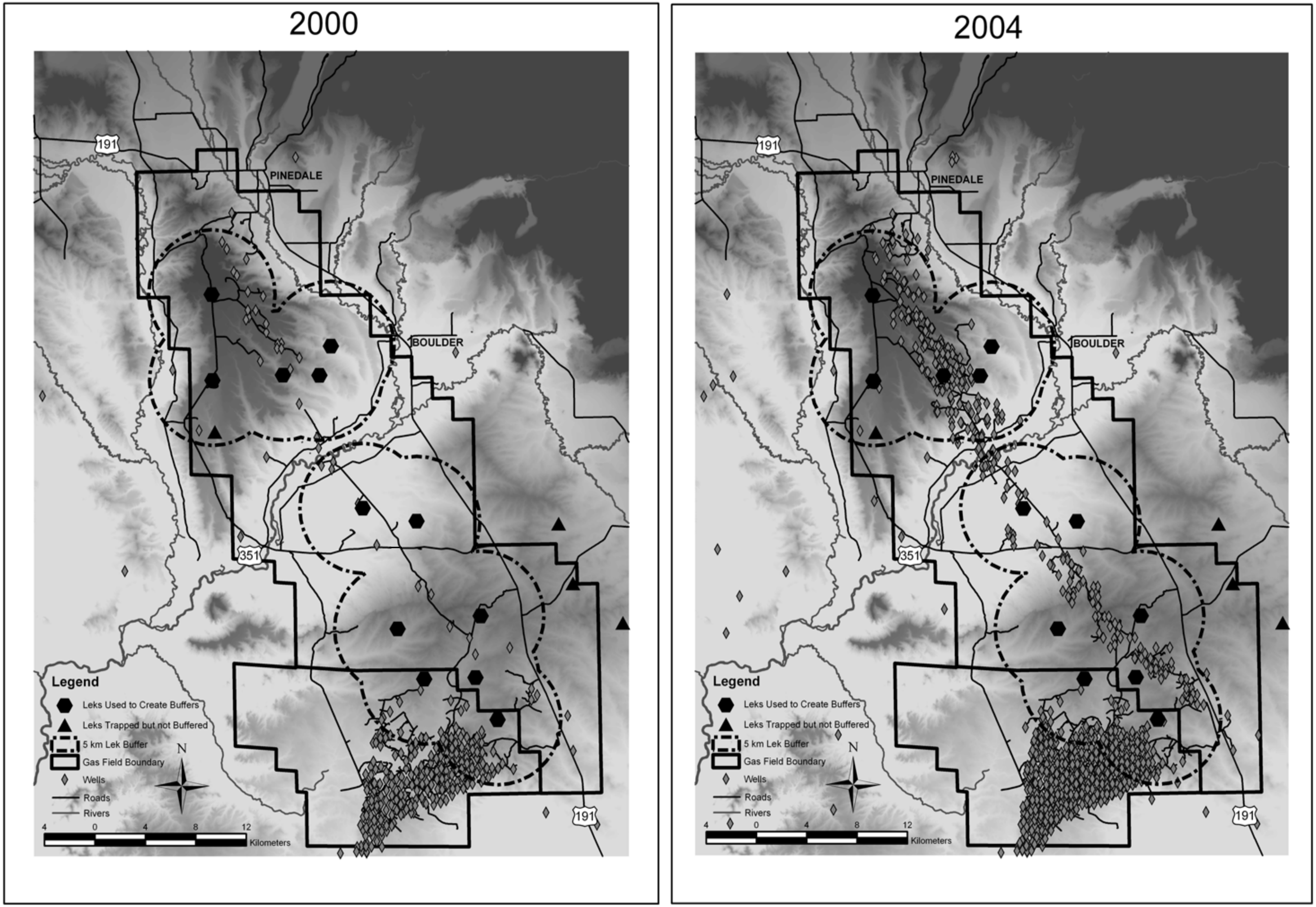

1998
191
PINEDALE
BOULDER
351
191
Legend
Study Lek Locations
Gas Field Boundary
Wells
Roads
Rivers
N
4
0
4
8
12
Kilometers
2004
191
PINEDALE
BOULDER
351
191
Legend
Study Lek Locations
Gas Field Boundary
Wells
Roads
Rivers
N
4
0
4
8
12
Kilometers

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
PINEDALE
BOULDER
191
351
191
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

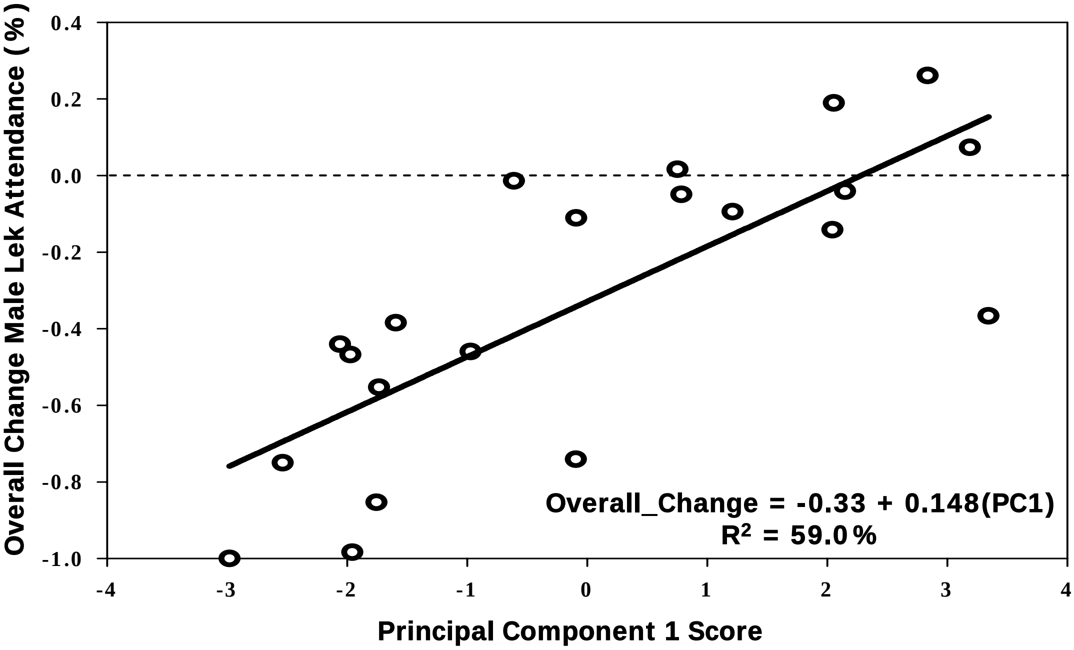

Overall Change Male Lek Attendance (%)
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-4
-3
-2
-1
0
1
2
3
4
Principal Component 1 Score
Overall_Change = -0.33 + 0.148(PC1)
R² = 59.0%

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

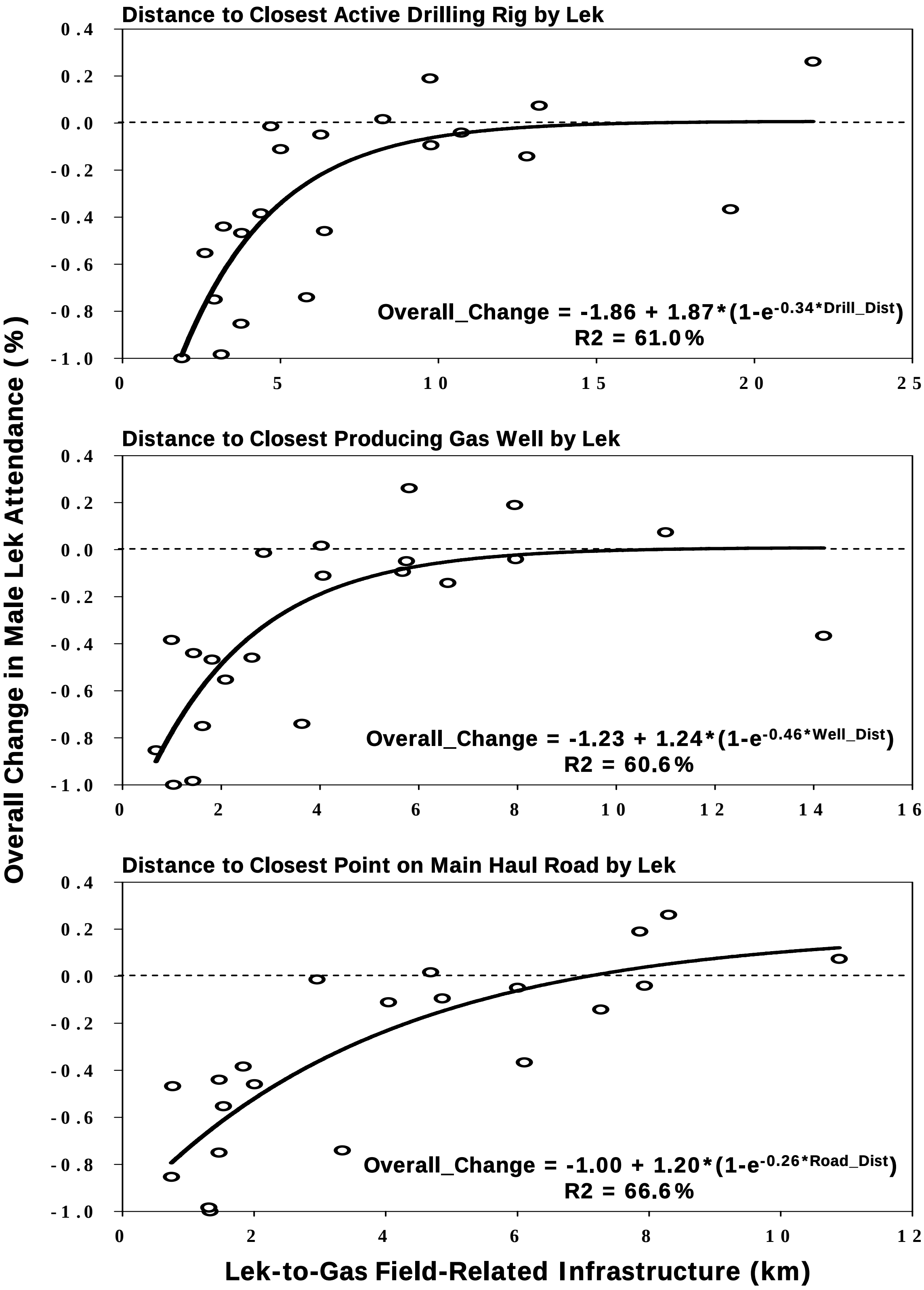
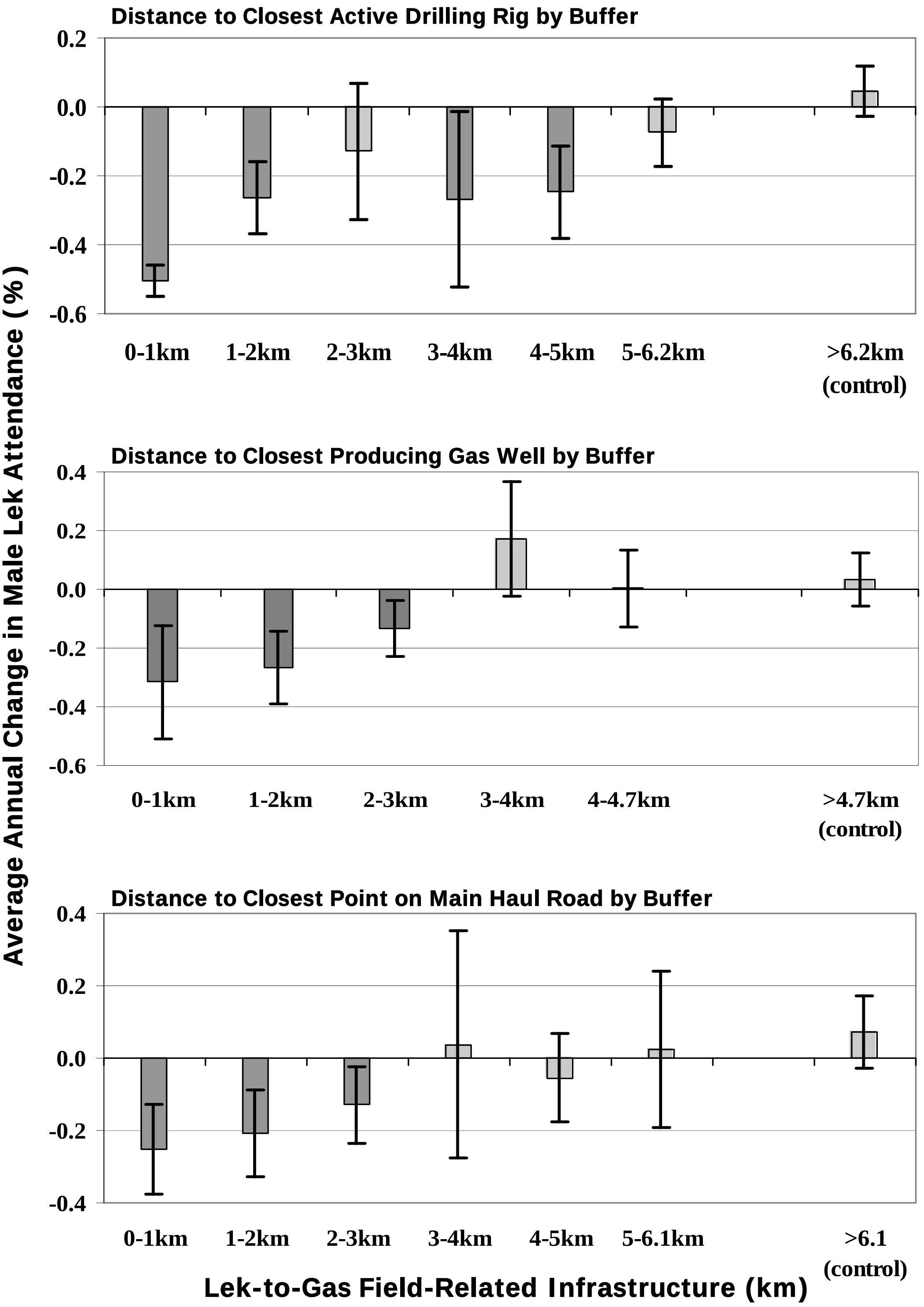

Distance to Closest Active Drilling Rig by Lek
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
0
5
10
15
20
25
Overall_Change = -1.86 + 1.87*(1-e^{-0.34*Drill_Dist})
R2 = 61.0%
Distance to Closest Producing Gas Well by Lek
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
0
2
4
6
8
10
12
14
16
Overall_Change = -1.23 + 1.24*(1-e^{-0.46*Well_Dist})
R2 = 60.6%
Distance to Closest Point on Main Haul Road by Lek
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
0
2
4
6
8
10
12
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

Distance to Closest Producing Gas Well by Buffer

Distance to Closest Point on Main Haul Road by Buffer

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

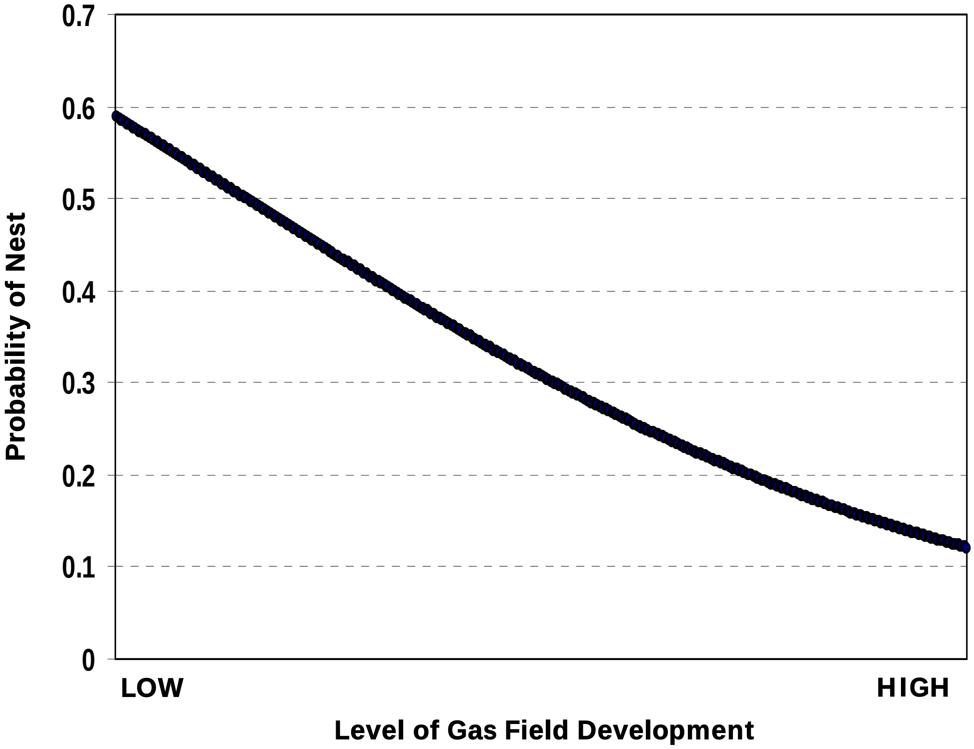
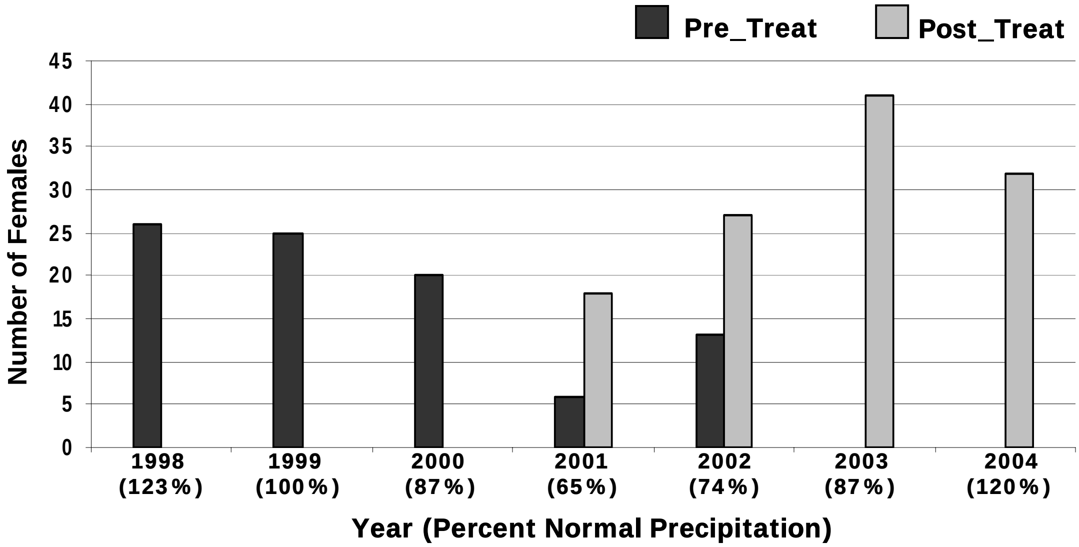

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Probability of Nest
LOW
HIGH
Level of Gas Field Development

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.

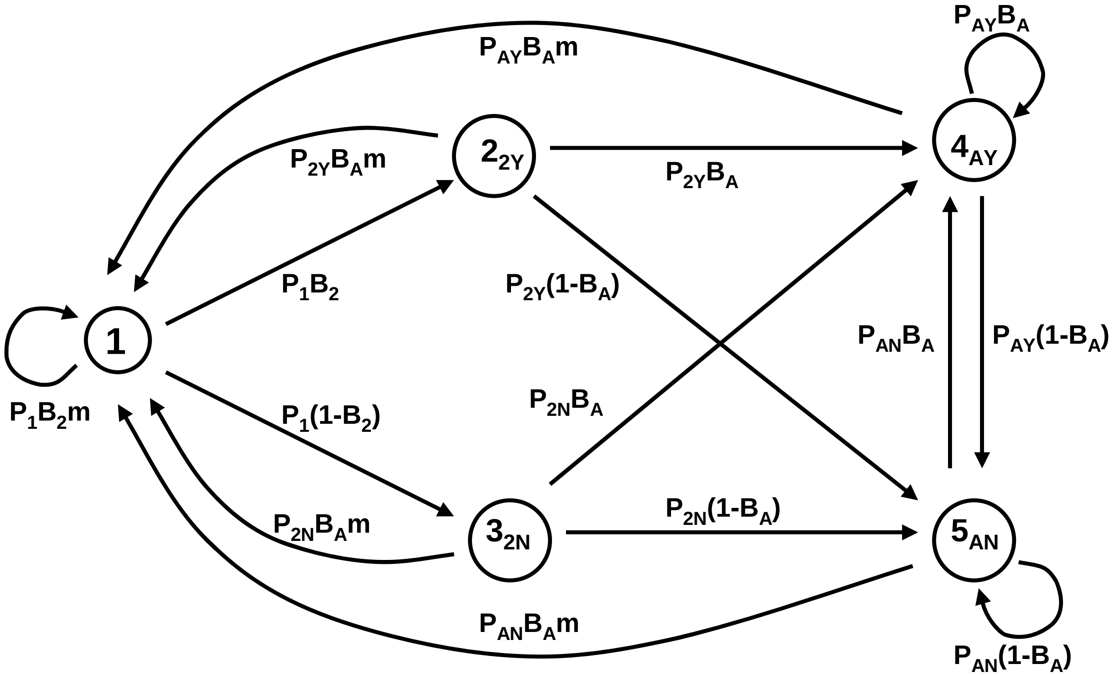
Figure 8



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

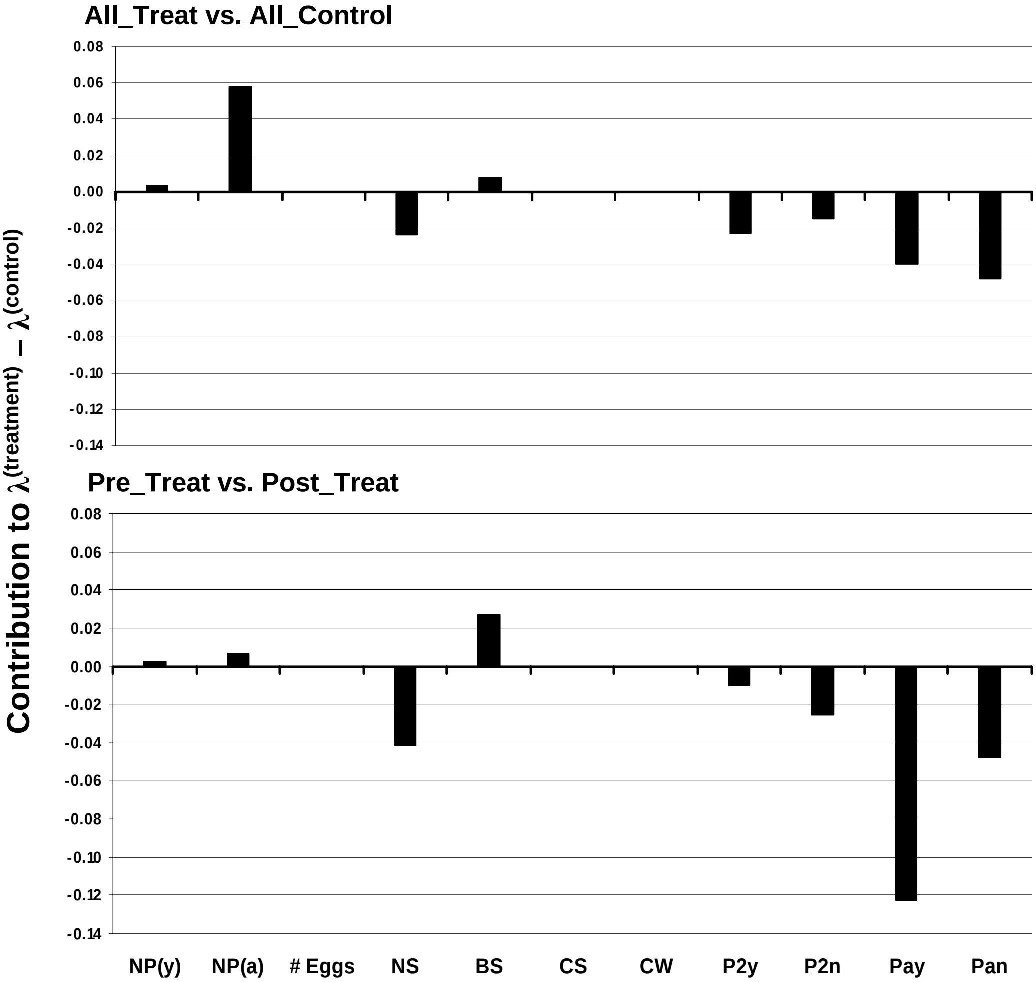
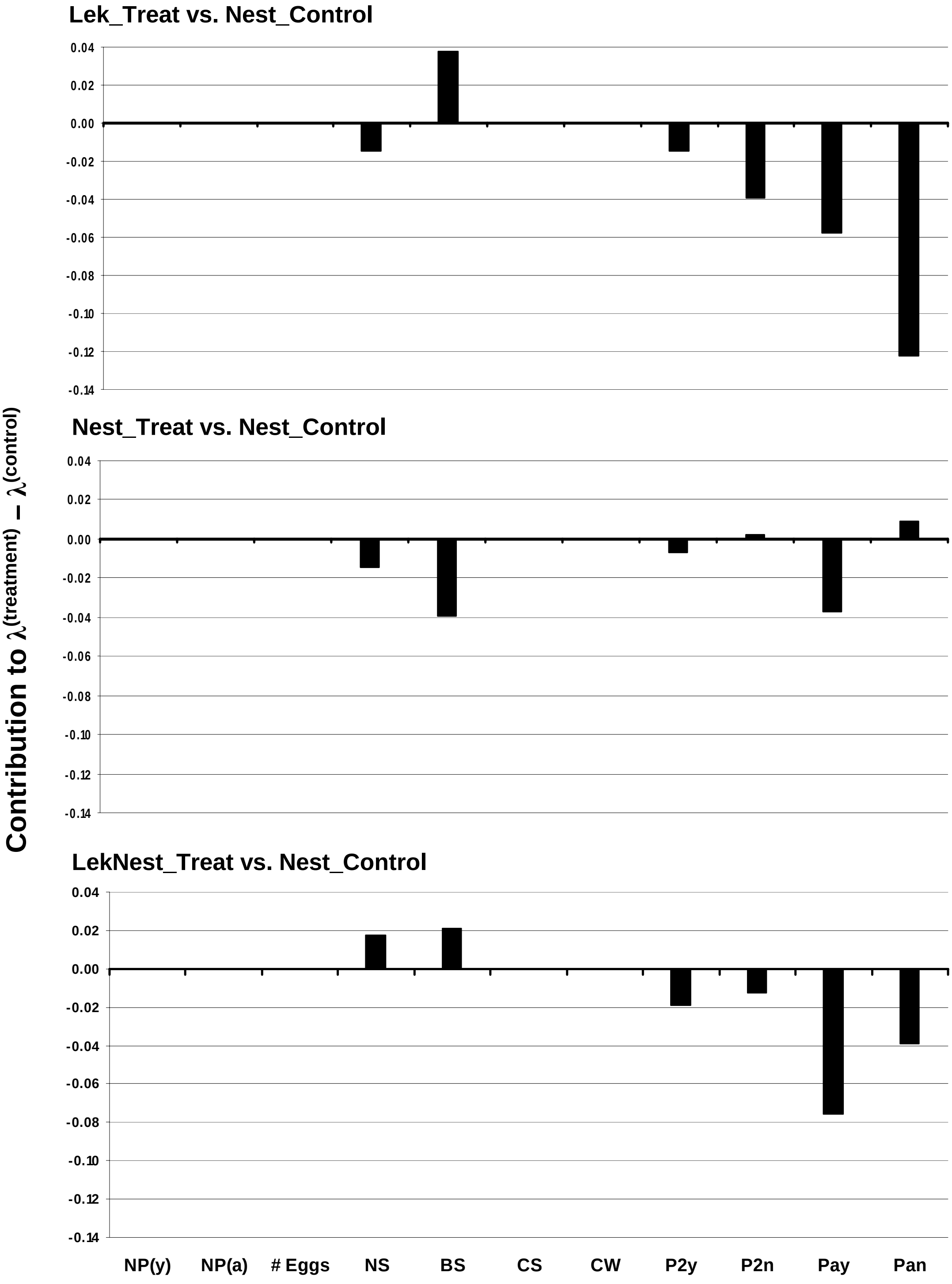

All_Treat vs. All_Control
0.08
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.12
-0.14
Pre_Treat vs. Post_Treat
0.08
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.12
-0.14
Contribution to $\lambda^{(treatment)} - \lambda^{(control)}$
NP(y)
NP(a)
# Eggs
NS
BS
CS
CW
P2y
P2n
Pay
Pan

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

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.

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APPENDIX A

Abridged Title. Greater Sage-Grouse Nest Distribution

SPATIAL DISTRIBUTION OF GREATER SAGE-GROUSE NESTS IN RELATIVELY CONTIGUOUS SAGEBRUSH HABITATS

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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 (2nd year successful median = 382 m, $n = 27$; 2nd year unsuccessful median = 415 m, $n = 41$; $U = 625$; $P = 0.37$) or for females whose first documented nest was unsuccessful (2nd year successful median = 497 m, $n = 15$; 2nd 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.

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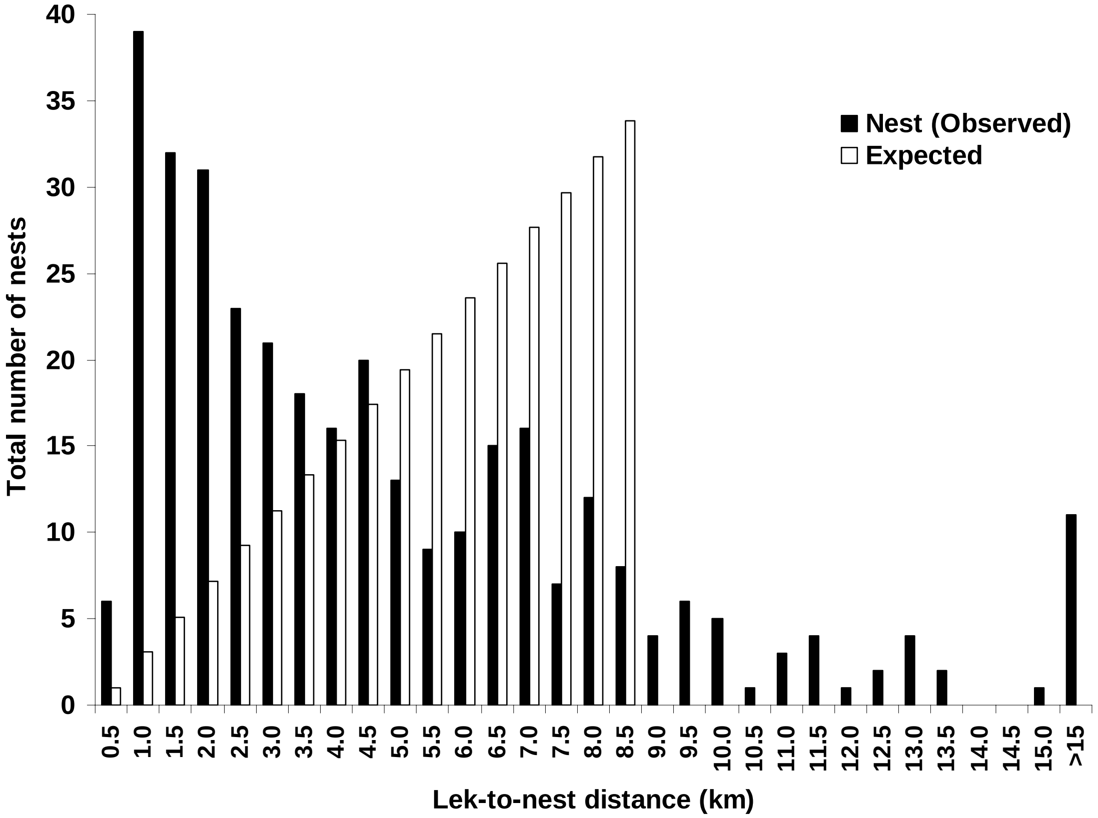
FIGURE 1. Distribution of Greater Sage-Grouse nests (*n* = 340) based on lek-of-capture to nest distances in central and western Wyoming, 1994-2003 and expected numbers assuming uniformly distributed nests (*n* = 296) within 8.5 km of a lek.



40
35
30
25
20
15
10
5
0
Total number of nests
■ Nest (Observed)
☐ Expected
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
Lek-to-nest distance (km)

APPENDIX B

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RH: Sage-grouse early brooding

GREATER SAGE-GROUSE EARLY BROOD-REARING HABITAT USE AND PRODUCTIVITY IN WYOMING

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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., ΔAIC_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.

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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 ΔAIC$_c$ $\leq$2 are presented.

Model[a]	K[b]	ΔAIC$_c$ [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 $\geq$3 cm and $\leq$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

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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).

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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 20th 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 20th 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 4th 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 2nd 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 20th 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 2nd and 3rd 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 ≥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 4th 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.

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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.

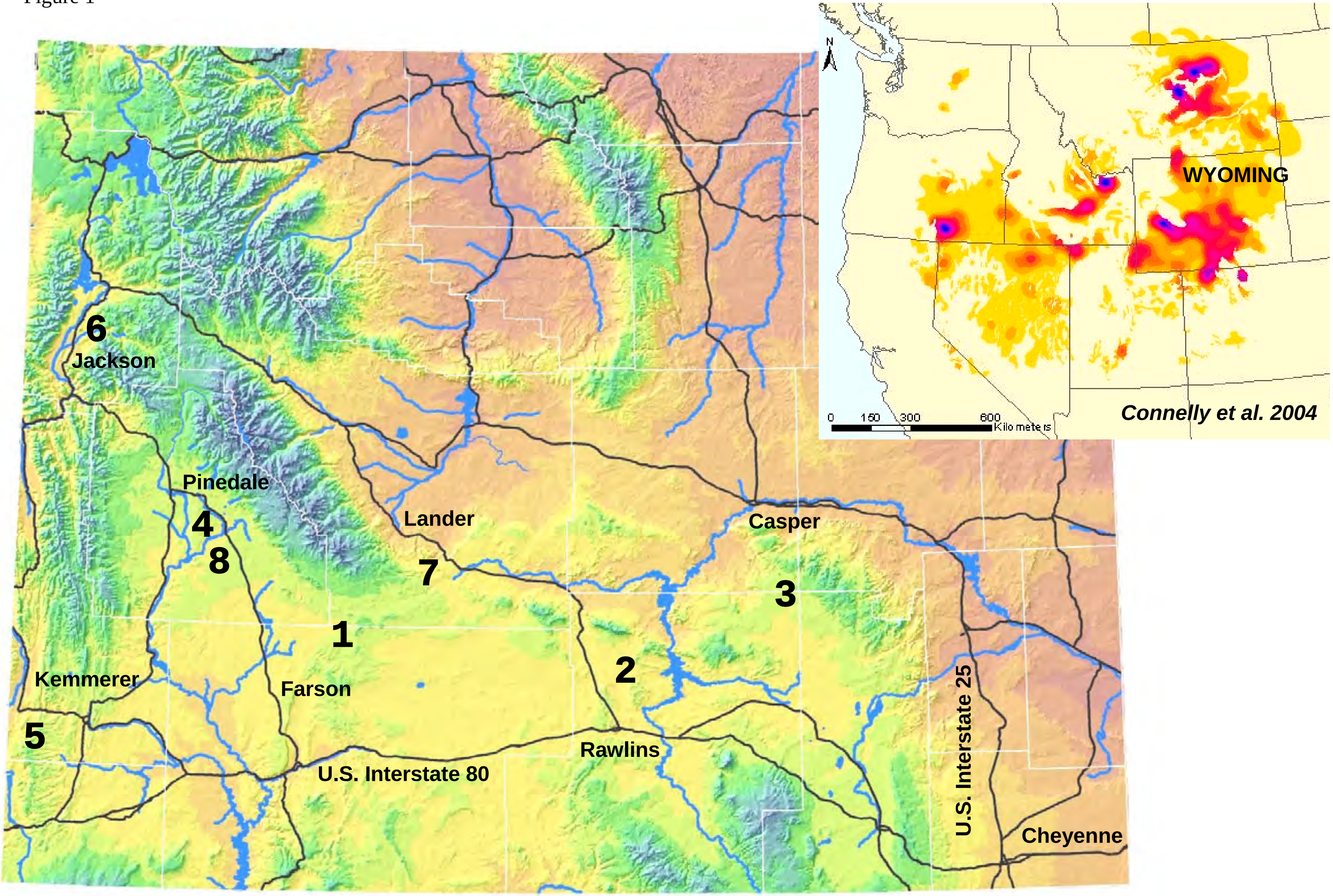
Study Area	Year	n[a]	Nesting Propensity	Nesting Success	Brooding Success	Chicks per Female[b]
Farson	1994	29	24/29 (83%)	9/24 (38%)	4/9 (44%)	8/29 (0.28)
	1995	41	33/37 (89%)	9/36 (25%)	8/9 (89%)	24/37 (0.65)
	1996	25	21/24 (88%)	11/23 (48%)	10/11 (91%)	38/24 (1.58)
Rawlins	1996	24	19/23 (83%)	15/19 (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



WYOMING
Connelly et al. 2004
0 150 300 600 Kilometers
N
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

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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 ≤ 9 ([36 PPM/60 sec] × 15) and for 45 PPM transmitters ≤ 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.

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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.

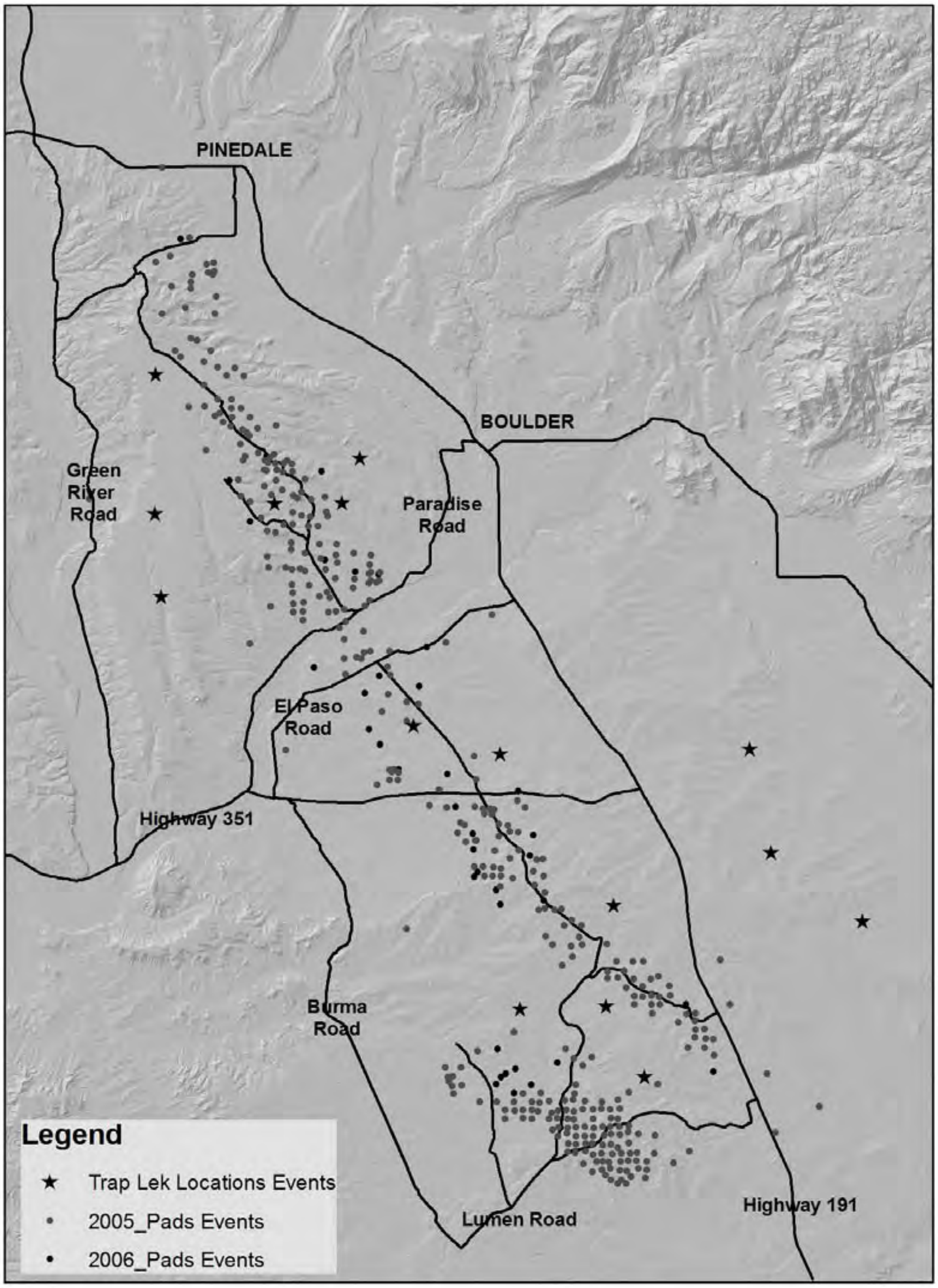


Figure 2. Yearling greater sage-grouse study location in southwestern Wyoming, 2005-06. The figure illustrates producing well pads and main haul roads present during the breeding seasons of 2005 and 2006; well pads within 5 km of trapped leks are included. Natural gas field infrastructure were buffered 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).

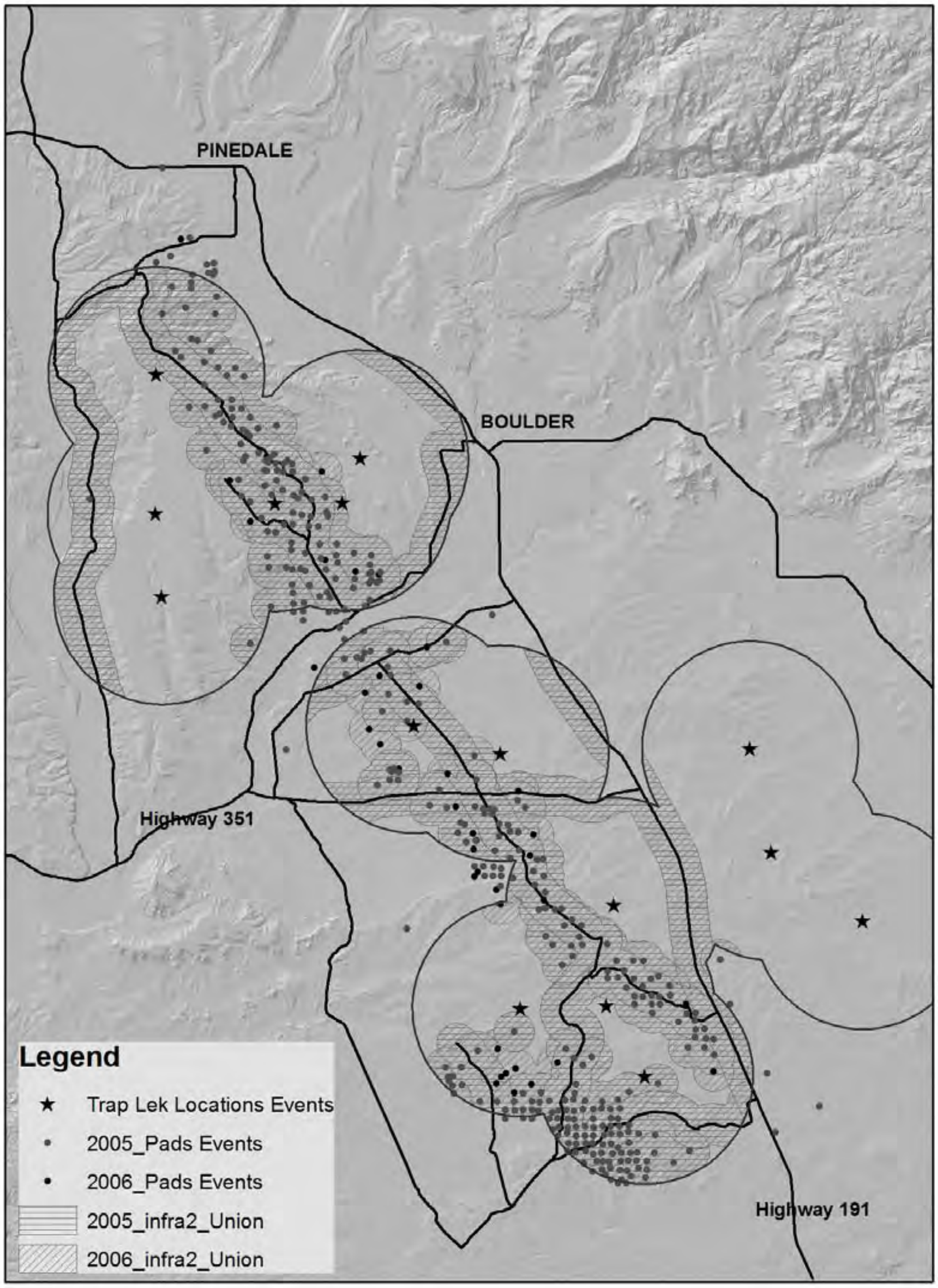
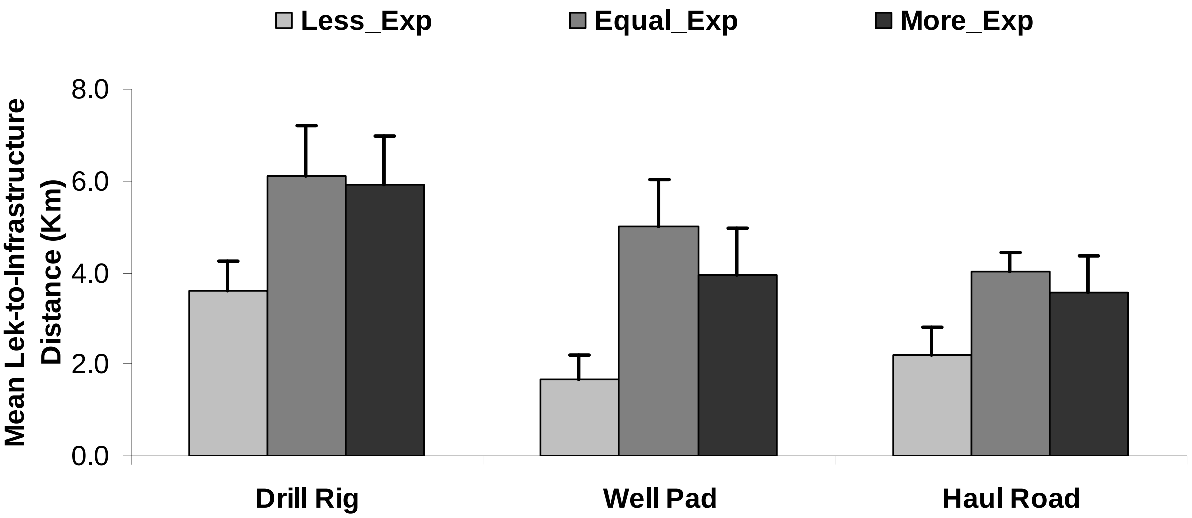


Figure 3. Mean (standard error) distances (km) from greater sage-grouse leks to natural gas field infrastructure in southwestern Wyoming, 2005-06. Leks were categorized as recruiting significantly less than, equal to, or more than expected numbers of males based on Chi-squared analyses of annual changes in the maximum number of males documented on leks during lek count procedures.



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Research Article

Winter Habitat Use of Greater Sage-Grouse Relative to Activity Levels at Natural Gas Well Pads

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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

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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

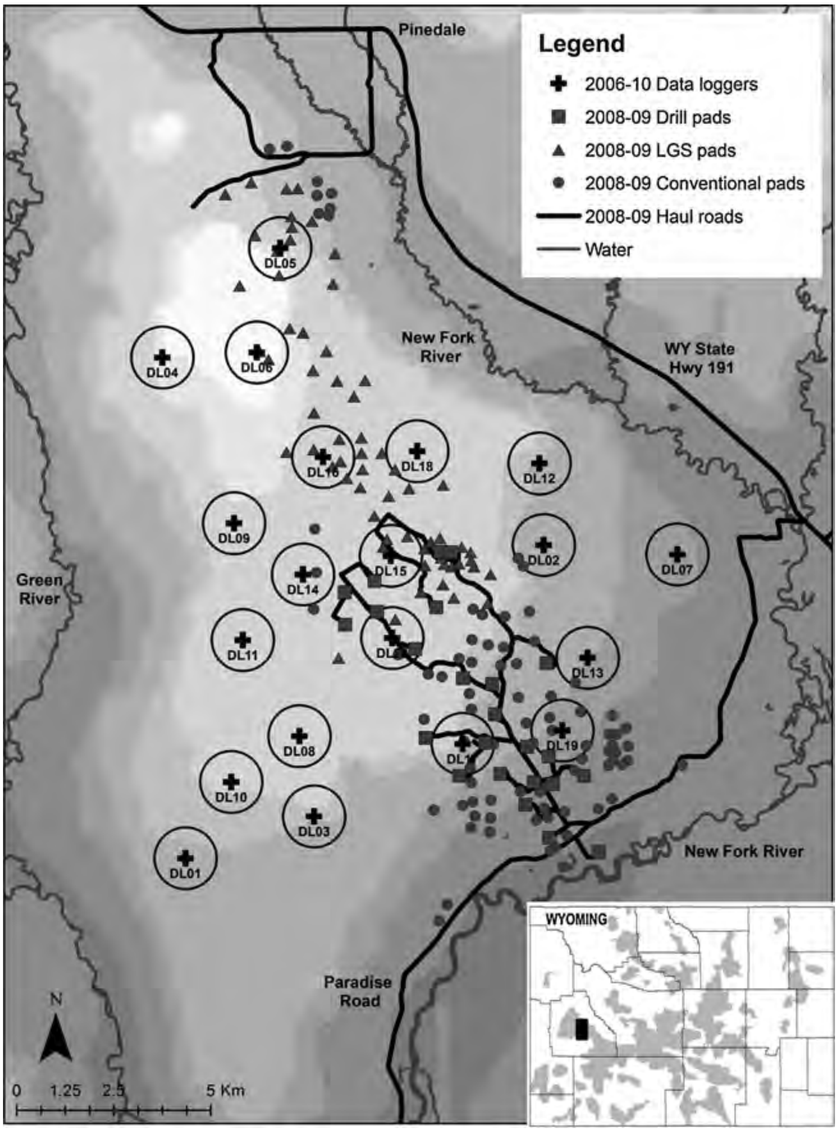

Figure 1. Data logger station locations and 0.8-km radius buffers generally delineating the area monitored by each station for radio-equipped greater sage-grouse on the Pinedale Mesa in Sublette County, Wyoming, 2005–2006 through 2009–2010 winters. Natural gas field infrastructure, including well pads 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 × 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 $>2\ \Delta\mathrm{AIC}_c$ 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 $\Delta\mathrm{AIC}_c$ 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.

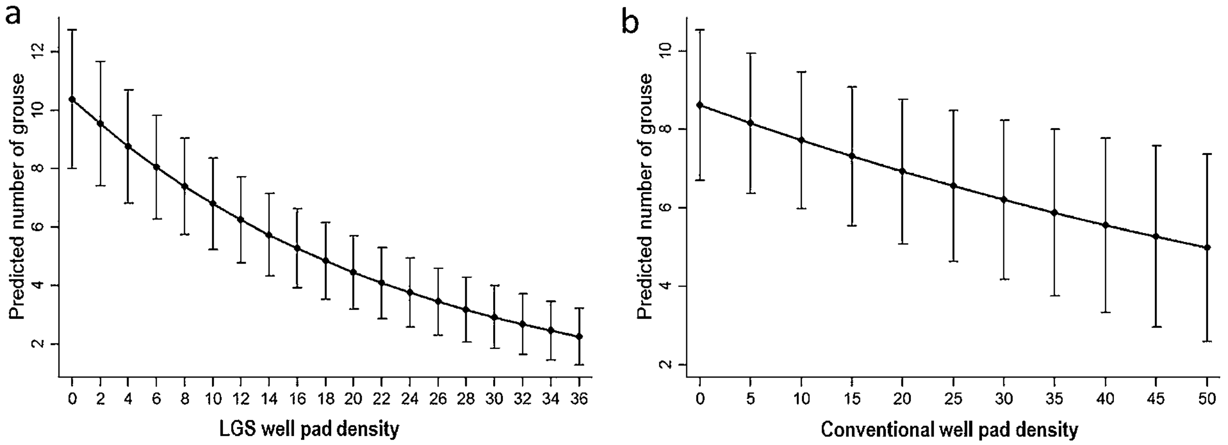

Figure 2. Predicted marginal effects (95% CI) of the density (no. of well pads within a 2.8-km radius of data logger stations) of a) well pads with off-site liquid gathering systems (LGS) and b) well pads with liquids gathered conventionally on the predicted number of sage-grouse visiting a location 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 ≥ 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.

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CHAPTER EIGHT

Nesting Success and Resource Selection of Greater Sage-Grouse

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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.

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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.).

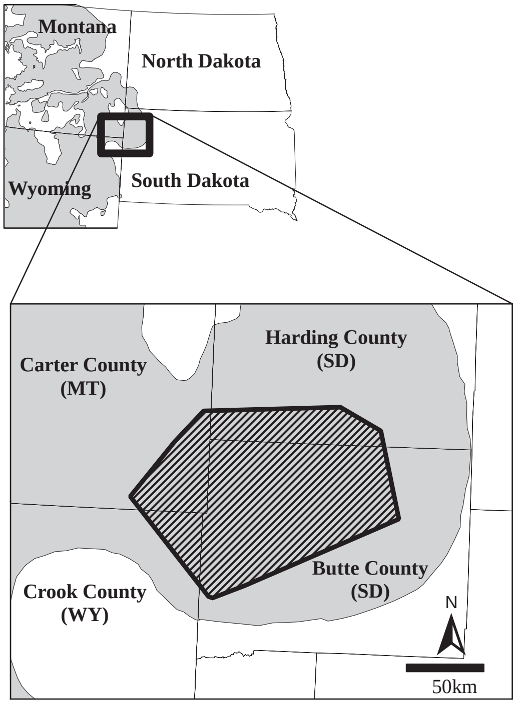

Figure 8.1. Location of study area for Greater Sage-Grouse in Butte, Carter, Crook, and Harding counties, 2006–2007. The hatched area encompasses all locations; the gray area is the current range of Greater Sage-Grouse (Schroeder et al. 2004).

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 ($\mathrm{AIC_c}$) to evaluate models (Burnham and Anderson 2002). We ranked our models based on differences between $\mathrm{AIC_c}$ for each model and the minimum $\mathrm{AIC_c}$ model ($\Delta\mathrm{AIC_c}$), and Akaike weights (w_i) to assess the weight of evidence in favor of each model and the sum $\mathrm{AIC_c}$ weight for each variable (Beck et al. 2006). In addition, we investigated the slope of the coefficient estimates (β) 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 $\Delta AIC_c < 2.0$.

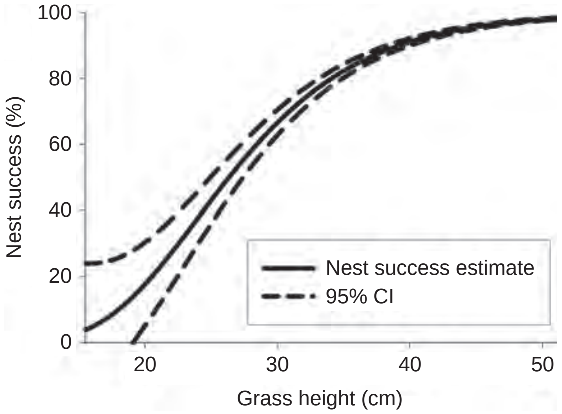

Figure 8.2. Effect of grass height on nest success of Greater Sage-Grouse in northwestern South Dakota, 2006–2007. Nest success estimates were derived from back-transformed beta estimates included in top model. Confidence intervals estimated from the delta method (Seber 1982).

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 ≥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.

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NESTING AND BROOD-REARING SUCCESS AND RESOURCE SELECTION OF GREATER SAGE-GROUSE IN NORTHWESTERN SOUTH DAKOTA

BY

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A thesis submitted in partial fulfillment of the requirements for the

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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

David W. Willis 4/14/08

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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.

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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*).

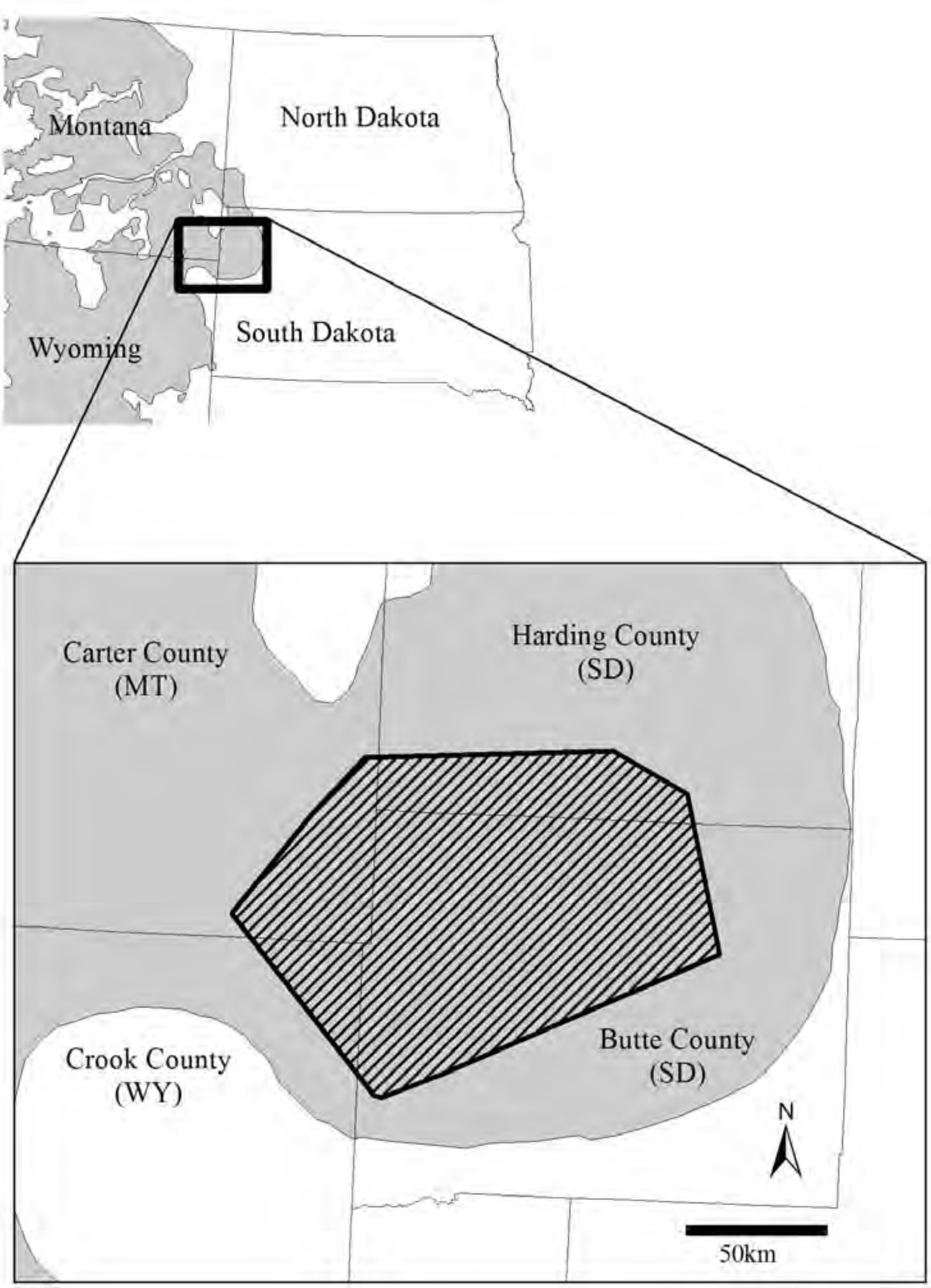

Figure 1. Study area of Butte, Carter, Crook, and Harding counties where we researched greater sage-grouse during 2006-2007. The dashed area encompasses all locations and the grayed area is current sage-grouse range (Schroeder et al. 2004).

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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 ($\beta = 0.15$ SE = 0.03) on nest success (Figures 5 & 6) and was present in all of the models considered. In contrast, litter cover negatively ($\beta = -0.08$ 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 ($\beta = 29.45$ SE = 40.35), and the 1-day lag effect negatively influenced nest success ($\beta = -1.89$ 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**		
	2006	**2007**		**2006**	**2007**		**Nest**	**Random**	
Variable	**(*n* = 34)**	**(*n* = 39)**	**P-value**	**(*n* = 35)**	**(*n* = 39)**	**P-value**	**(*n* = 73)**	**(*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 ± 2.8 *n* = 13	3 June ± 2.6 *n* = 13	7.9 ± 0.3 *n* = 26	10 May ± 1.5 *n* = 2	16 June ± 1.5 *n* = 2	7.3 ± 0.5 *n* = 4
2007	21 April ± 1.7 *n* = 17	29 May ± 1.5 *n* = 17	8.5 ± 0.2 *n* = 30	9 May ± 4.7 *n* = 3	12 June ± 3.2 *n* = 3	5.5 ± 0.9 *n* = 4
Avg.	24 April ± 1.6 *n* = 30	31 May ± 1.5 *n* = 30	8.3 ± 0.2 *n* = 56	9 May ± 2.6 *n* = 5	14 June ± 2.0 *n* = 5	6.4 ± 0.6 *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

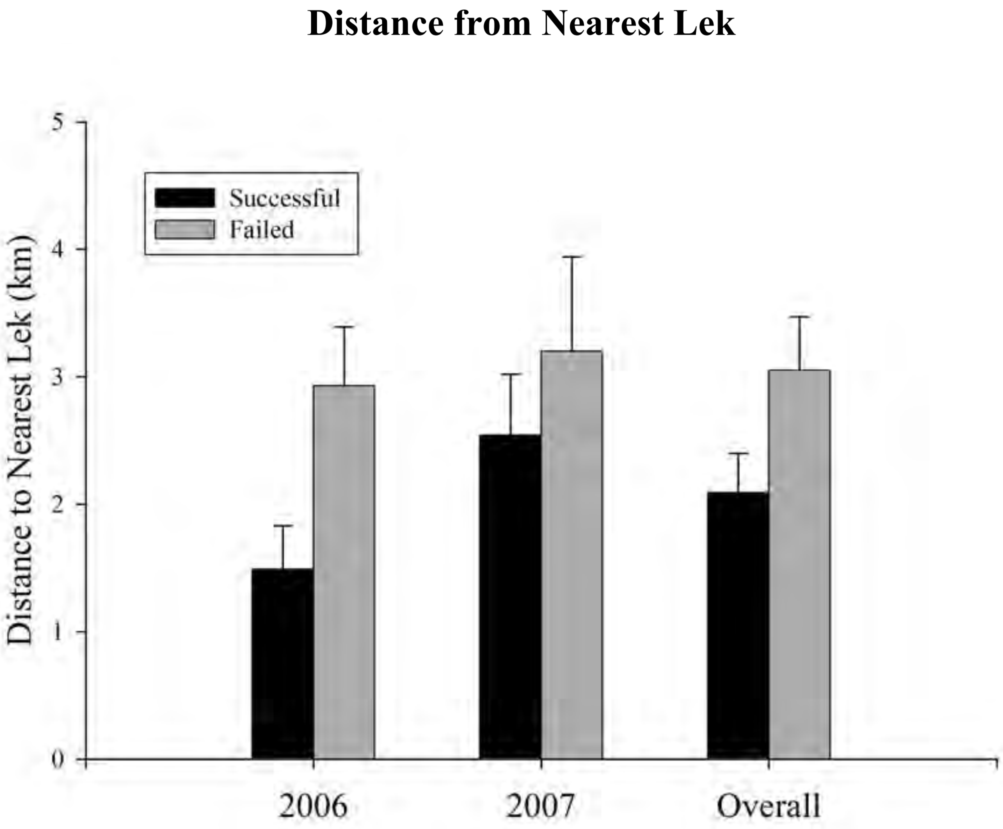
Table 6. Parameter Estimates, odds ratios, and corresponding confidence intervals for the best-approximating model of greater sage-grouse nests sites versus random sites in northwestern South Dakota, 2006-2007.

	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



Distance from Nearest Lek

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

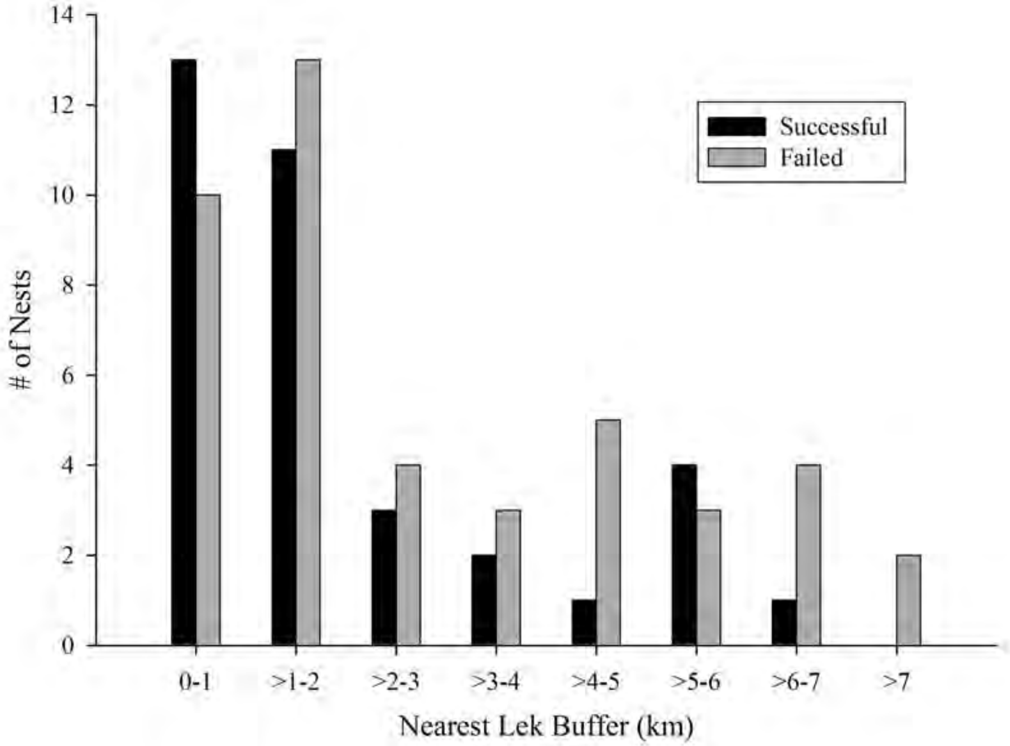


Figure 3. Distribution of successful and failed nests to nearest documented lek distances for greater sage-grouse in northwestern South Dakota, USA, 2006-2007.

Monthly Precipitation

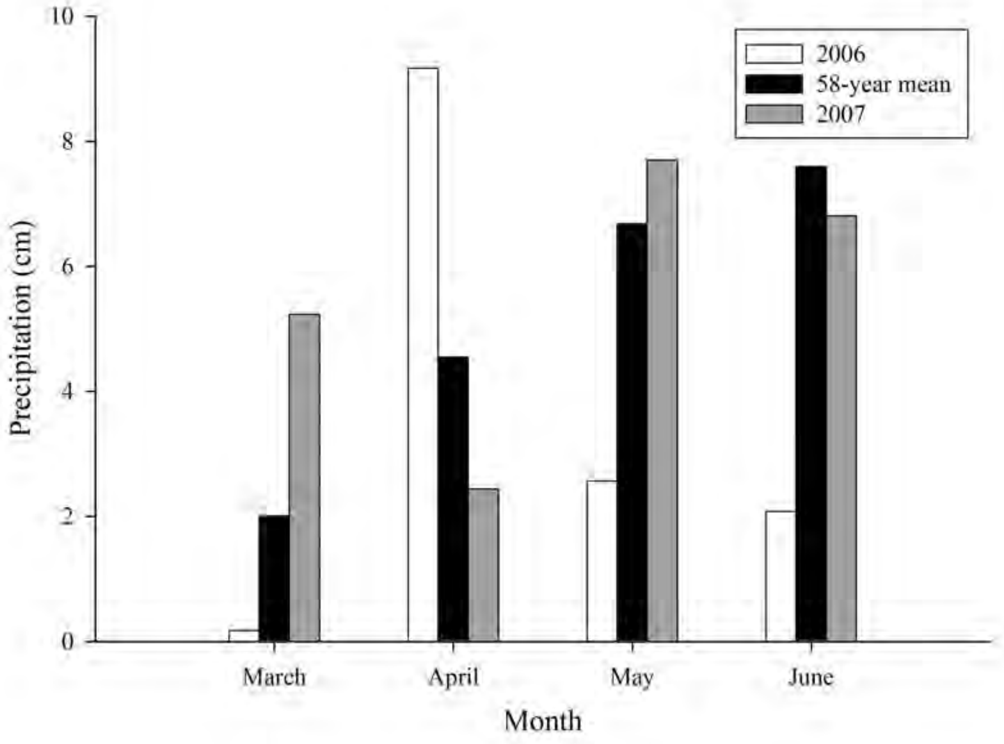


Figure 4. Monthly precipitation received during the breeding and nesting periods in 2006 – 2007 compared to the 58-year mean from the nearest daily weather station (Nisland, SD).

Effect of Grass Height on Nest Success

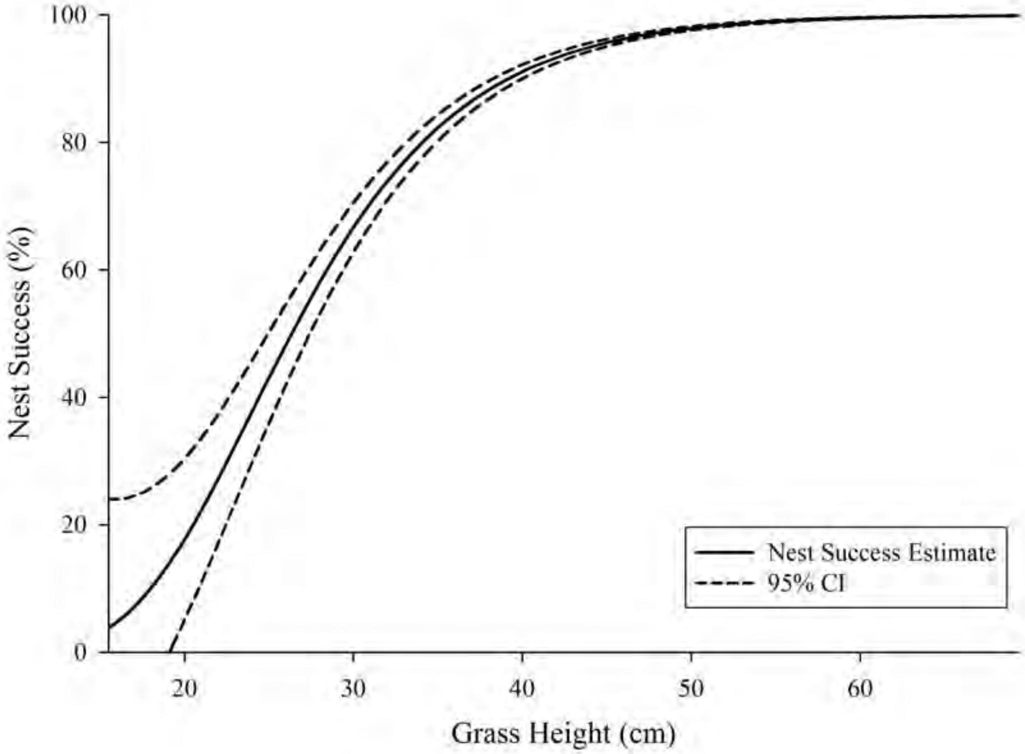


Figure 5. Effect of grass height on greater sage-grouse nest success in northwestern South Dakota, USA, 2006-2007. Nest success estimate derived from back-transformed beta estimates included in top model. Confidence intervals estimated from the delta method (Seber 1982).

Effect of Grass Height and Litter on Nest Success

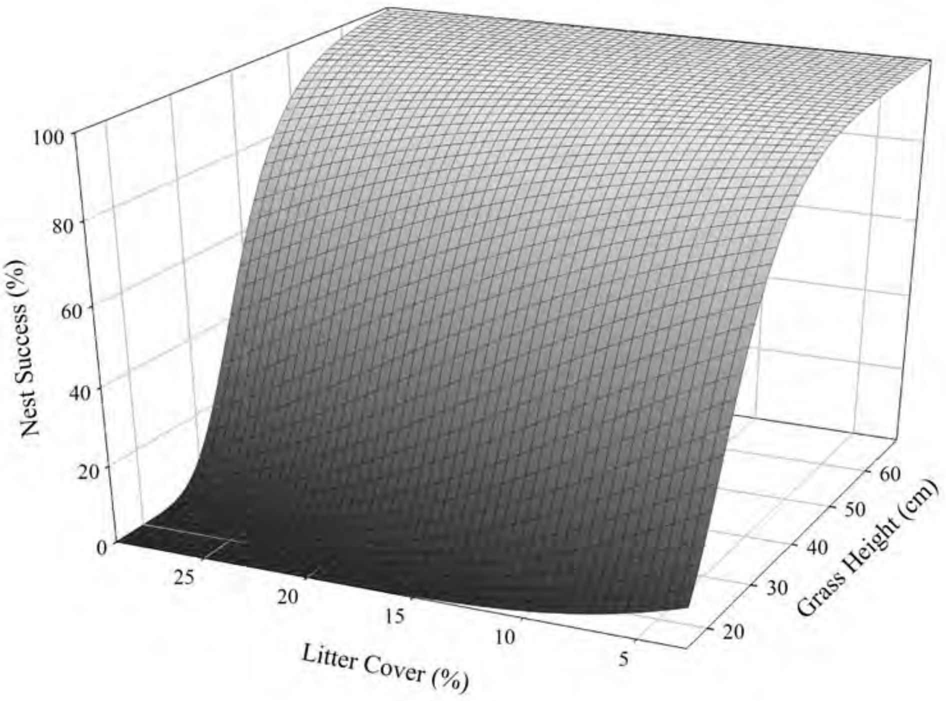


Figure 6. Effect of grass height and litter canopy coverage on greater sage-grouse nest success in northwestern South Dakota, USA, 2006-2007. Nest success estimate derived from back-transformed beta estimates included in top model.

Effect of Litter Canopy Coverage on Nest Success

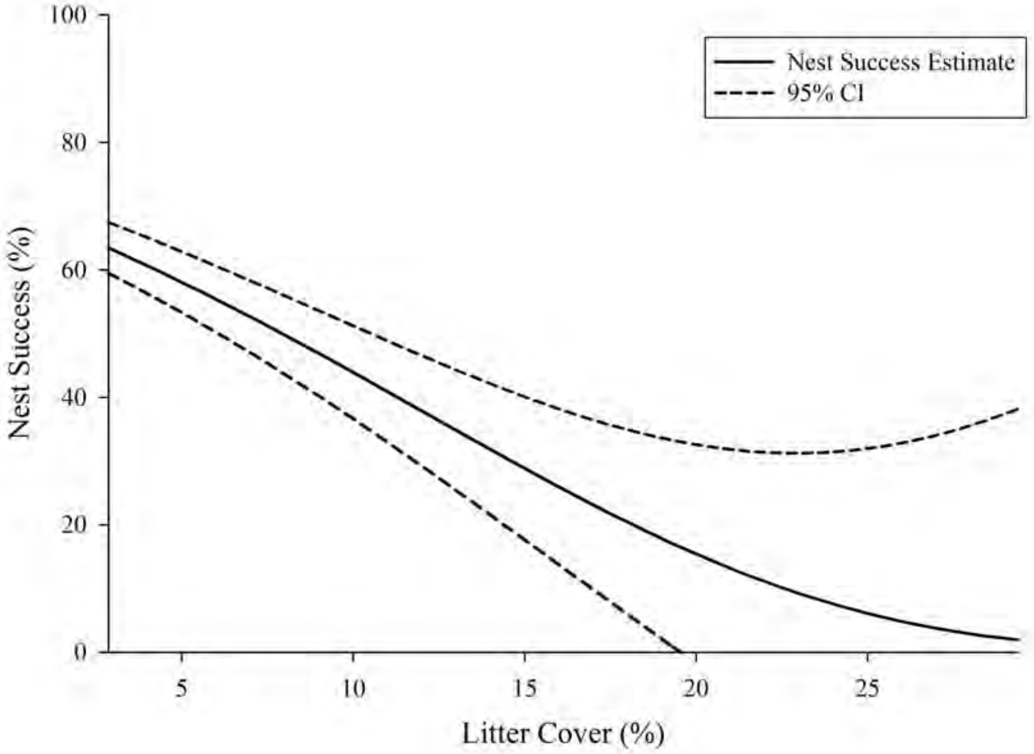


Figure 7. Effect of litter canopy coverage on greater sage-grouse nest success in northwestern South Dakota, USA, 2006-2007. Nest success estimate derived from back-transformed beta estimates included in top model. Confidence intervals estimated from the delta method (Seber 1982).

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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

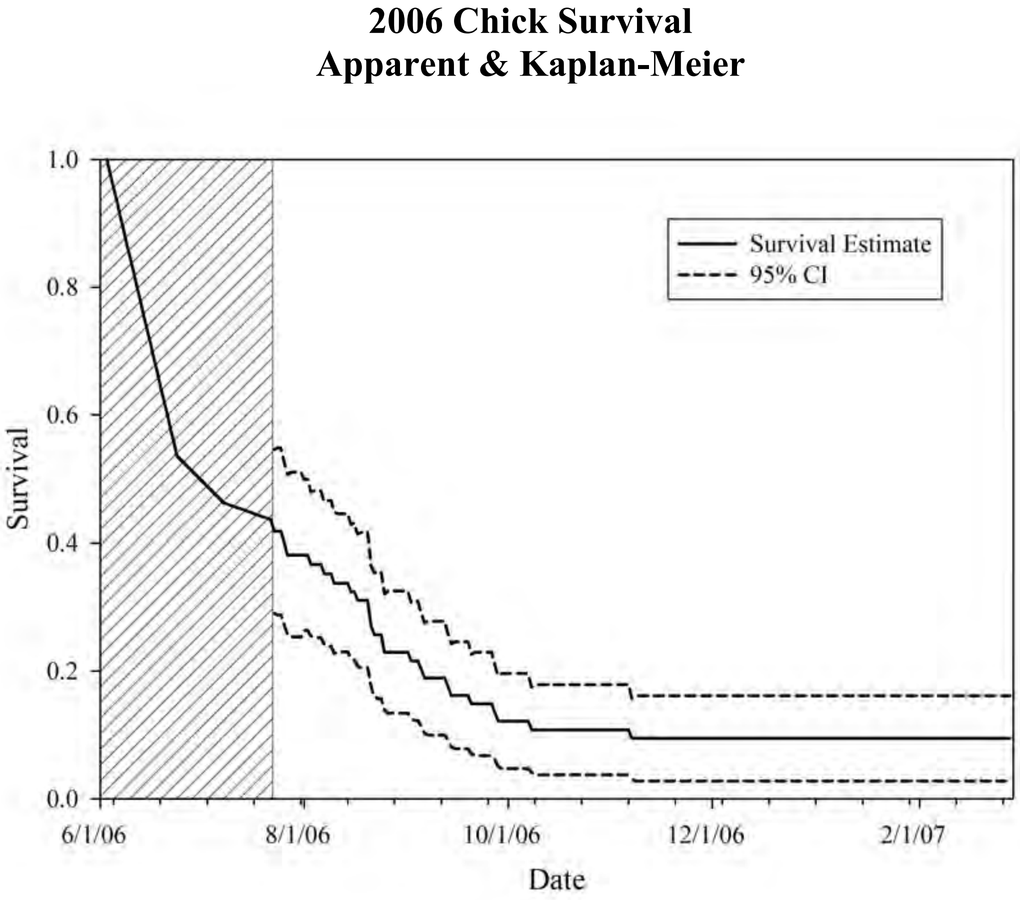

Figure 8. Greater sage-grouse apparent chick survival to 7 weeks post hatch (dashed area), and recruitment as of 1 March 2007 using a Kaplan-Meier product-limit method (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989) in northwestern South Dakota, USA, 2006-2007. A sample size of *n* = 31, was used in the Kaplan-Meier analysis.

2007 Chick Survival
Apparent & Kaplan-Meier

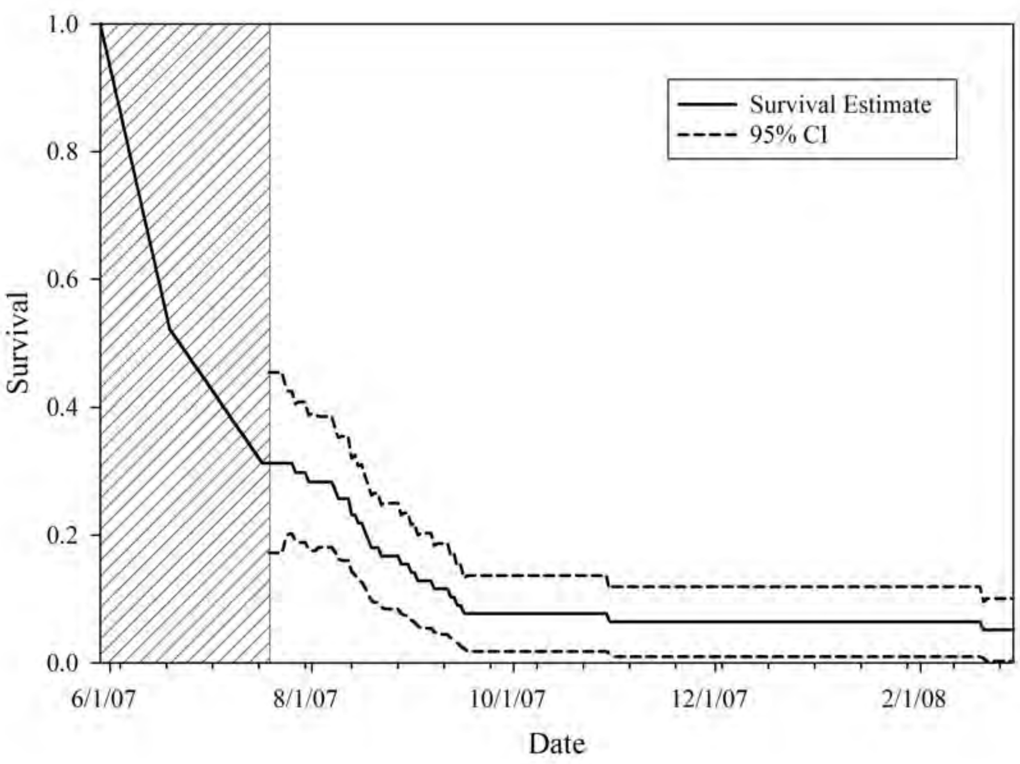

Figure 9. Greater sage-grouse apparent chick survival to 7 weeks post hatch (dashed area), and recruitment as of 1 March 2008 using a Kaplan-Meier product-limit method (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989) in northwestern South Dakota, USA, 2007-2008. A sample size of *n* = 24, was used in the Kaplan-Meier analysis.

Effect of Visual Obstruction and Bluegrass Cover
On Brood-rearing Habitat Selection

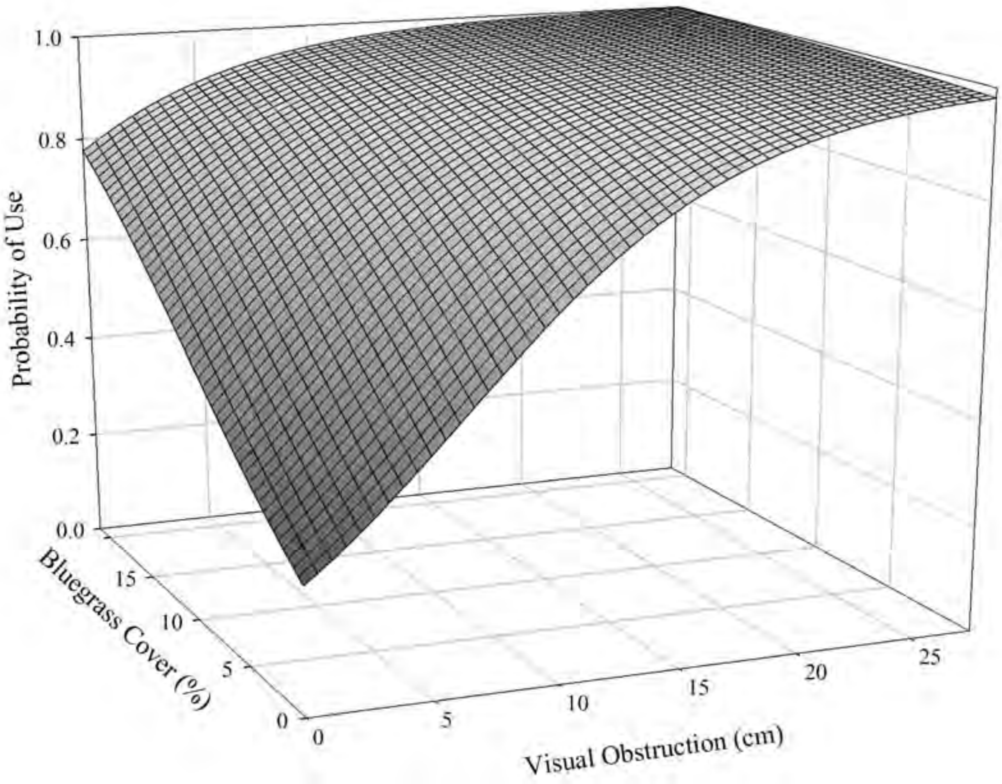

Figure 10. Effect of visual obstruction and bluegrass cover on greater sage-grouse brood-rearing habitat selection in northwestern South Dakota, USA, 2006-2007. Probability of use derived from parameter estimates in best approximated model (visual obstruction + bluegrass cover).

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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.

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Ecological minimums, greater sage-grouse, landscape modeling, partitioned Mahalanobis D^2, population connectivity, sagebrush, species distribution models.

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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

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.

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 ≥ 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 ≤ 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 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 ≤ 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).

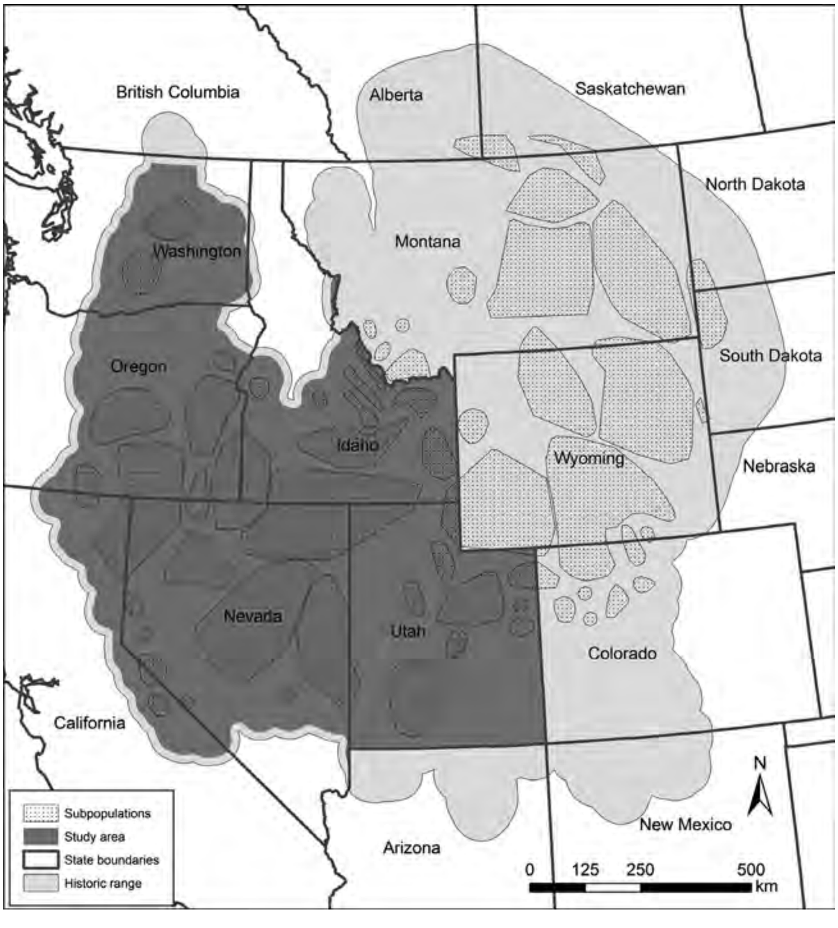

Figure 2. Study area and greater sage-grouse population boundaries within the historic sage-grouse range in western North America.

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 ≤ 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

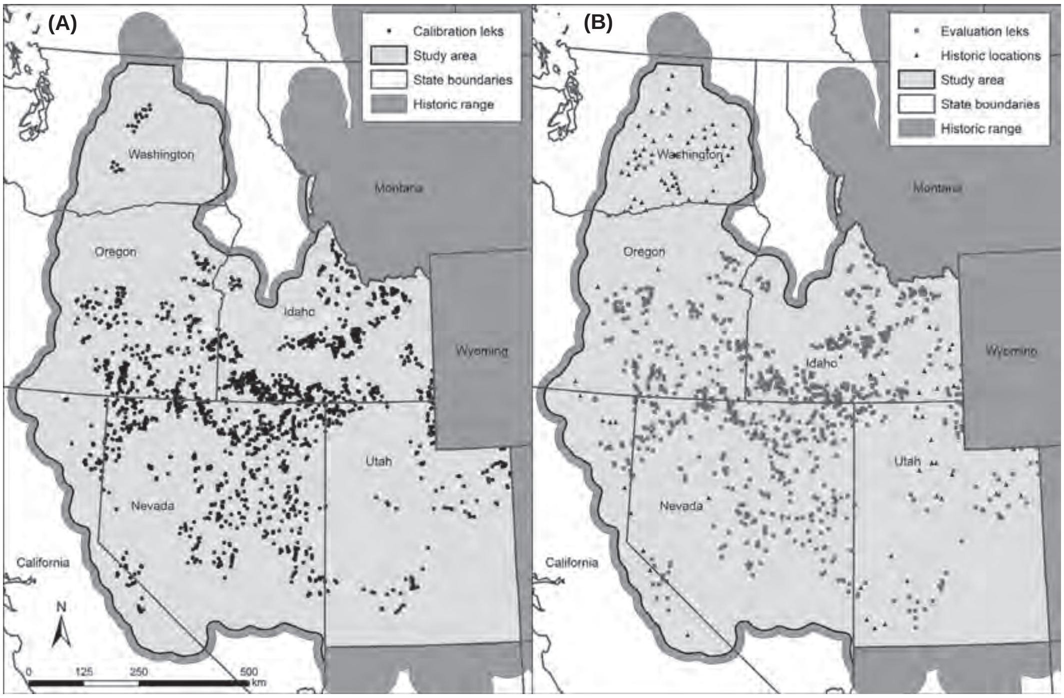

Figure 3. Distribution of greater sage-grouse lek locations active between 1998 and 2007 in the western range used to calibrate and evaluate models. Leks were randomly selected into calibration (A, black circles) and evaluation subsets (B, gray squares). Historic, but currently unoccupied sage-grouse 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 (≥ 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 ≥ 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

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		Eigenvector
Environmental variables	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range	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 (≥ 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).

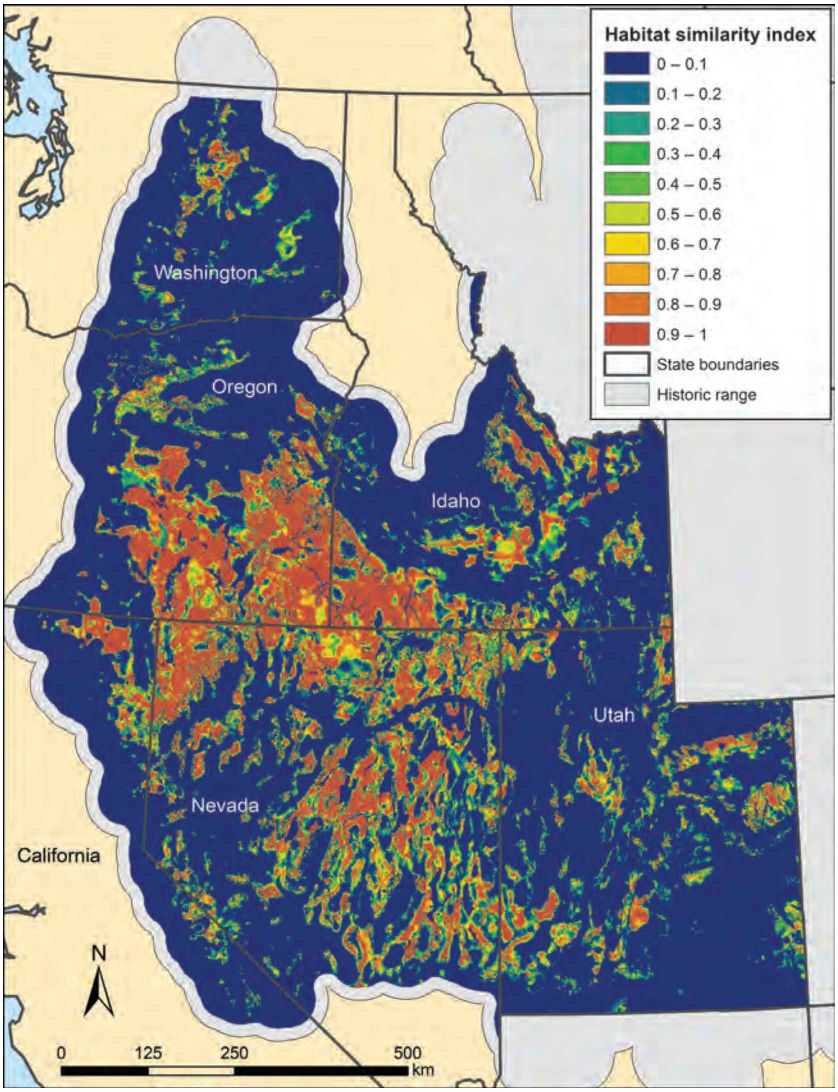

Figure 4. Habitat similarity index (HSI) values for greater sage-grouse across their western range. HSI values represent the relationship of environmental values at map locations to the multivariate model of minimum requirements for sage-grouse defined by land cover, anthropogenic variables, soil, topography, 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

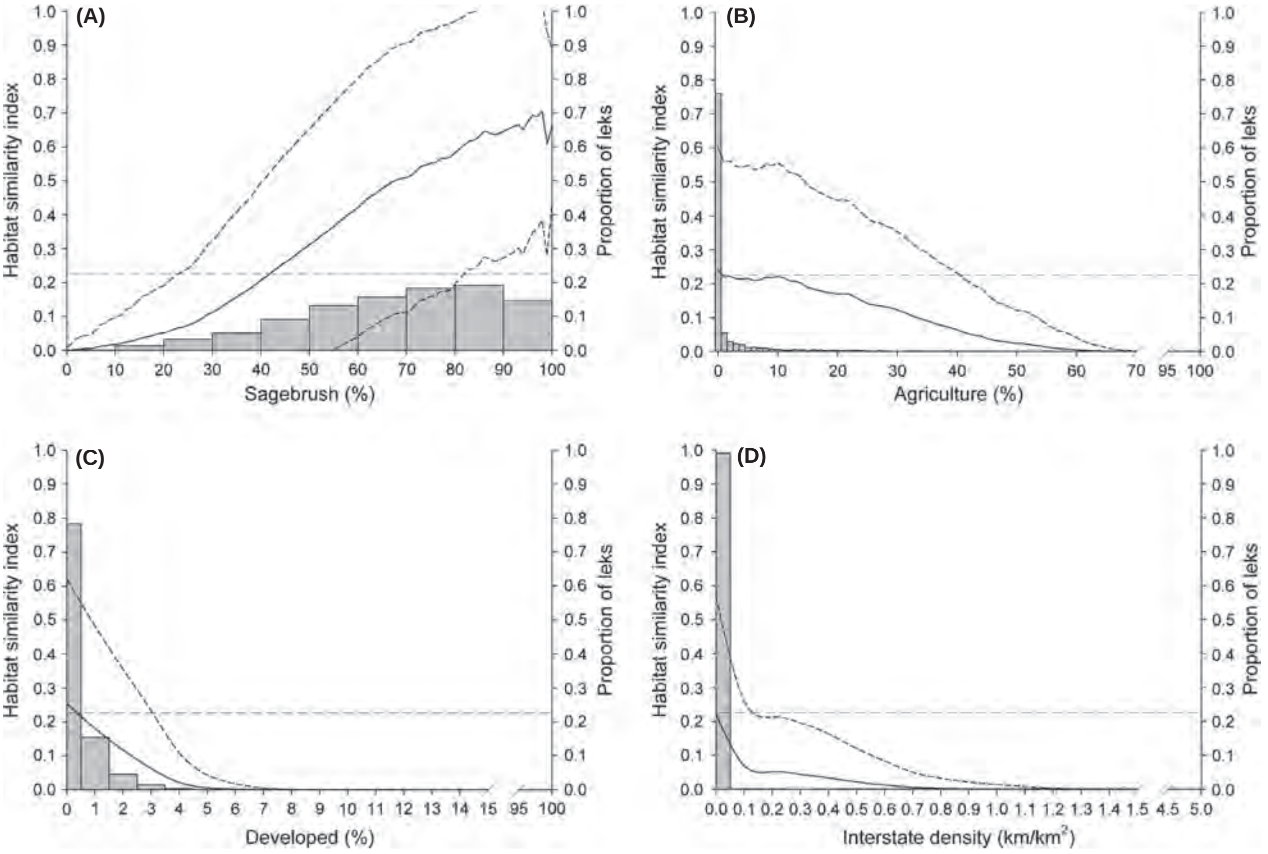

Figure 5. Changes in the habitat similarity index (HSI) relative to (A) sagebrush, (B) agriculture, (C) developed lands, and (D) density of interstate highways in the landscape within 5 km. Mean HSI values for study area (black line, ±1 SD [stippled lines]) and proportion of total leks (gray bars) were 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-

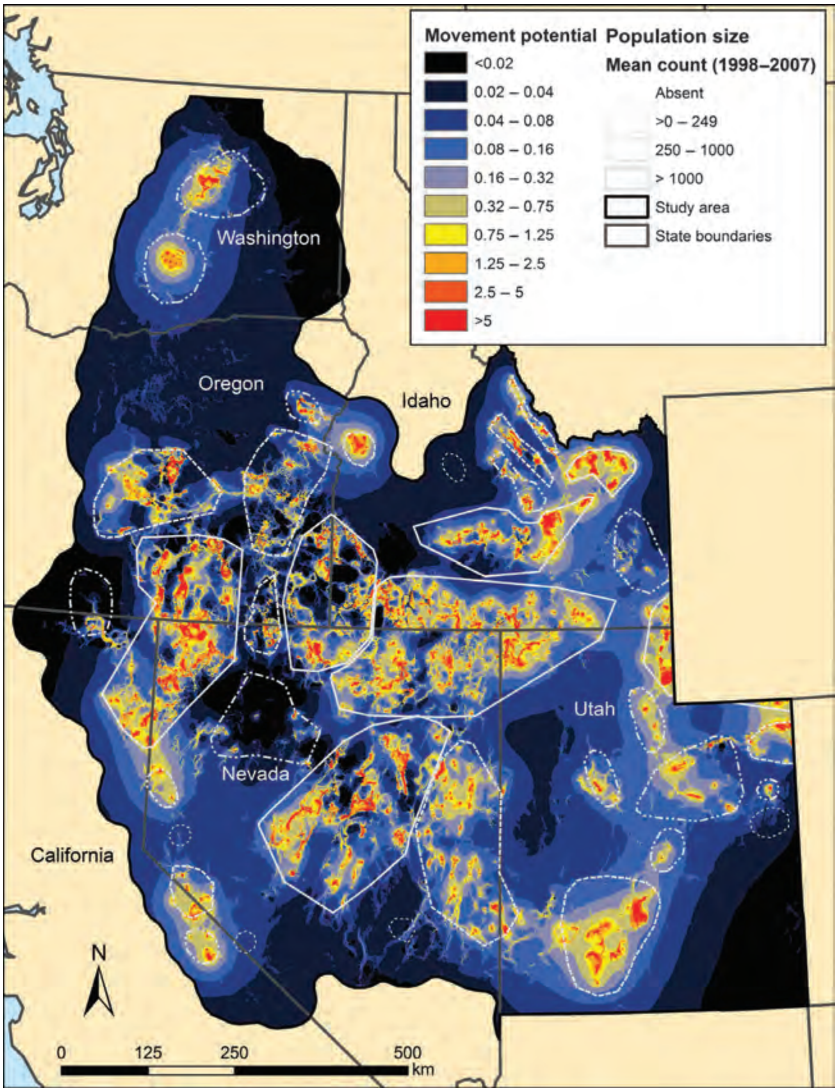

Figure 6. Estimated potential for sage-grouse movement among sage-grouse leks (Circuitscape; McRae 2006). Rescaled HSI values were used as a measure of landscape resistance.

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 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.

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Conflict of Interest

None declared.

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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

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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).

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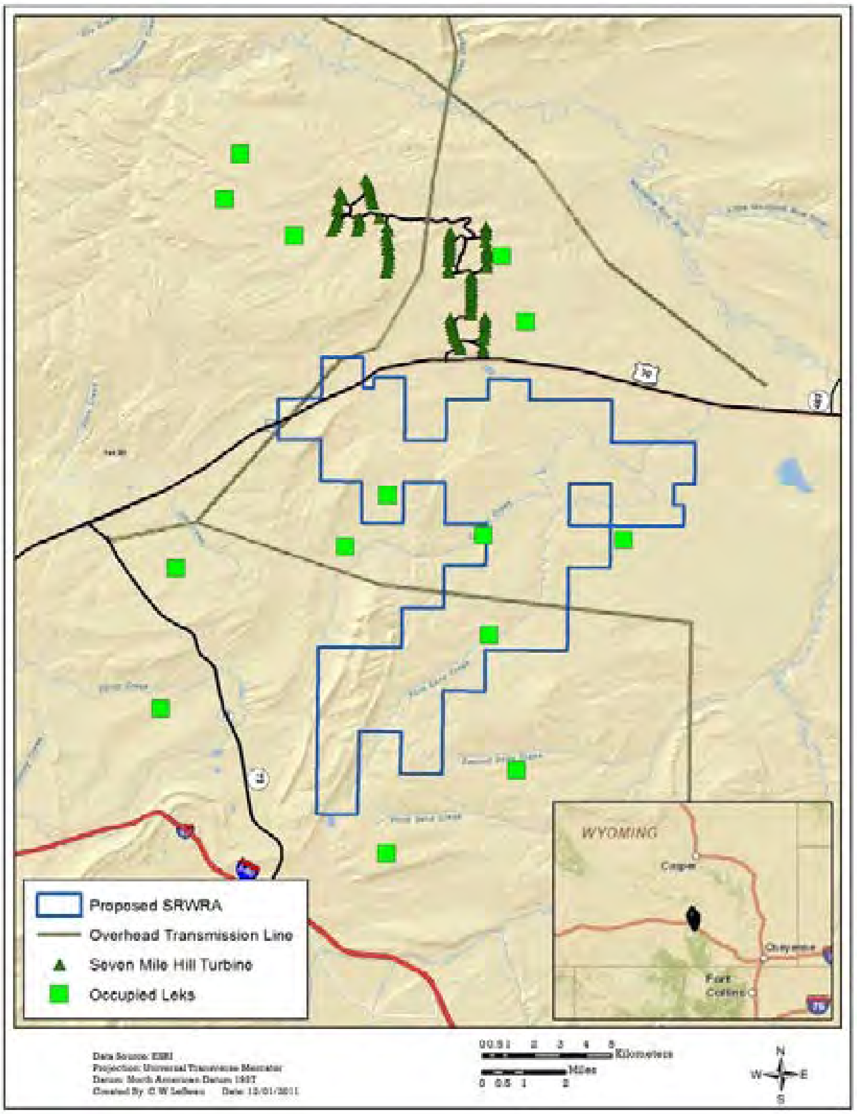

Figure 1-1. Seven Mile Hill and Simpson Ridge study areas located in Carbon County, Wyoming, USA. The Seven Mile Hill Wind Energy facility consisted of 79, 1.5-MW wind turbines. The Simpson Ridge study area comprised of the area within and surrounding the Simpson Ridge Wind Resource Area (SRWRA).

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 β 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 5th percentile of the 1,000 estimates represented the lower limit of a 90% confidence limit and the value at the 95th 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(β_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 ΔAIC*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 ΔAIC*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 (ΔAIC*c* = 2.10) or have a significant slope (β = -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; β = 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 ΔAIC*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.

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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 (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.

Model	log[L]	K	AIC*c*	ΔAIC*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 (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.

Model	log[L]	K	AIC*c*	ΔAIC*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

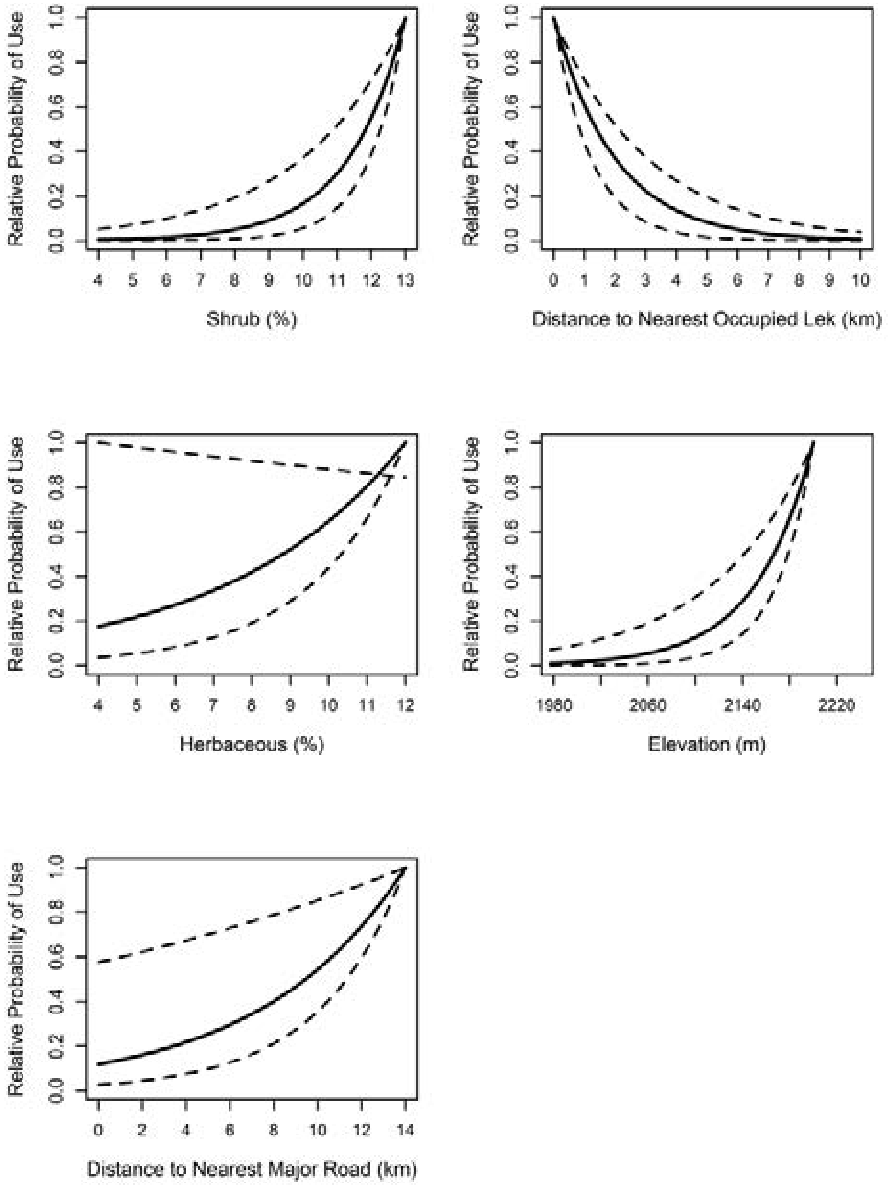

Figure 2-1. Odds ratios or relative probability of sage-grouse nest site selection and 90% confidence intervals (dashed lines) within the Seven Mile Hill study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value. Overlapping confidence limits indicate a non-significant estimate.

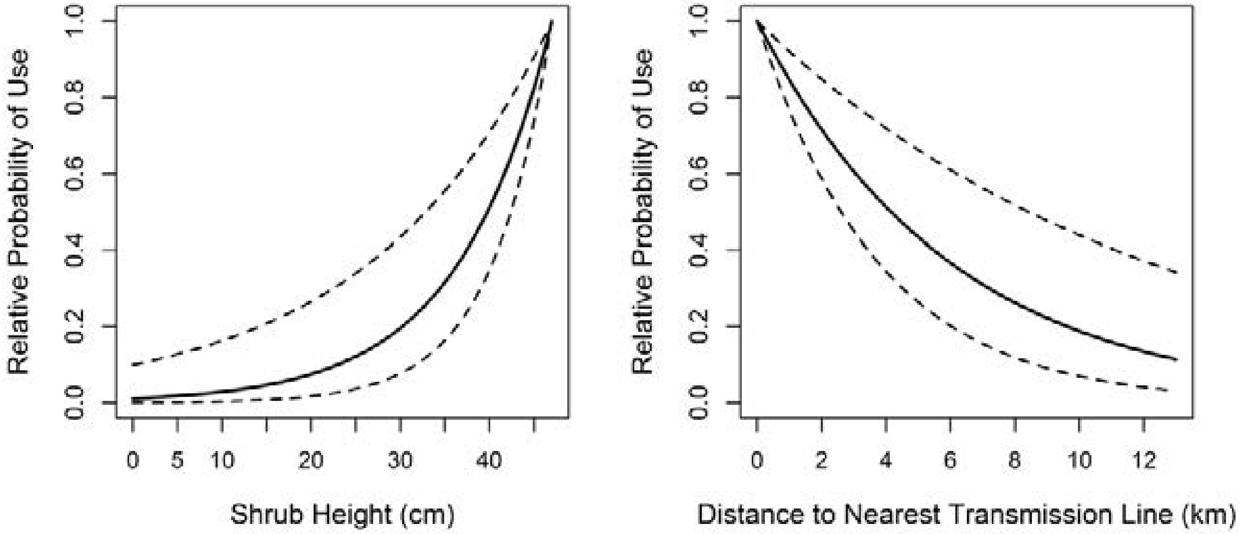

Figure 2-2. Odds ratios or relative probability of sage-grouse nest site occurrence and 90% confidence intervals (dashed lines) within the Simpson Ridge study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value.

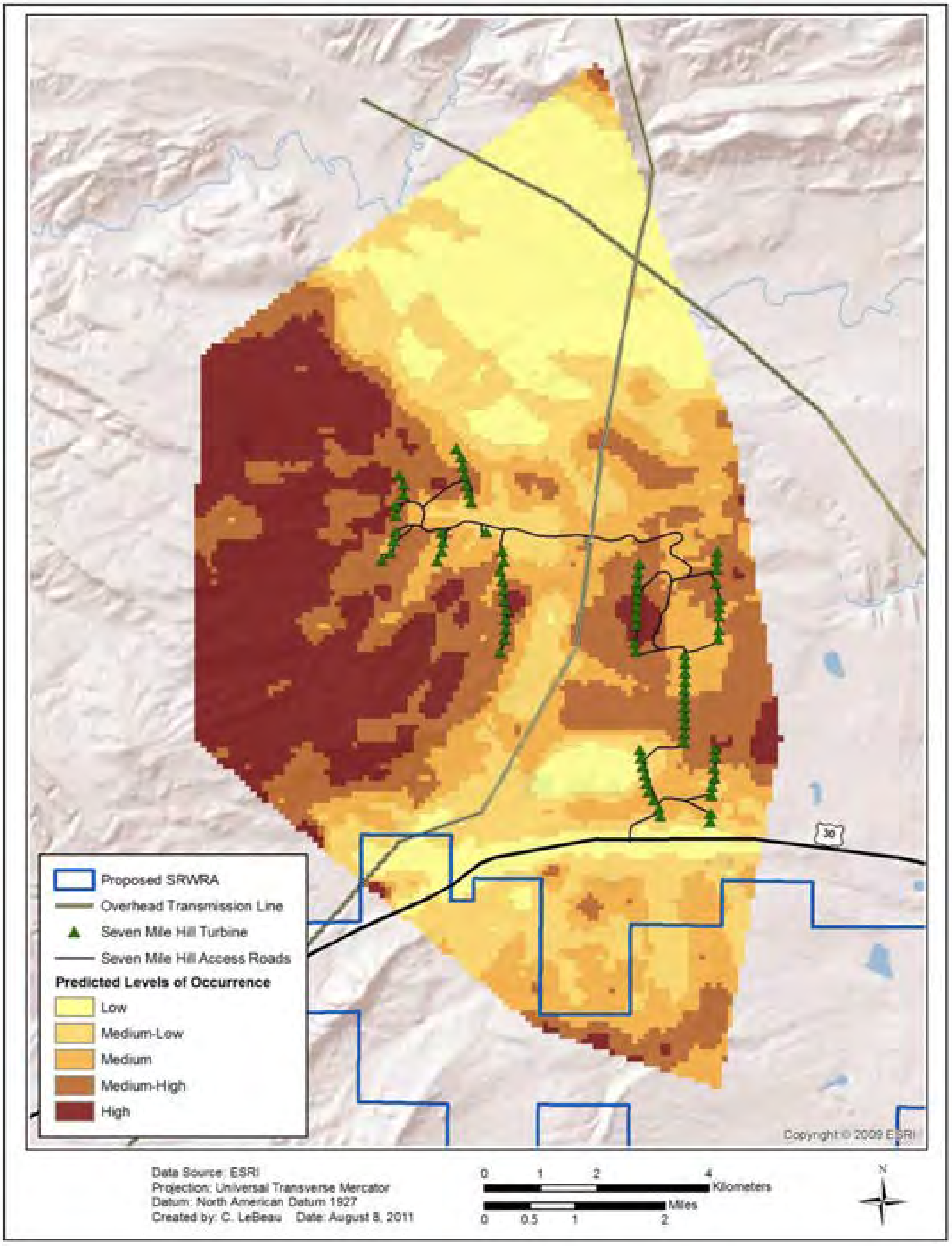

Figure 2-3. Predicted nesting habitat used within a 129 km^2 minimum convex polygon by sage-grouse within the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010.

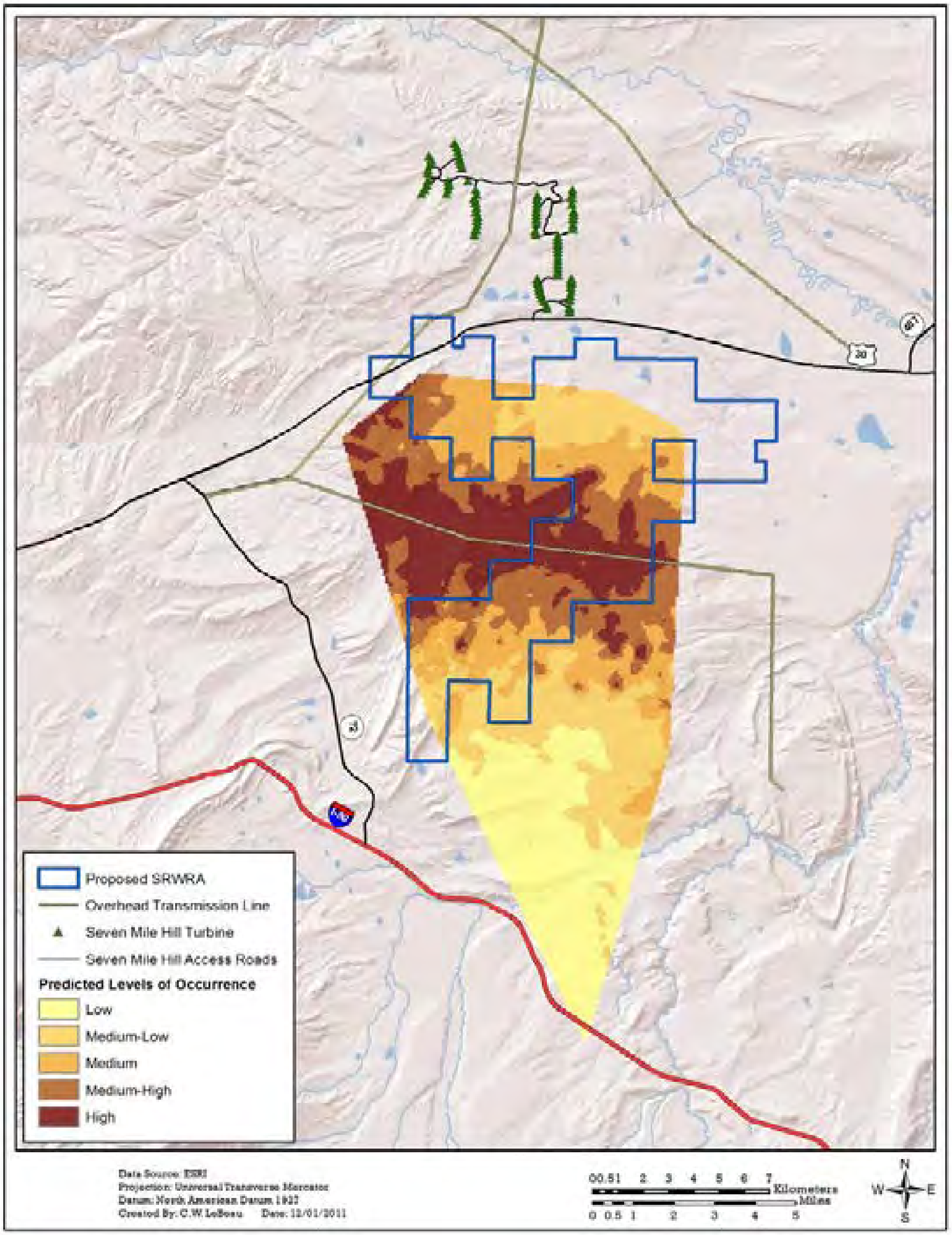

Figure 2-4. Predicted nesting habitat used within a 217 km^2 minimum convex polygon by sage-grouse within the Simpson Ridge Study area, Carbon County, Wyoming, USA, 2009 and 2010.

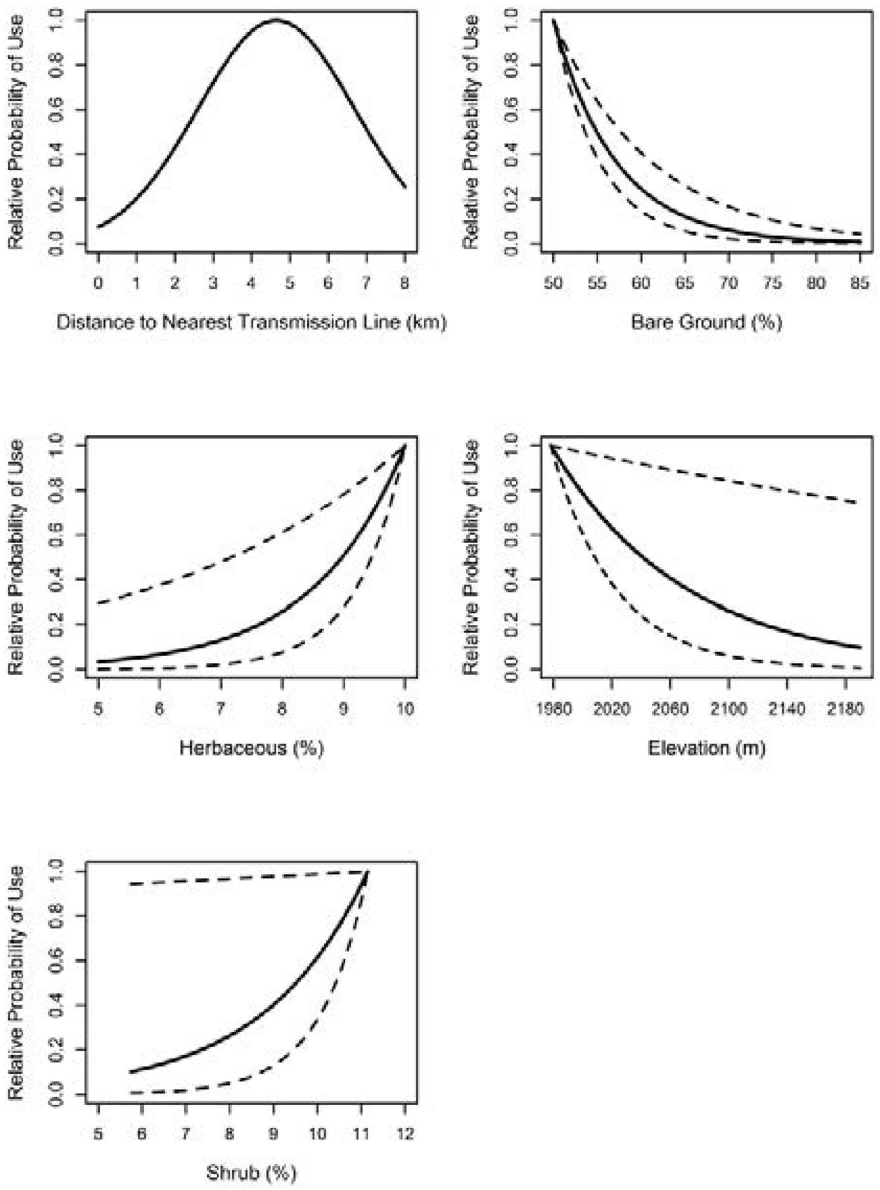

Figure 2-5. Odds ratios or relative probability of sage-grouse brood-rearing selection and 90% confidence intervals (dashed lines) within the Seven Mile Hill study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. Confidence intervals were not calculated for distance to transmission line because confidence intervals for quadratic effects depend on values of other covariates.

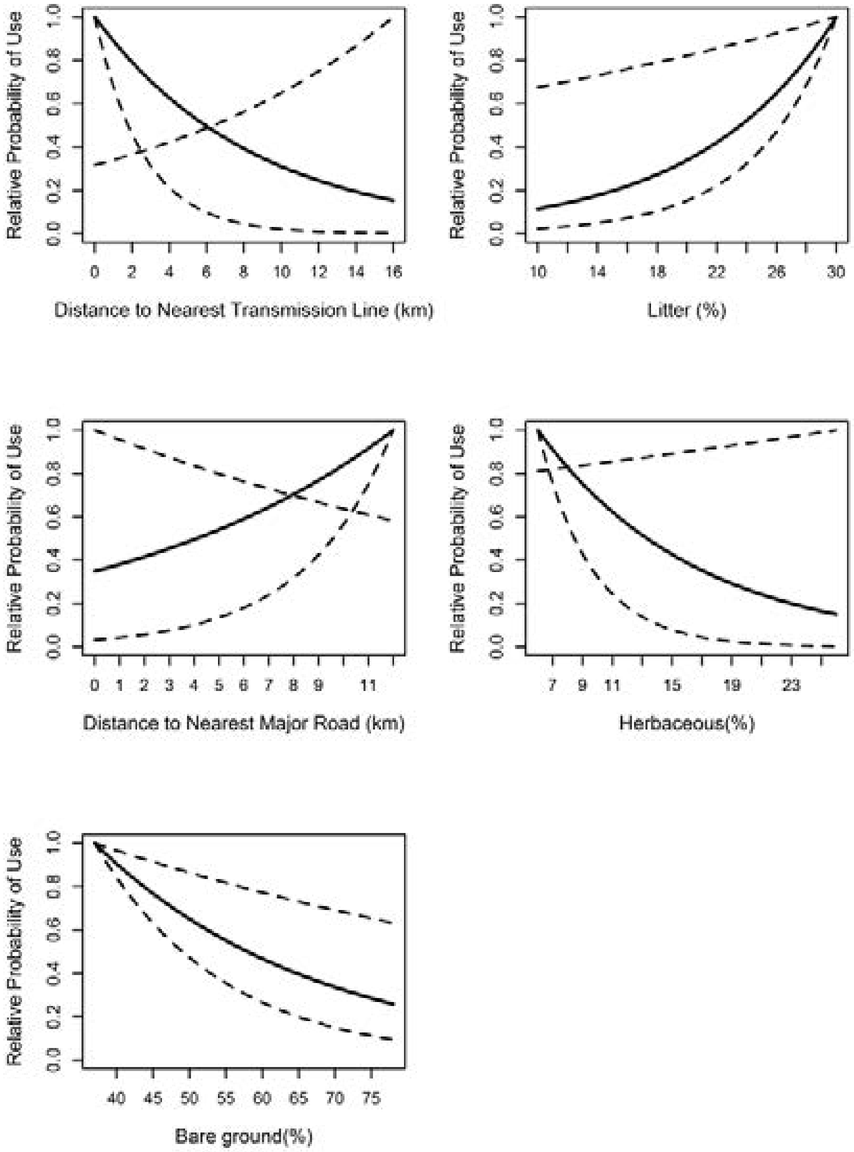

Figure 2-6. Odds ratios or relative probability of sage-grouse brood-rearing occurrence and 90% confidence intervals (dashed lines) within the Simpson Ridge study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value. Overlapping confidence limits indicate a non-significant estimate.

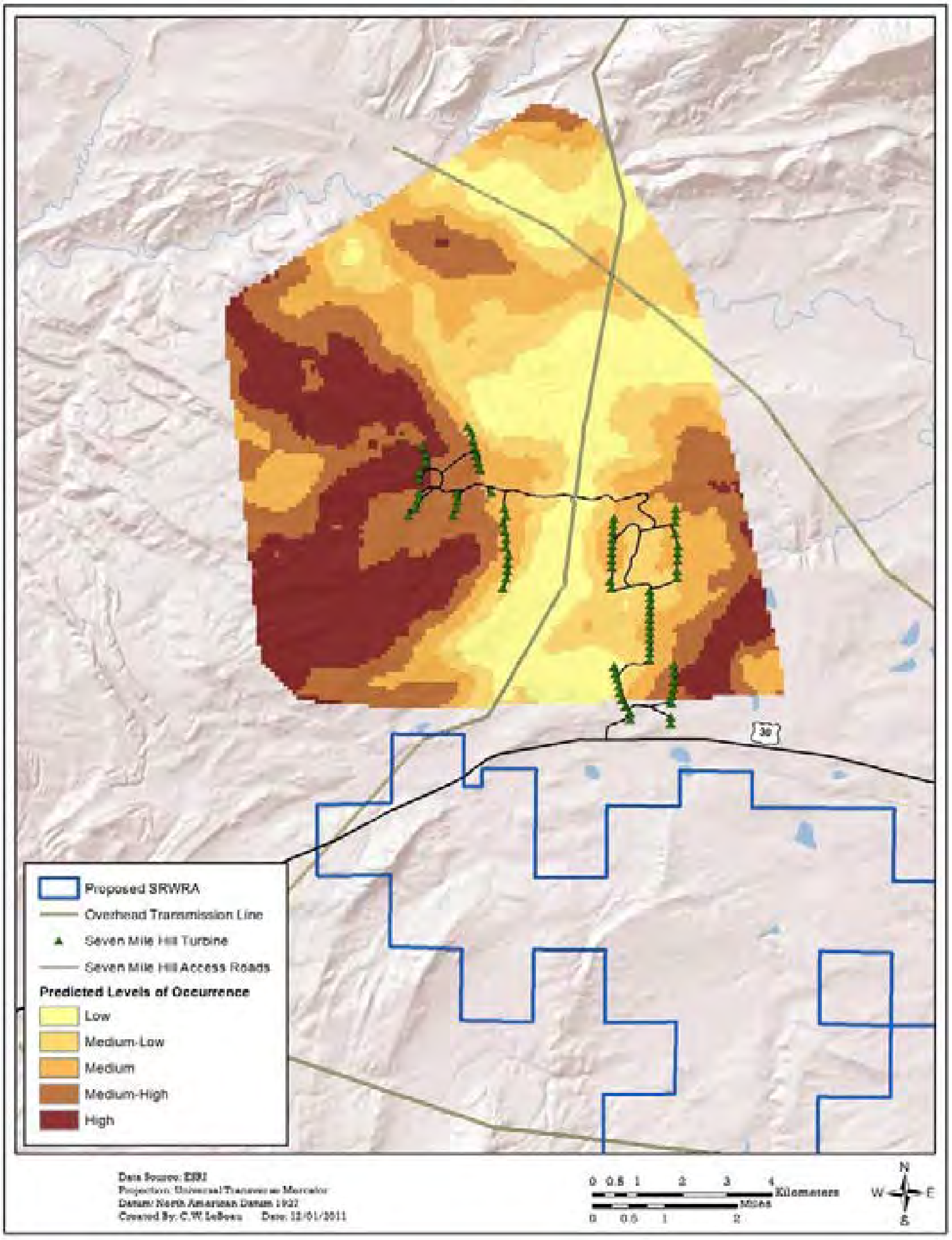

Figure 2-7. Predicted brood-rearing habitat used within a 126 km^2 minimum convex polygon by sage-grouse within the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010.

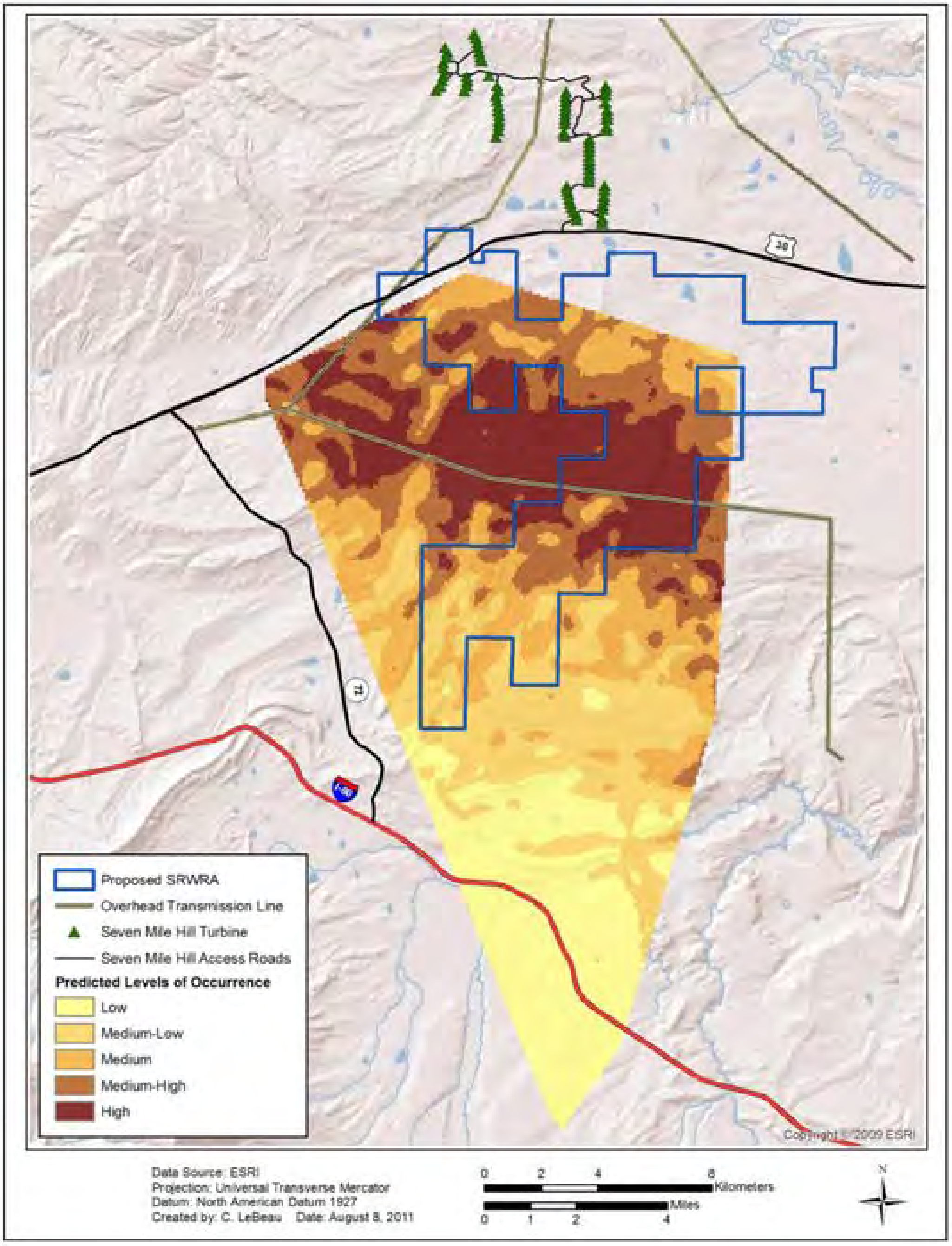

Figure 2-8. Predicted brood-rearing habitat used within a 650 km^2 minimum convex polygon by sage-grouse within the Simpson Ridge study area, Carbon County, Wyoming, USA, 2009 and 2010.

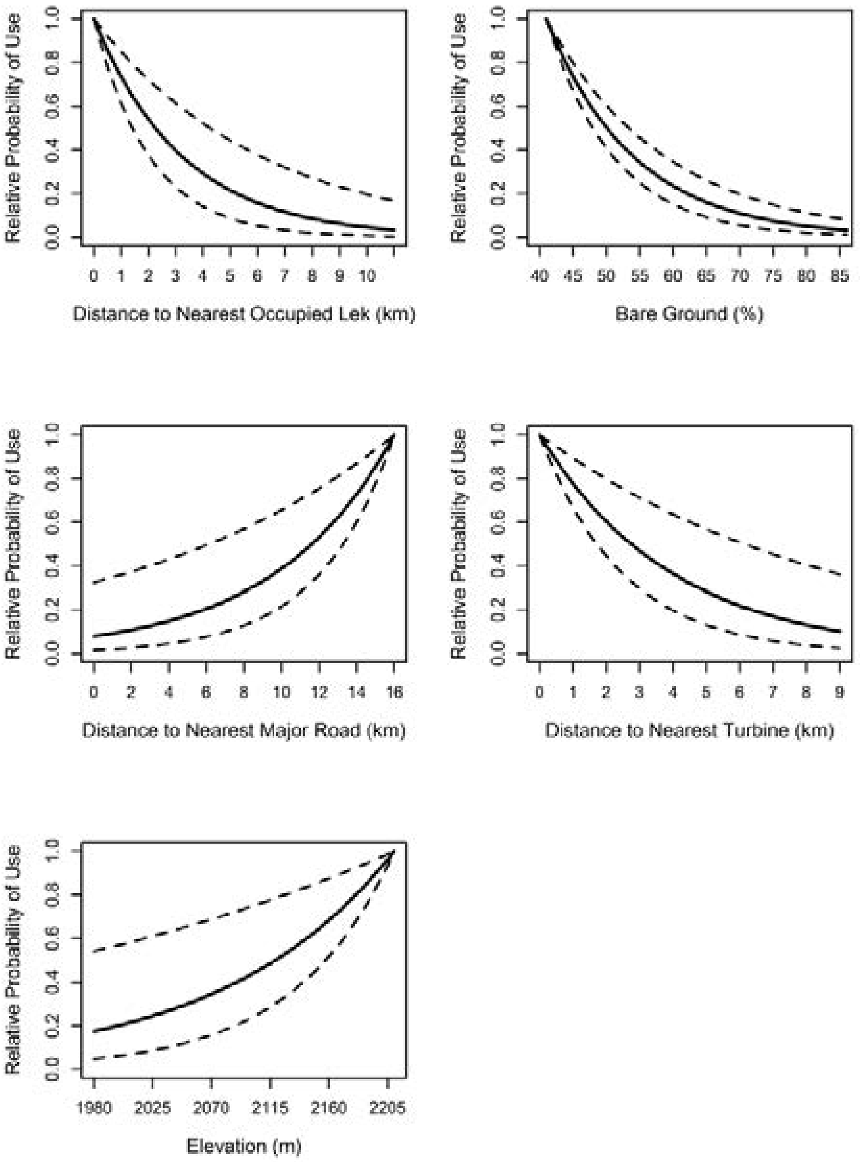

Figure 2-9. Odds ratios or relative probability of female sage-grouse summer occurrence and 90% confidence intervals (dashed lines) within the Seven Mile Hill study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model were held constant at their mean value.

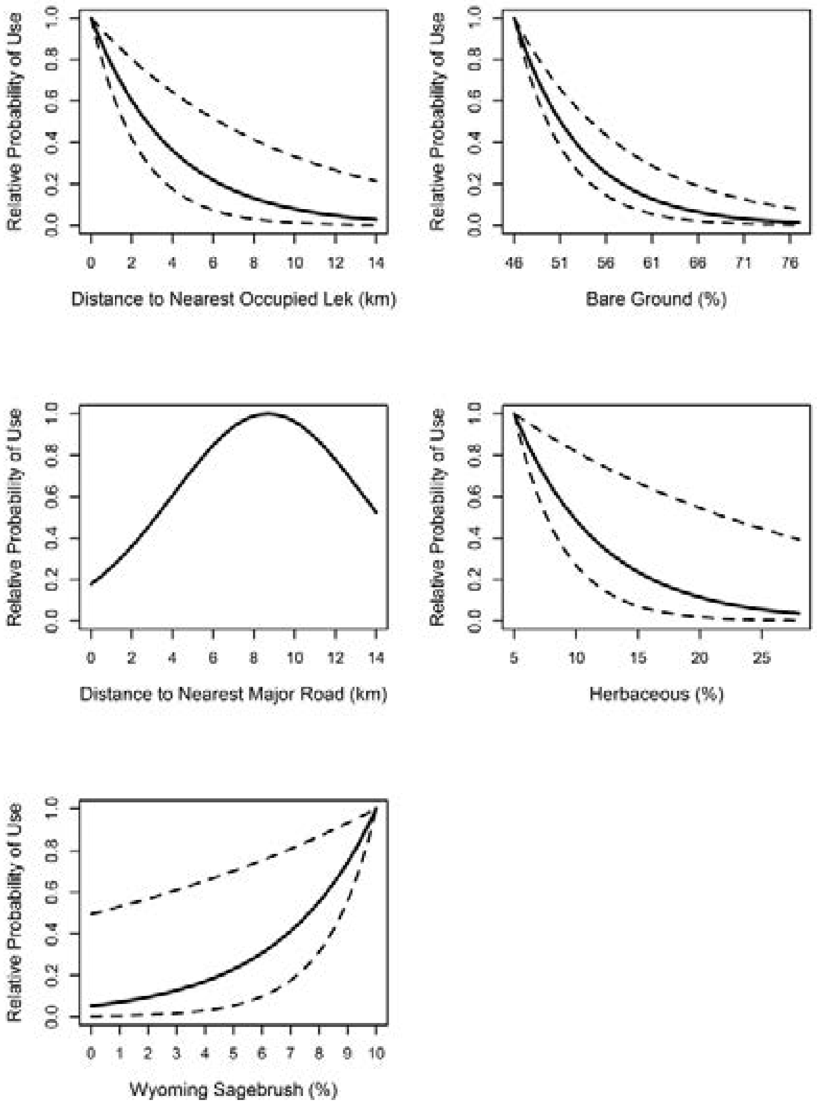

Figure 2-10. Odds ratios or relative probability of female sage-grouse summer occurrence and 90% confidence intervals (dashed lines) within the Simpson Ridge study area as a function of top model covariates, Carbon County, Wyoming, USA, 2009 and 2010. All other covariates in the best approximating model 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.

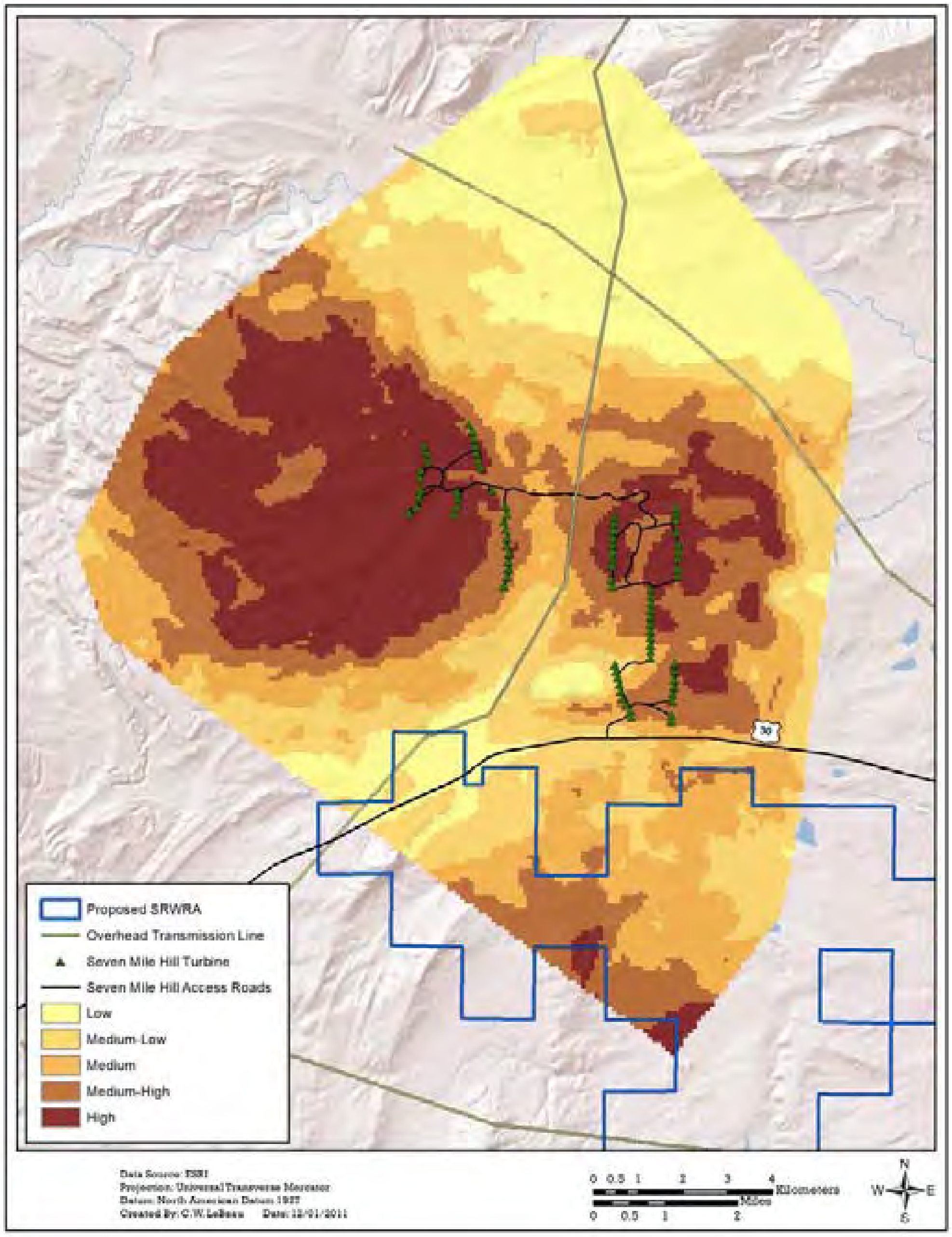

Figure 2-11. Predicted summer habitat used within a 243 km^2 minimum convex polygon by sage-grouse within the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010.

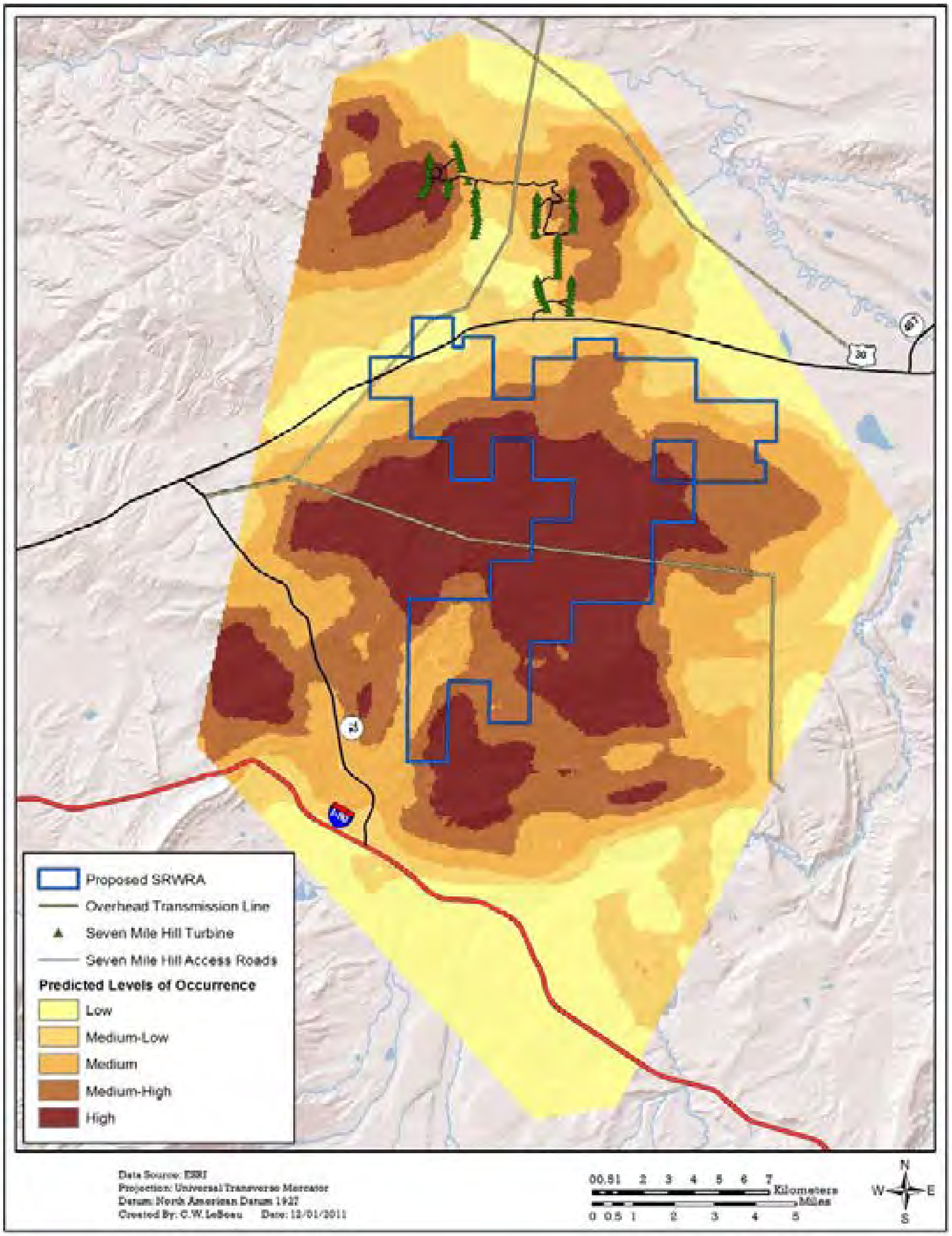

Figure 2-12. Predicted summer habitat used within a 751 km^2 minimum convex polygon by sage-grouse within the Simpson Ridge study area, Carbon County, Wyoming, USA, 2009 and 2010.

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 $\Delta \mathrm{AIC}c$ 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(β_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 25th percentile) within 0.30 km, farther from an overhead transmission line (4.9 km, 75th percentile), and closer to turbines (2.0 km, 25th percentile; Fig. 3-2). Habitats with good survival would consist of a higher SD of shrub height (8.8 cm, 75th percentile) within 0.30 km, closer to overhead transmission lines (1.3 km, 25th percentile), and farther from turbines (11 km, 75th 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 (ΔAIC*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 ≥5 Δ 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 (ΔAIC*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 (λ). 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.

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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

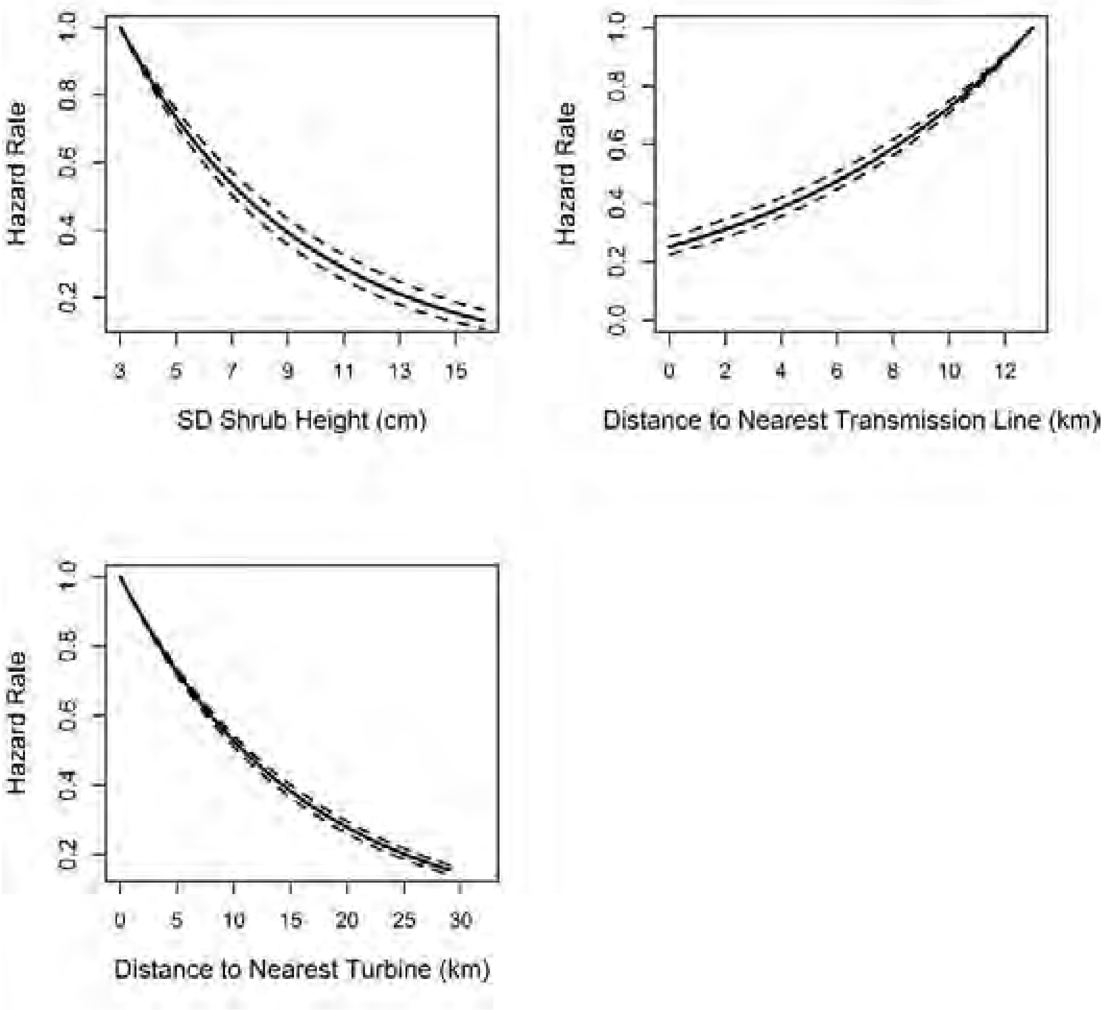

Figure 3-1. Relative hazard rate of nest survival adjusted for the SD of shrub height within 0.30 km, and the distance to nearest turbine and transmission line at the Simpson Ridge and Seven Mile Hill study areas, Carbon County, Wyoming, USA, 2009 and 2010. Dashed lines indicate the lower and upper 90% confidence limits.

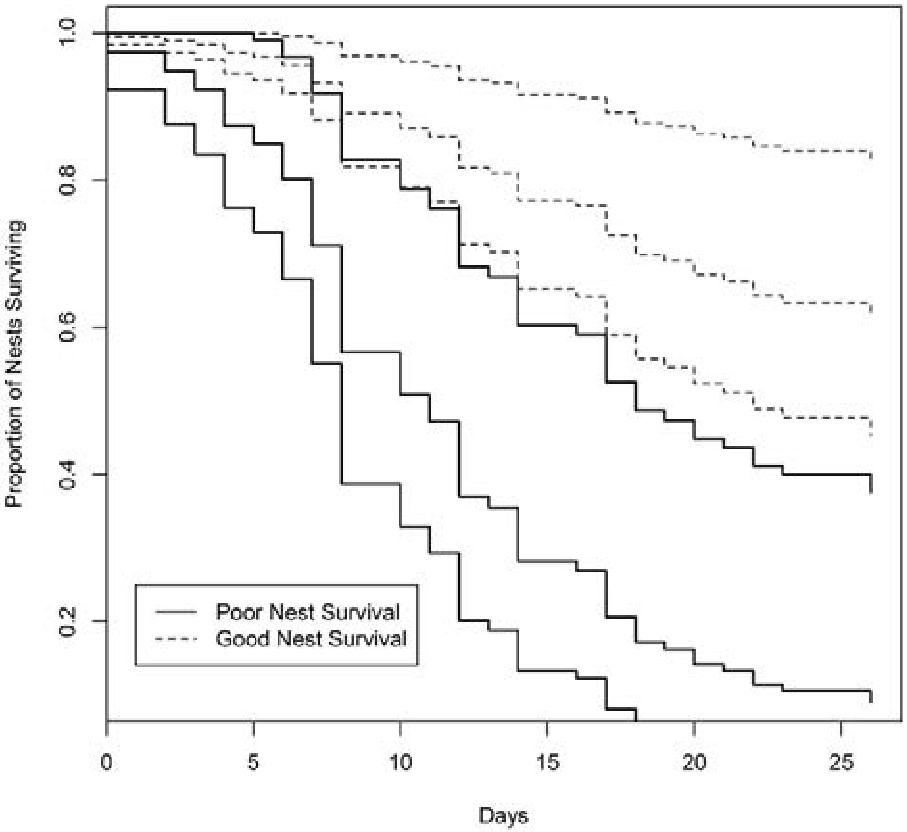

Figure 3-2. Expected nest survival and 90% confidence intervals for nests located in higher risk habitats (closer to turbines, further from transmission lines, and higher SD of shrub height within 0.30 km; poor nest survival) and for nests located in lower risk habitats (good nest survival) within the Simpson Ridge and Seven Mile Hill study areas Carbon County, Wyoming, USA, 2009 and 2010.

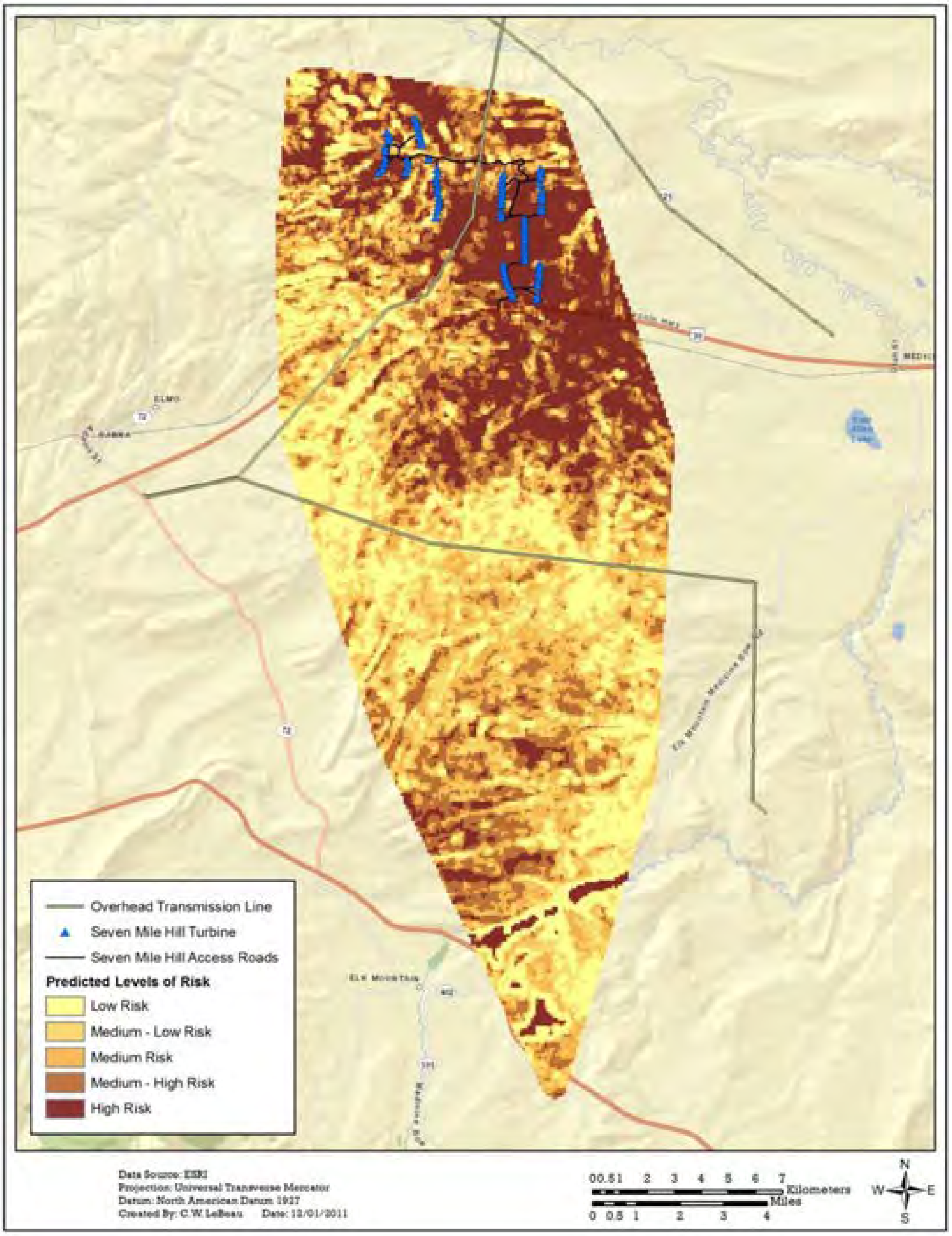

Figure 3-3. Spatial variation in the predicted relative risk of sage-grouse nest failure (low – high) within the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010.

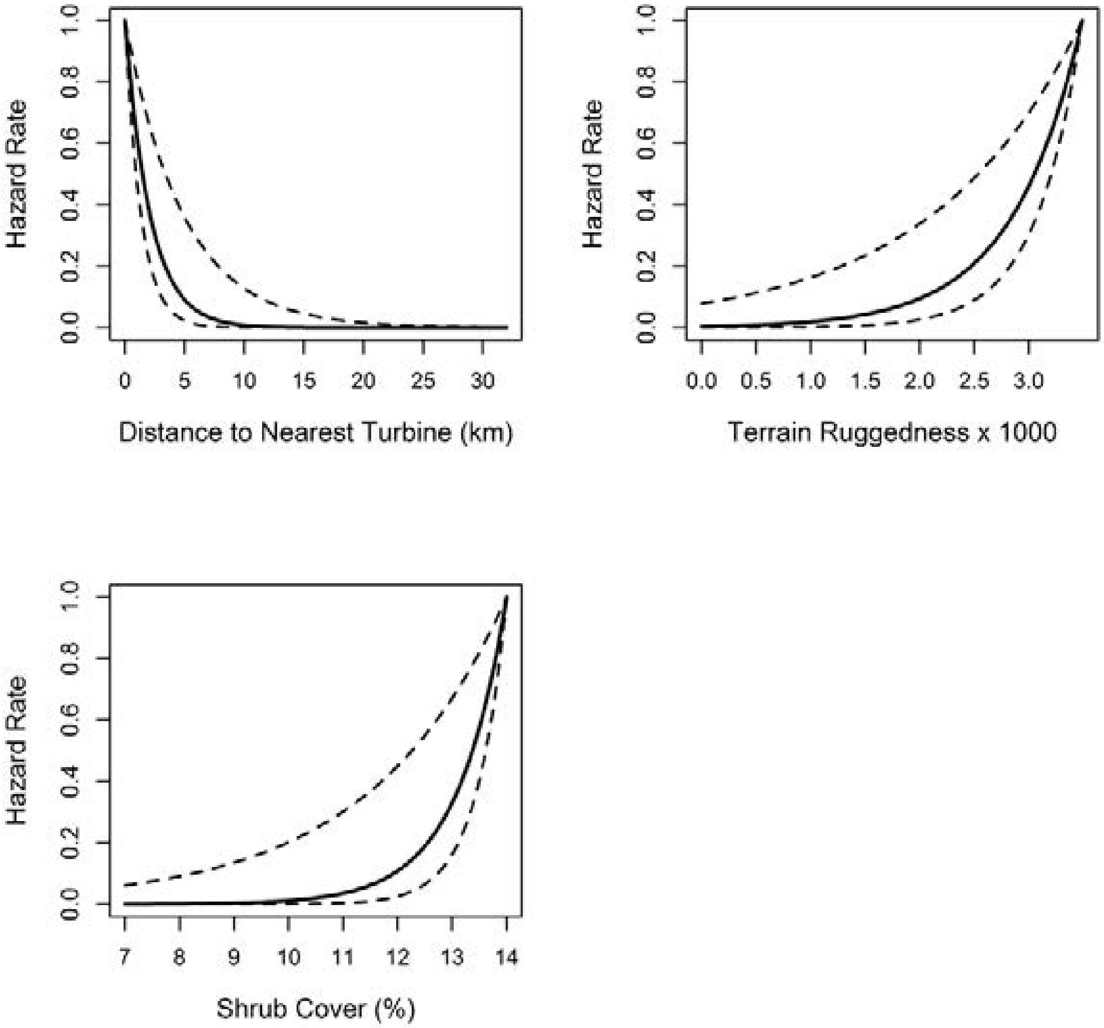

Figure 3-4. Relative hazard rate of brood survival adjusted for distance to nearest turbine, terrain ruggedness, and percent shrub cover at the Simpson Ridge and Seven Mile Hill study areas, Carbon County, Wyoming, USA, 2009 and 2010. Dashed lines indicate the lower and upper 90% confidence limits.

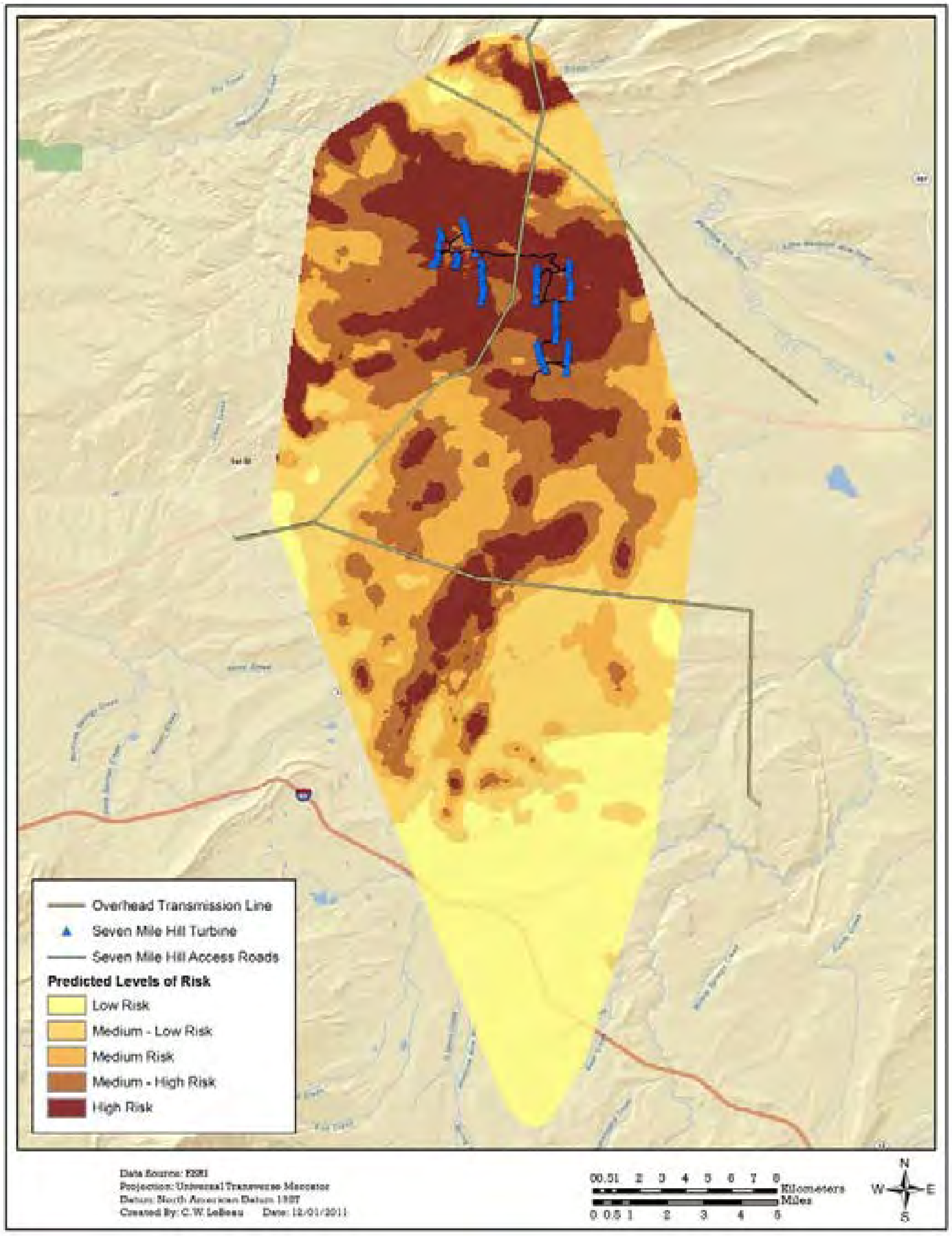

Figure 3-5. Spatial variation in the predicted relative risk of sage-grouse brood failure (low – high) within the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010.

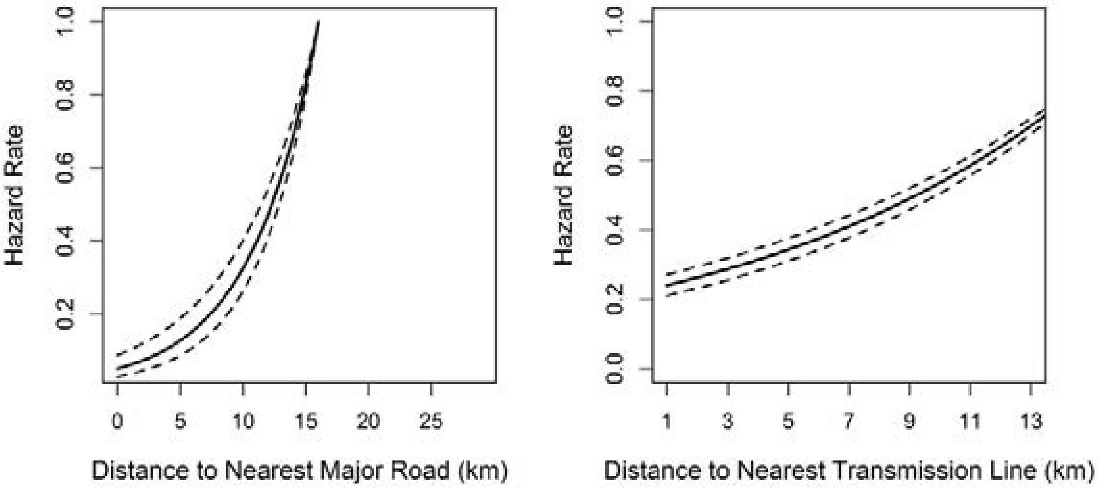

Figure 3-6. Relative hazard rate of female survival adjusted for the distance to nearest major road and distance to nearest overhead transmission line at the Simpson Ridge and Seven Mile Hill study areas, Carbon County, Wyoming, USA, 2009 and 2010. Dashed lines indicate the lower and upper 90% confidence limits.

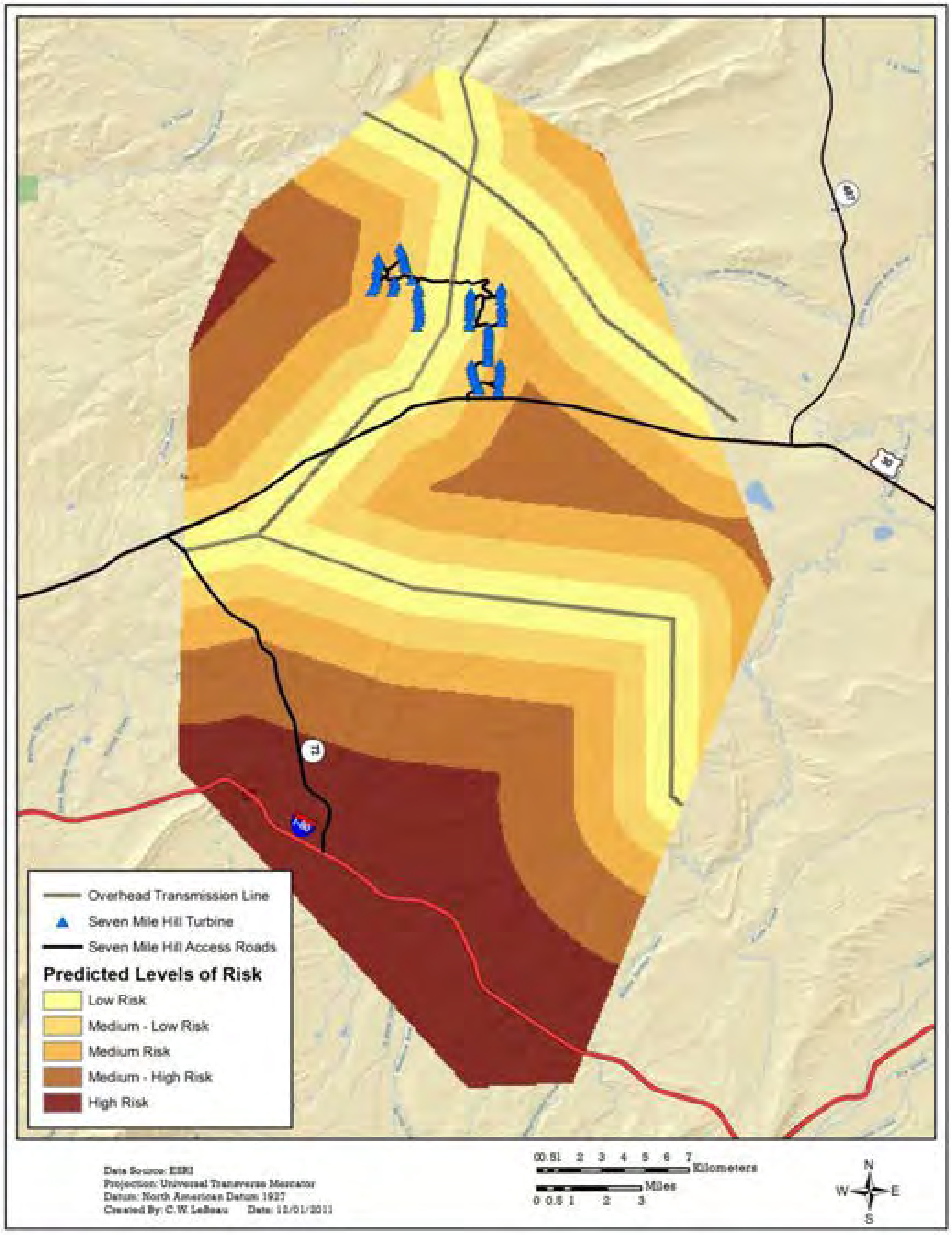

Figure 3-7. Spatial variation in the predicted relative risk of sage-grouse summer mortality (low – high) within the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009 and 2010.

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*, ω_i was a random lek effect, ε_{ij} were error terms for each lek and year assumed to be normally distributed, and β_0(intercept), β_1, and β_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 (ΔAIC = 0.402); however, this interaction was insignificant (β =

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 (β = -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).

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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

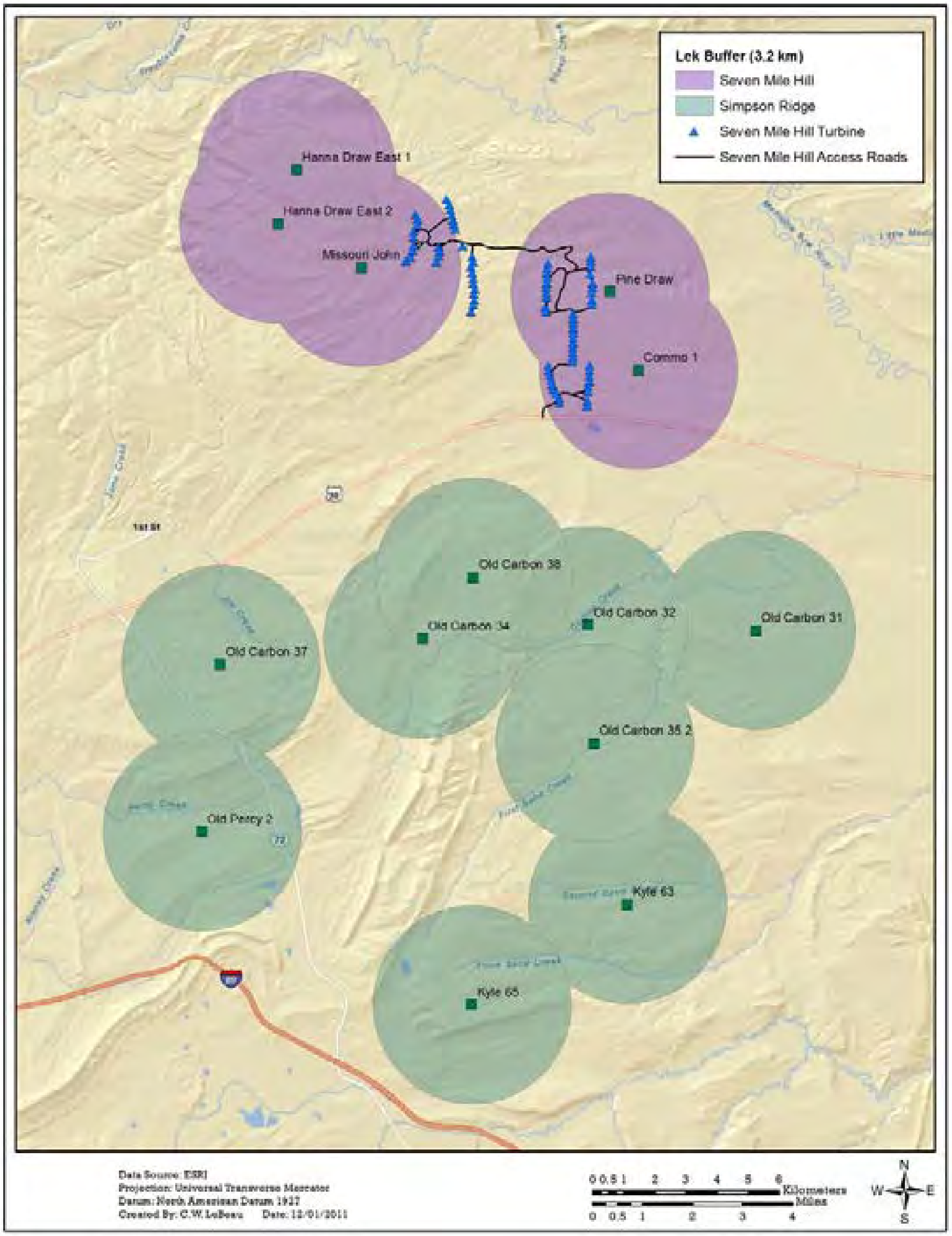

Figure 4-1. Lek locations within the Seven Mile Hill and Simpson Ridge study areas located in Carbon County, Wyoming, USA, 2008–2011.

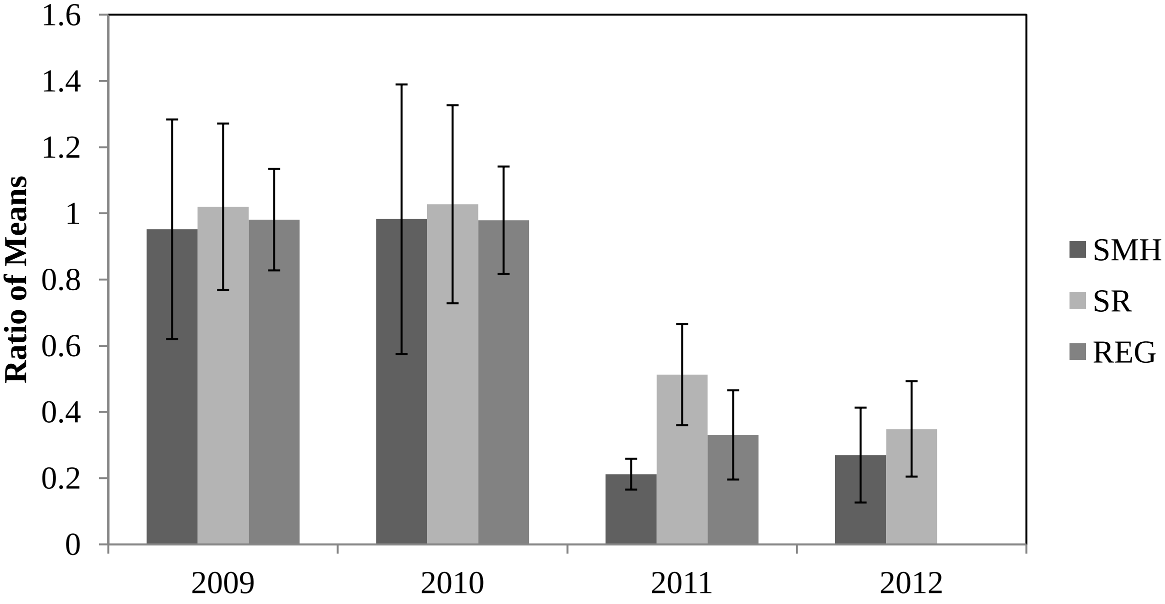

Figure 4-2. Ratio of means (± 90% CI) of peak male lek attendance observed at Simpson Ridge (SR), Seven Mile Hill (SMH), and regional (REG) leks from 2008–2012, Carbon County Wyoming, USA. Pre-development (2008) counts were used as the baseline to detect changes in peak male lek attendance to 4 years post development. The 2012 lek data was not available for the regional lek population at time of publication.

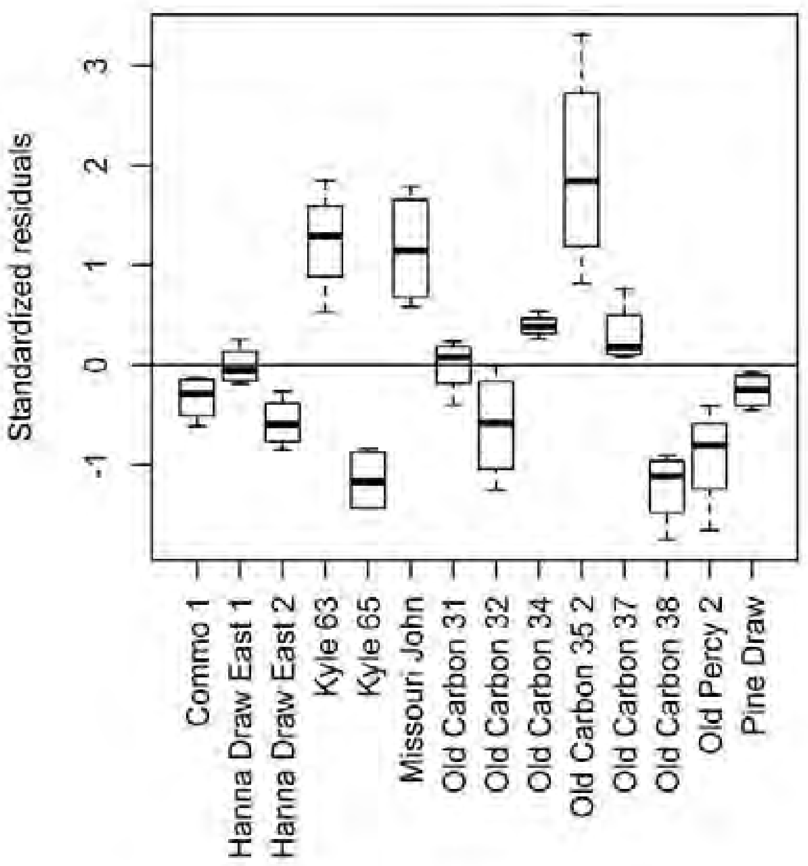

Figure 4-3. The distribution of standardized residuals from the linear regression model comparing male lek attendance to year and study area in Carbon County, Wyoming, USA, 2008–2012. The standardized residuals were plotted against individual leks within both study areas. Leks located above and below the zero residual line indicate within lek correlation. Boxes include the interquartile range (25th–75th 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.

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Management and Conservation

Short-Term Impacts of Wind Energy Development on Greater Sage-Grouse Fitness

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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

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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 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.

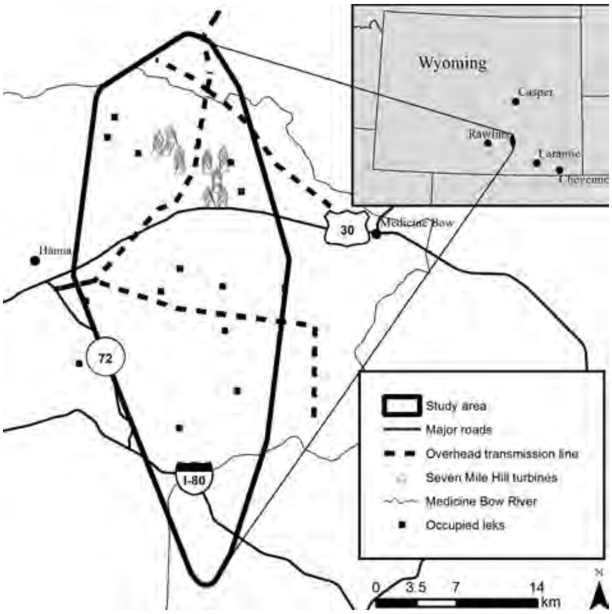

Figure 1. Seven Mile Hill study area in Carbon County, Wyoming, USA and occupied greater sage-grouse leks in 2009 and 2010. The Seven Mile Hill Wind Energy facility consisted of 79, 1.5-MW wind turbines.

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) $\geq$1 egg to be a successful nesting attempt (Rotella et al. 2004). We considered nests that failed to successfully hatch $\geq$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 $\geq$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 $\leq$35–37 days post-hatch; Walker 2008). We considered females to be successful through the early brood-rearing period if $\geq$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 [$\exp(\beta)$] 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 (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. Competing models were limited to models with improved AIC_c scores.

Model[a]	log[L]	*K*	AIC_c	ΔAIC_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.

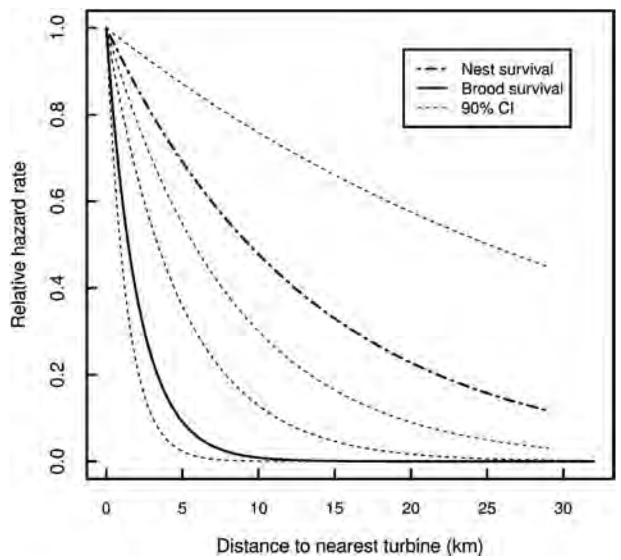

Figure 2. Relative hazard rate of sage-grouse nest and brood survival adjusted for the distance to nearest turbine at the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010. Dotted lines indicate the lower and upper 90% confidence limits.

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.

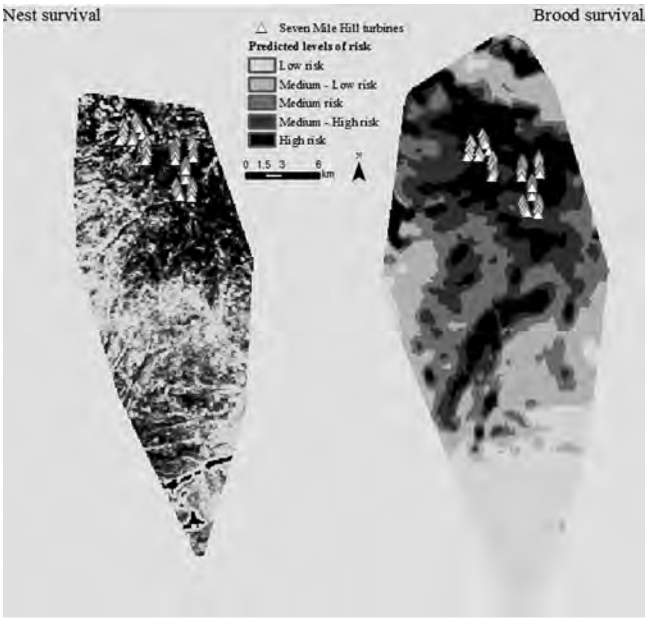

Figure 3. Spatial variation in the predicted relative risk of sage-grouse brood failure and nest failure (low to high) within the Seven Mile Hill study area, Carbon County, Wyoming, USA, 2009 and 2010.

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.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

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

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Contents

Table

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

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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$^{(\text{distance /–1km})}$; 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.

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Symbols in this section refer to citations in Table 1.

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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

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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.

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[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

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[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).

Priority sage-grouse habitat areas

- 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

Priority sage-grouse habitat areas

- 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.

General sage-grouse habitat areas

- 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

Priority sage-grouse habitat areas

- 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

Priority sage-grouse habitat areas

- 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]

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[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 (Eisworth 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.

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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*).

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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).

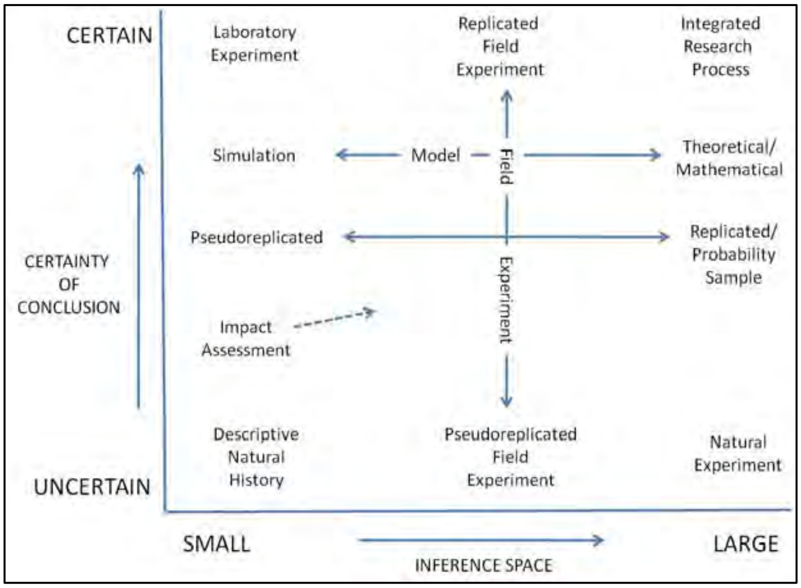

Figure 1. The spectrum of types of wildlife studies that can produce results and conclusions with a large amount of certainty over a very large area of applicability (adapted from Ratti and Garton 1994 and Garton et al. 2005).

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.

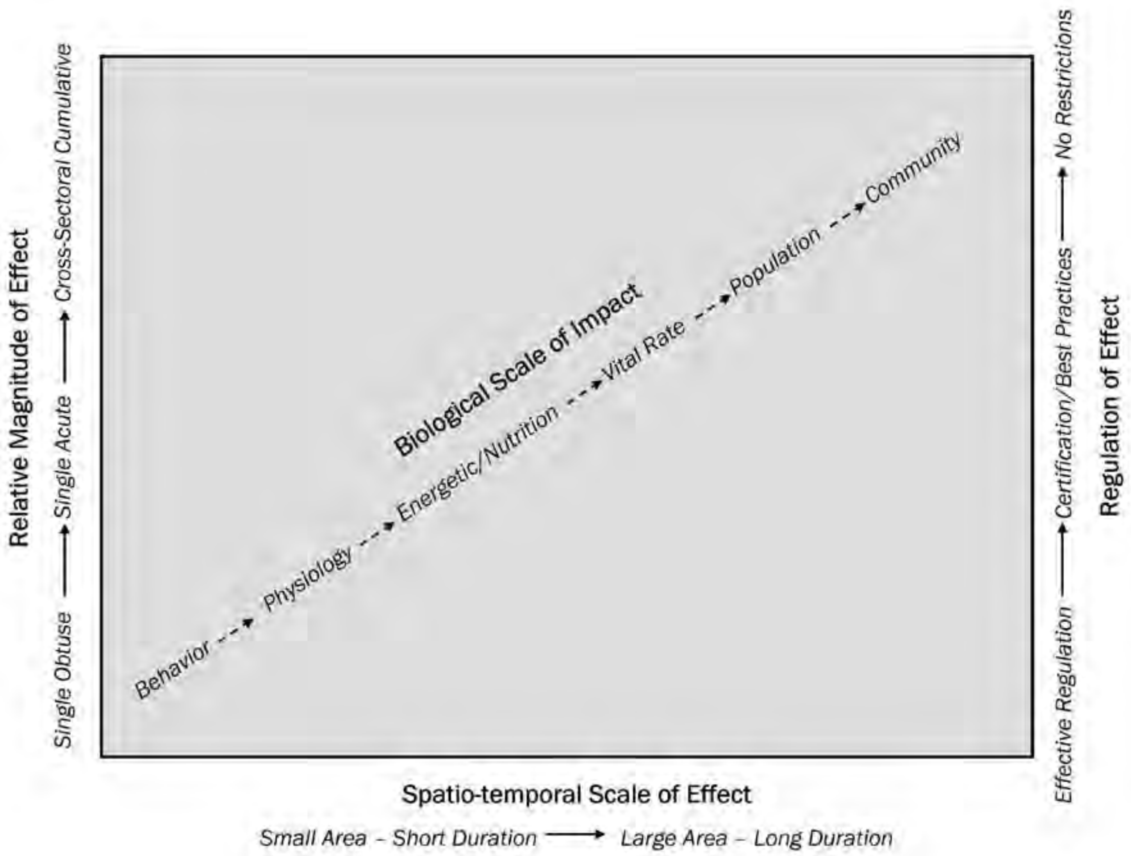

Figure 2. Schematic representation of a typology for classifying and predicting the impacts of human-wildlife interactions (as modified from Johnson and St-Laurent 2011).

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).

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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.

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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.

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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.

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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

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Dynamics of Greater Sage-grouse (*Centrocercus urophasianus*) Populations in Response to Transmission Lines in Central Nevada

Progress Report: Year 9

December 2011

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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 (β = 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 ± 0.18 SE) compared to the year of lowest NDVI (f = 0.08 ± 0.03 SE). We found a similar positive influence on male survival, but the effect was not as strong (β = 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 (β = -0.62; 95% CI = -0.82 to -0.41) and annual survival (β = - 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 (γ=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 (γ=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 (λ) and male breeding propensity. A linear regression comparing annual lek count trends to realized λ, annual variation in breeding propensity, and unexplained error, showed that lek counts produced a good fit to realized λ (R^2 = 0.760). However, the remaining error was sufficient to cause discrepancies between lek counts and realized λ 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; Φ_B = 0.947 ± 0.007) and during the fall (August-October; Φ_F = 0.922 ± 0.009). We detected a substantial cost of reproduction on survival, where females that successfully raised $\geq$ 1 chick to 45 days of age had lower annual survival (Φ_A = 0.498 ± 0.057) than unsuccessful females (Φ_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 (β = 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 (Ψ_S = 0.277 ± 0.089) compared to previously unsuccessful hens (Ψ_U = 0.094 ± 0.025). NDVI had a strong positive influence on female success (β = 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 (λ) 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 (γ) 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 (ΔAIC <3.0), and their β 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 (Φ) as a function of NDVI, temporary emigration (γ) 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 (λ_A), and realized λ (λ_R) using Pradel models. We then used a linear regression to partition the variance in λ_A that was associated with realized rate of growth (λ_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 ≥ 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 (Ψ; 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 Ψ_t) and carryover (effect of NDVI_{t-1} on Ψ_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 ($\beta = 0.28$; 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 ($\beta = 0.21$; 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 λ_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 γ = 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 γ = 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 γ. 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 (β = -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 (β = 0.70, 95% CI = 0.19 to 1.21) compared to the quadratic effect (β = 0.39, 95% CI = -0.13 to 0.92). Model-averaged estimates of γ indicate a general decline in breeding propensity following years of high density (Fig 10).

The most competitive Pradel λ model indicated a positive relationship between NDVI and λ_R (β = 0.37, 95% CI = 0.21 to 0.54)(Table 10). Estimates of general population trajectory (i.e., increase or decline) were similar between λ_A and λ_R, however, annual estimates of λ_A only fell within 95% confidence intervals of model-averaged λ_R in 3 of 7 intervals (Fig. 11). Nevertheless, variance partitioning indicated a strong relationship between λ_A and λ_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 λ_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 λ_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 λ_A ($\lambda_A = 0.896 \pm 0.047$) and λ_R ($\lambda_R = 0.912 \pm 0.051$) 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; $\Phi_W = 0.983 \pm 0.003$), followed by summer (June-July; $\Phi_S = 0.980 \pm 0.006$), 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 ± 0.057, compared to annual survival of 0.610 ± 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* (Ψ_S = 0.277 ± 0.089) compared to females who were unsuccessful in year *t-1* (Ψ_U = 0.094 ± 0.025). There was a direct positive effect of NDVI on female breeding success (β = 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 ± 0.134 in 2006, to a low of 0.141 ± 0.075 in 2008. For previously unsuccessful hens, annual probability of success ranged from 0.191 ± 0.067 in 2006, to a low of 0.047 ± 0.022 in 2008 (Fig 15). The overall probability of female success, averaged across all individuals from 2006-2010, was 0.123 ± 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.

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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
Φ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_B$ + $NDVI_{SF}$	0.000	0.374	10	1271.273
Φ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_B$	0.025	0.369	9	1273.311
Φ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_{SF}$	4.878	0.033	9	1278.164
Φ Season + $Nest_S$ + $Brood_F$ * Age	4.975	0.031	8	1280.274
Φ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_F$	5.287	0.027	9	1278.573
.	.	.	.	.
.	.	.	.	.
.	.	.	.	.
Φ 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 (λ_R) 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 = Year; *p* = Year + secondary occasion; *c* = *p* (Blomberg et al).

Model[a]	ΔAIC_c	w_i	No. Param.	Deviance
λ_R (NDVI)	0.00	0.79	18	5023.76
λ_R (Trend)	3.70	0.12	18	5027.46
λ_R (Trend^2)	4.65	0.08	19	5026.32
λ_R (Year)	9.96	0.01	23	5023.22
λ_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 λ_R. Trend^2 = quadratic trend in annual λ_R. Year = full annual variation. . = λ_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
Φ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_B$ + $NDVI_{SF}$	0.000	0.374	10	1271.273
Φ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_B$	0.025	0.369	9	1273.311
Φ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_{SF}$	4.878	0.033	9	1278.164
Φ Season + $Nest_S$ + $Brood_F$ * Age	4.975	0.031	8	1280.274
Φ Season + $Nest_S$ + $Brood_F$ * Age + $NDVI_F$	5.287	0.027	9	1278.573
.	.	.	.	.
.	.	.	.	.
.	.	.	.	.
Φ 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]	ΔAIC_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 Ψ_t) or carry over (effect of $NDVI_{t-1}$ on Ψ_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:
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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

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[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

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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].

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[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].

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[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

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[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.

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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).

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[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].

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[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. <u>Therefore, we recommend that an ambient value of 20-22 dBA should be used for interim protections in sage-grouse habitat.</u> 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, <u>we recommend continuing to use the 10 dB threshold as an interim measure, combined with appropriate measures of ambient (i.e. 20-22 dBA).</u> 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

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[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

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[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.

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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

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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).

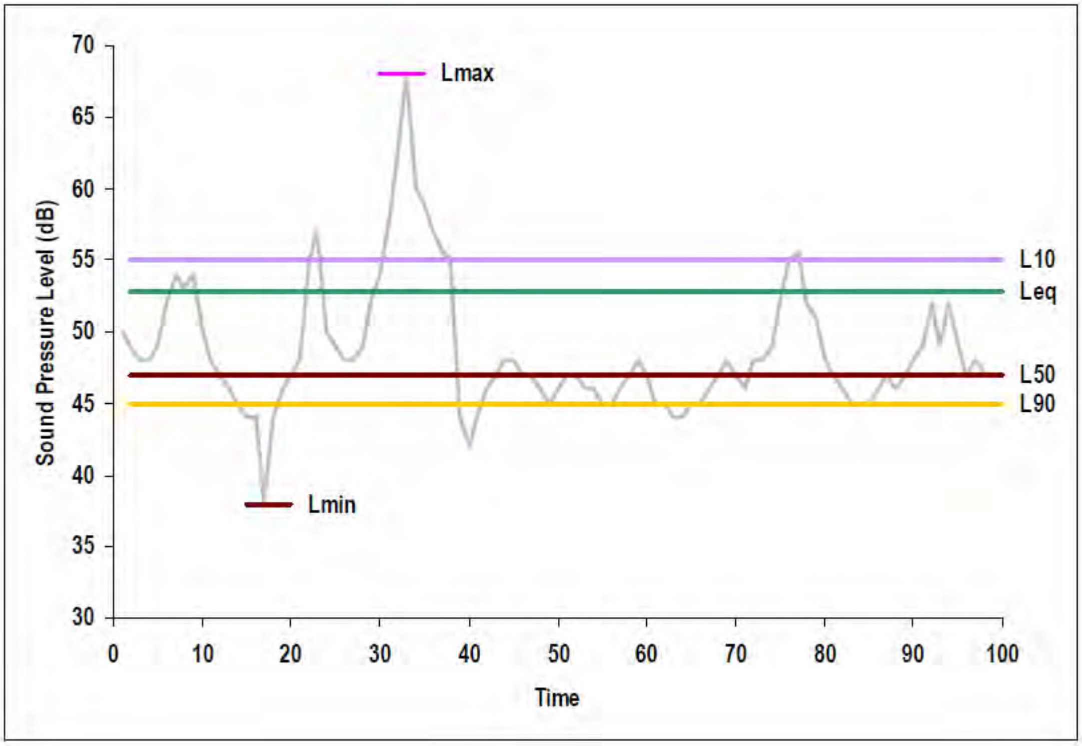


Table 1. Spring 2009 noise levels on leks in the Pinedale Anticline Project Area. Data were collected by KC Harvey Consultants (KC Harvey 2009) from multi-day deployments of four Type-2 sound level meters (Quest - SoundPRO-DL-2-1/3-10; noise floor 20-22 dB). All measures are presented in dBA. Weather 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).

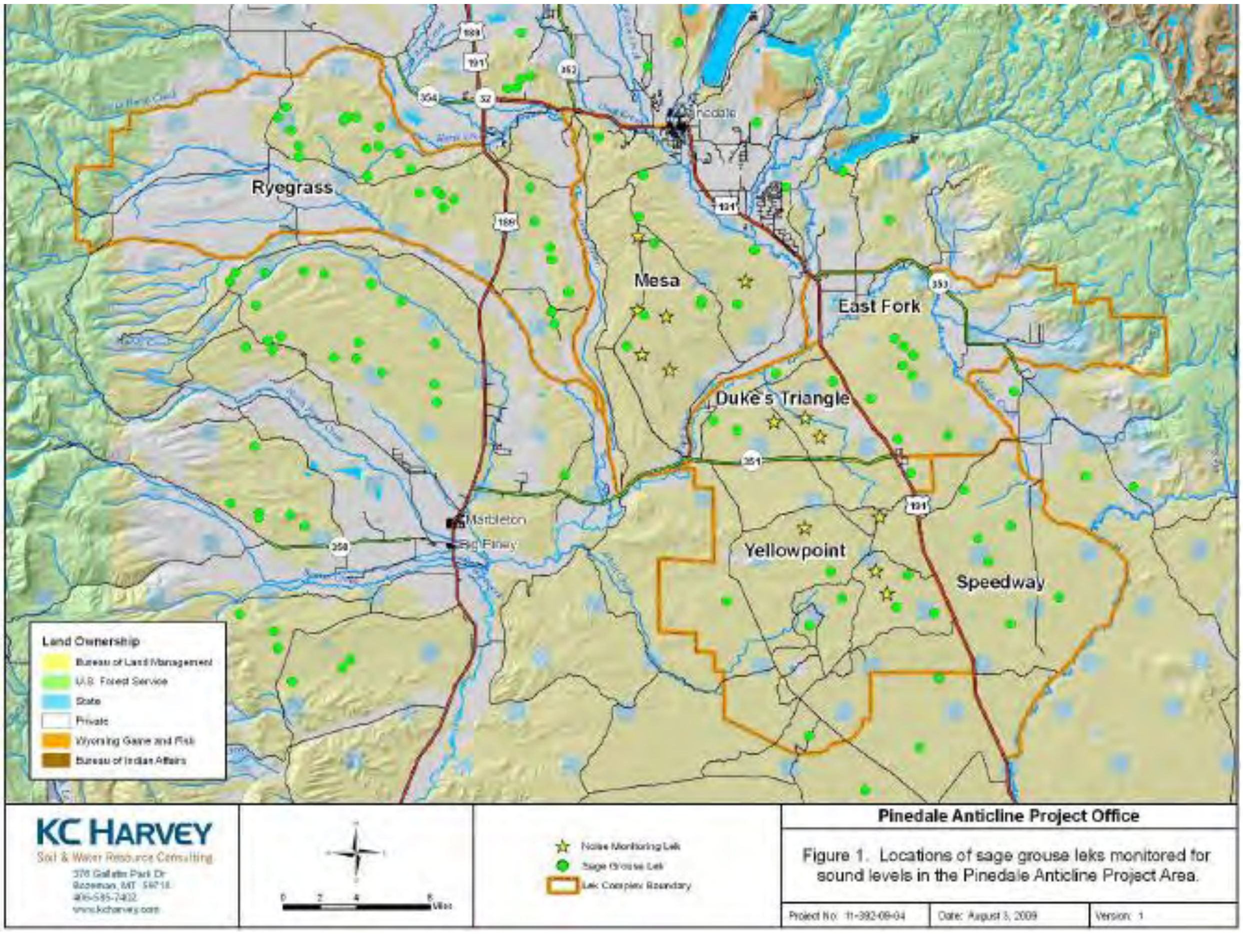


Figure 3. An illustration of noise levels surrounding a lek. This illustration shows a lek in the center, surrounded by a 0.6 mile buffer, a 1.9 mile buffer encompassing ~45% of nests, and a 4-mile buffer encompassing 74-80% of nests (Holloran & Anderson 2005; Moynahan 2004). Noise propagation is shown 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].

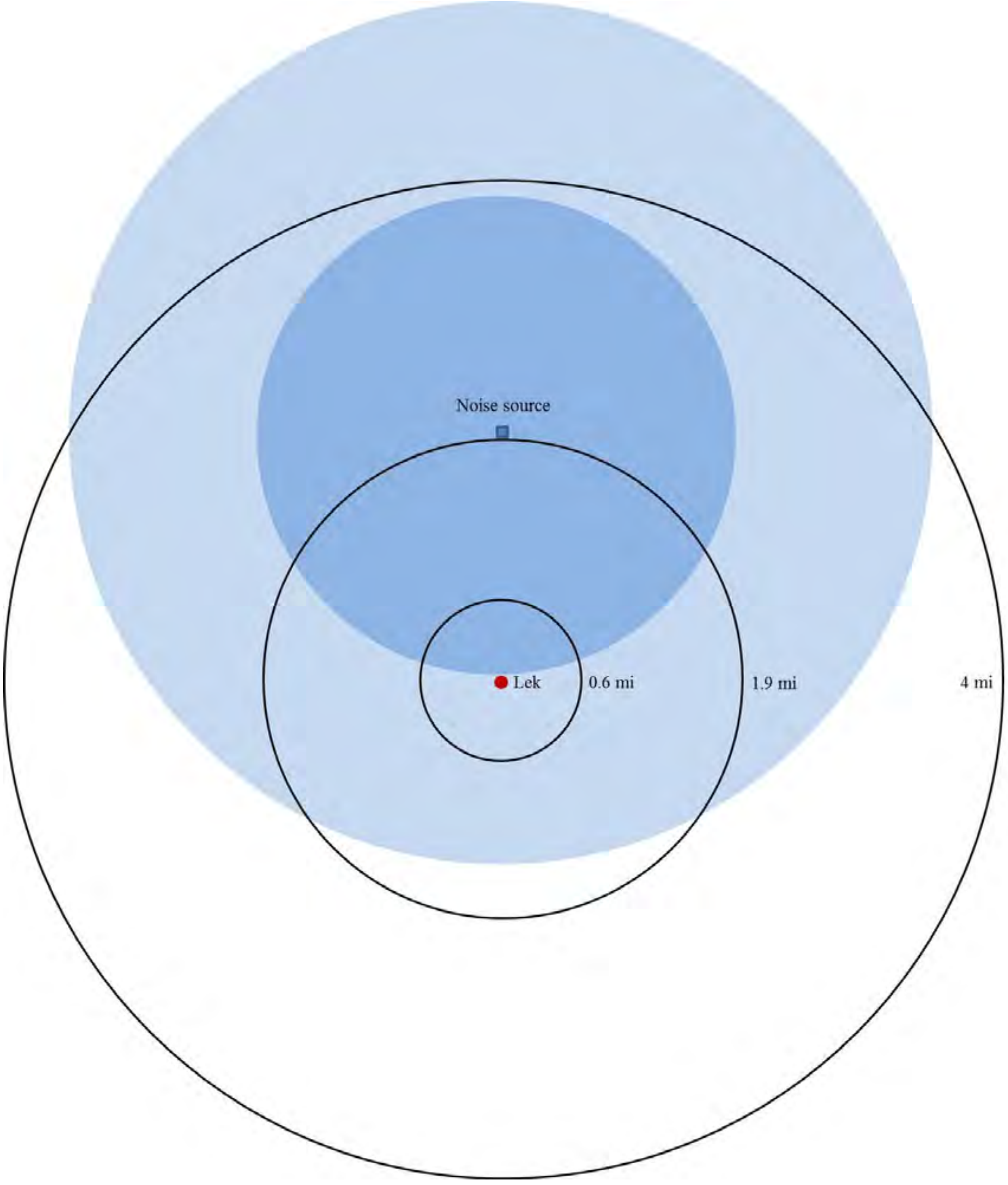
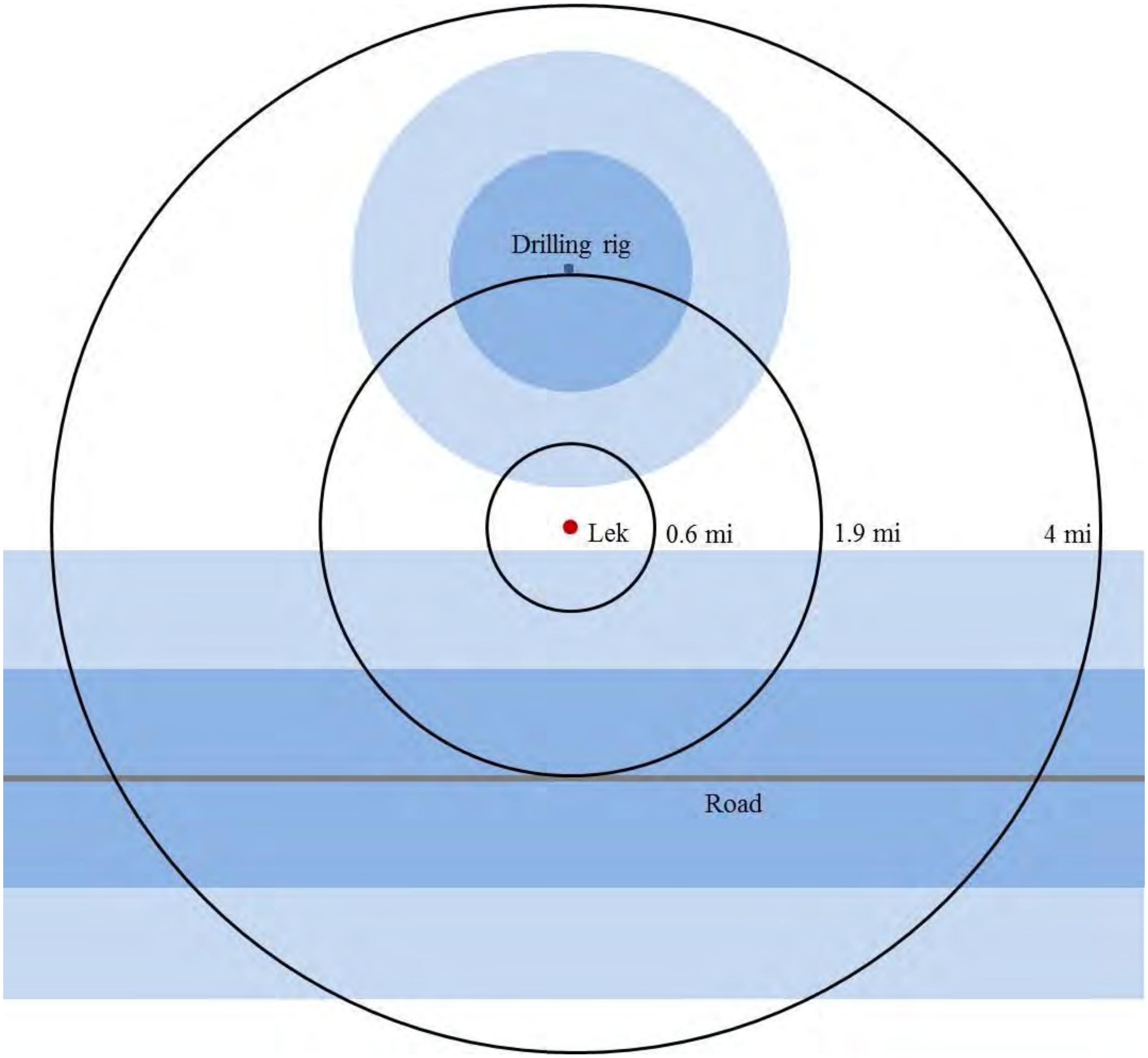


Figure 4. Traffic and drilling noise surrounding a lek. This illustration shows a lek in the center, surrounded by a 0.6 mile buffer, a 1.9 mile buffer encompassing ~45% of nests, and a 4-mile buffer encompassing 74-80% of nests (Holloran & Anderson 2005; Moynahan 2004). Noise from an example natural 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].



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ORIGINAL RESEARCH

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Phenology largely explains taller grass at successful nests in greater sage-grouse

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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 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):

$$\text{GrassHeight}_{\text{Hatch}} = \text{GrassHeight}_{\text{Fate}} - \left(\text{SurveyDate}_{\text{Fate}} - \text{SurveyDate}_{\text{Hatch}}\right) \times \beta_{\text{grass}}$$

where, for each study area and year, we fit a linear regression of measured grass height ($\text{GrassHeight}_{\text{Fate}}$) on day of nesting season ($\text{SurveyDate}_{\text{Fate}}$) to estimate β_{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 (β_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,

$$y_{i,t} \sim \text{Bern}(y_{i,t-1} S_{i,t})$$

and

$$\text{logit}\,(S_{i,t}) = \beta_0 + x_i{}'\beta$$

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 (μ=0; σ=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

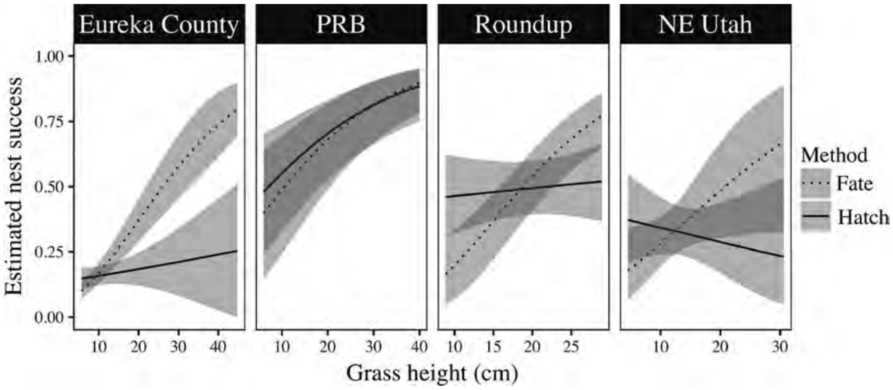

FIGURE 1 Predicted response of sage-grouse nest success (and 95% CI [Eureka County] or CRI [other studies]) to live grass height using measurements collected with a biased method following determination of nest fate (dotted lines), and those measured or corrected to the predicted hatch date of nests (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 (χ^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).

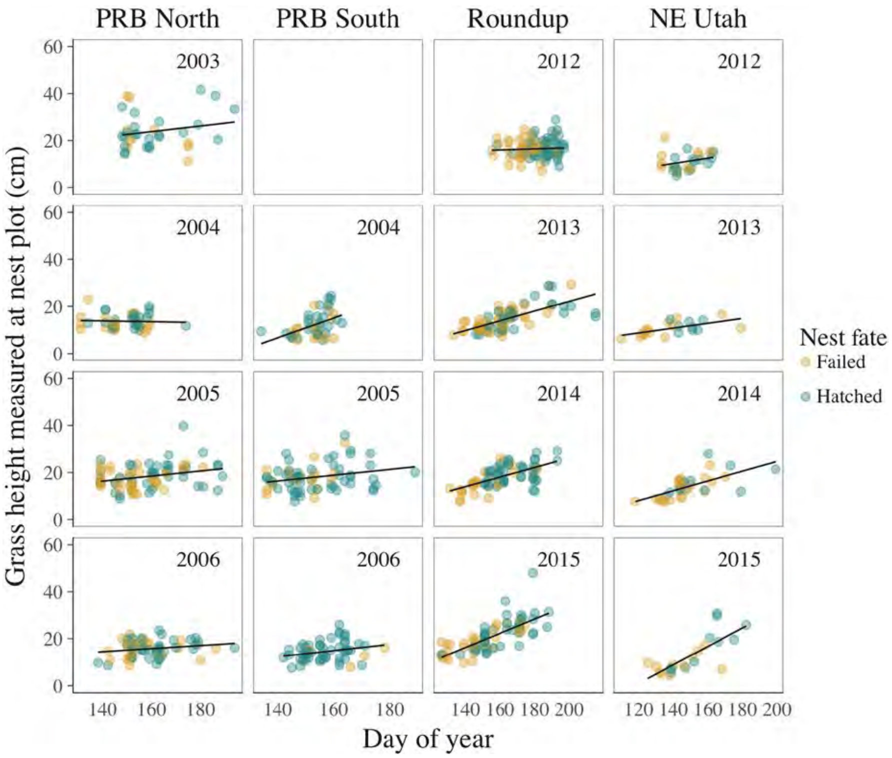

FIGURE 2 Average grass height surrounding successful and failed sage-grouse nests (*n* = 808) at the ordinal date of measurement by year (rows) and study area (columns). After accounting for phenology, a difference in grass height between successful and failed nests was not supported

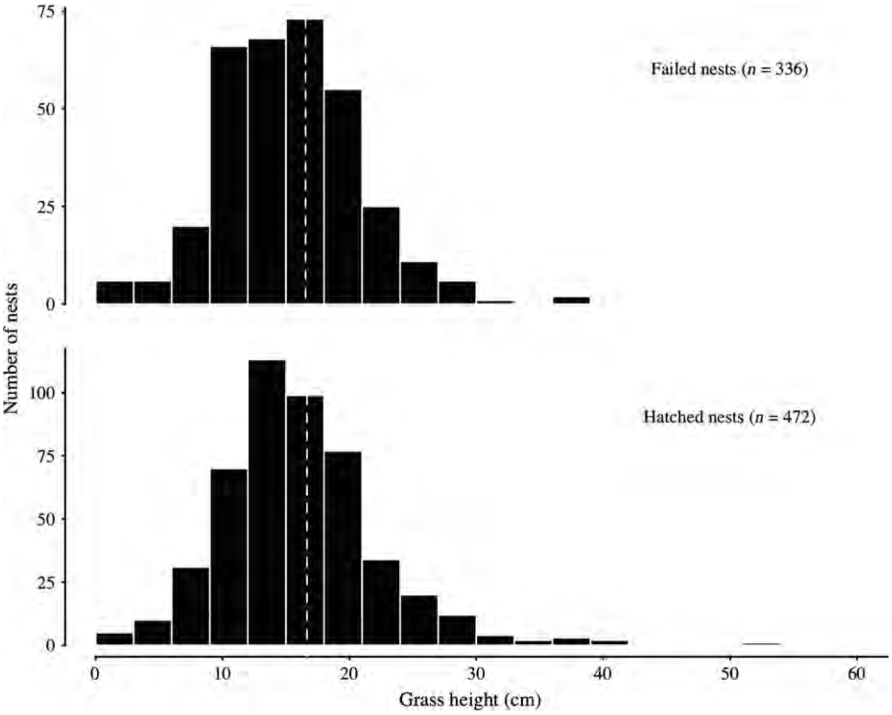

FIGURE 3 Grass heights surrounding greater sage-grouse nests (*n* = 808) corrected to hatch date. Median height of grass-surrounding nests (dashed vertical lines) was 15.26 cm at successful nests and 15.14 cm at failed nests. A one-sided Kolmogorov–Smirnov test provided no evidence that the distributions 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 α 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.

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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.

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Reproductive state leads to intraspecific habitat partitioning and survival differences in greater sage-grouse: implications for conservation

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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.

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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 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 20×50 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 20×50 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 ± 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 ± 116 m (s.e.) for brood-rearing females and 1539 ± 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

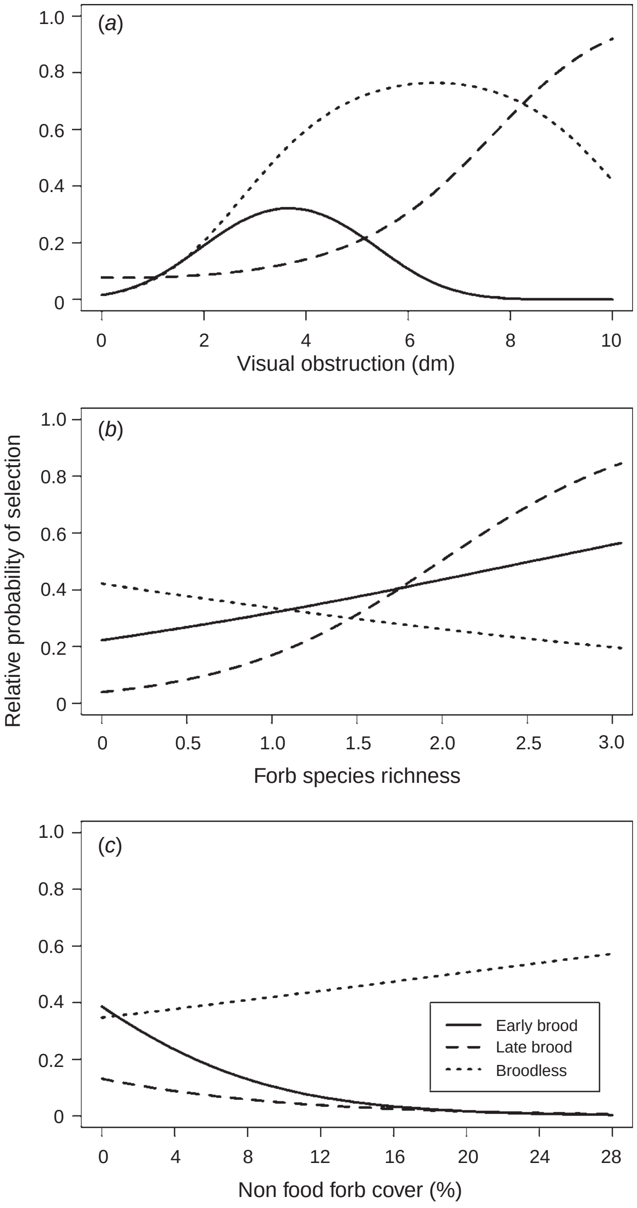

Fig. 1. Relative probability of selection of early-brood, late-brood, and broodless female summer habitats as a function of (*a*) visual obstruction, (*b*) forb species richness, and (*c*) non-food forb cover in central Wyoming, USA, 2011–13.

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 ± 0.06 weeks, late brood = 8.2 ± 0.06 weeks, broodless = 1.2 ± 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

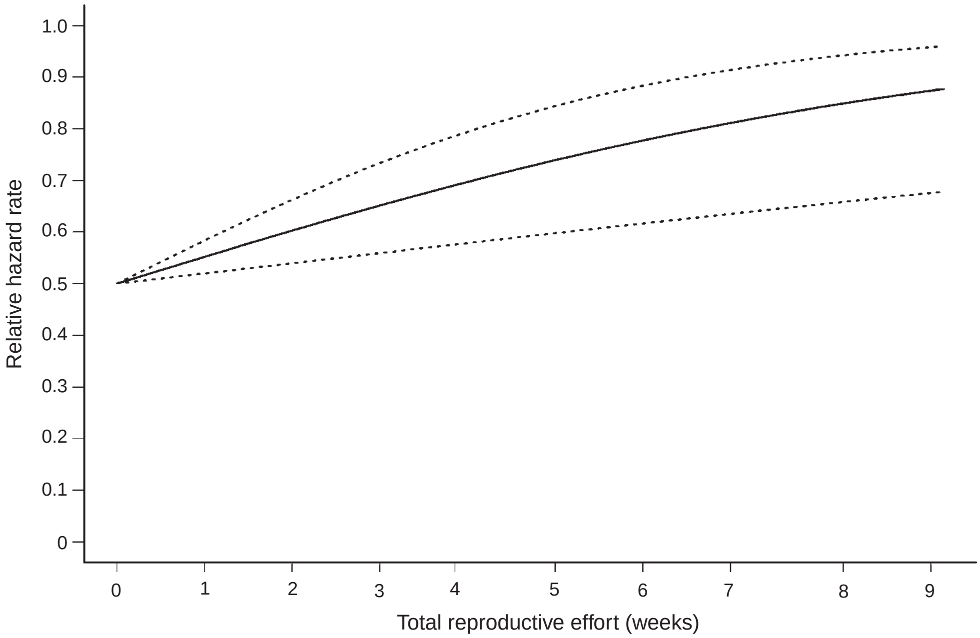

Fig. 2. Relative hazard rates for the most-supported model that included total reproductive effort (weeks) predicting adult female sage-grouse survival in central Wyoming, USA, 2011–13. Hazard rates were plotted with 90% confidence intervals (dashed lines).

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

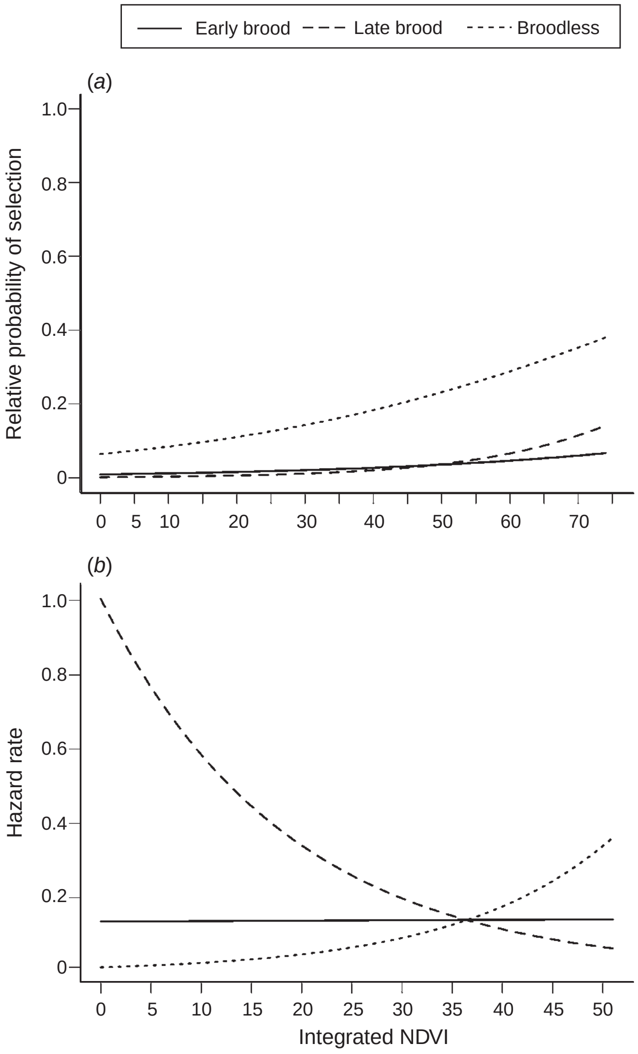

Fig. 3. Relative probability of selection of early-brood, late-brood, and broodless female summer habitats as a function of (*a*) INDVI, and (*b*) hazard rates relative to INDVI across reproductive states in central Wyoming, USA, 2011–13. We approximated each reproductive state by partitioning total 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.

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Tools and Technology

Mapping Sage-Grouse Fence-Collision Risk: Spatially Explicit Models for Targeting Conservation Implementation

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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*).

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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 × 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 × 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. (2012a) 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 (θ) and removal (ψ) 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 (ψ) 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 (θ) was modeled as a function of distance to lek, lek size, and TRI, and removal (ψ) 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; $\hat{y} = 78 \times \exp(\beta_0 + \beta_1 \times \mathrm{TRI} + \beta_2 \times \mathrm{distance})$). 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 (ΔAIC = 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]	ΔAIC	AIC
θ(TRI + distance) ψ(region)	5	0	403.505
θ(TRI + lsize + distance) ψ(region)	6	1.582	405.086
θ(TRI) ψ(region)	4	3.153	406.658
θ(TRI + lsize) ψ(region)	5	4.581	408.086
θ(distance) ψ(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 θ = daily collision rate and ψ = 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 (ΔAIC > 19).

[c] K = no. of model parameters.

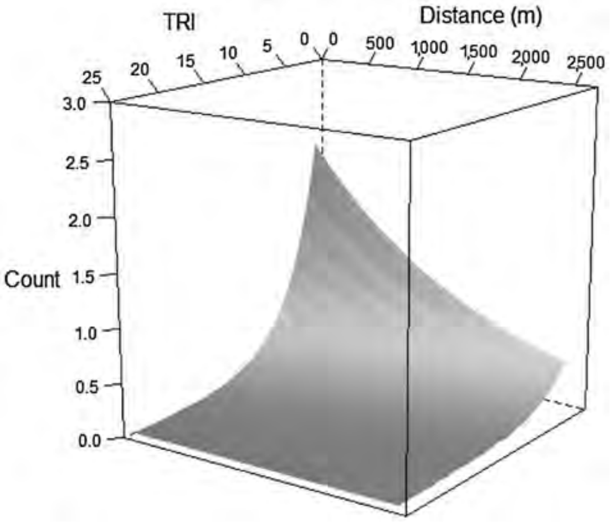

Figure 2. Maximum-likelihood estimates of total number of greater sage-grouse fence collisions over the 78-day lekking season from the top stochastic-linear-immigration-death model fit to data from southern Idaho, USA. Collision was a function of terrain ruggedness (TRI) and distance to the nearest lek. Maximum-likelihood estimates of total collisions from the top model = 78 × exp{$\beta_0 + \beta_1 \times \text{TRI} + \beta_2 \times \text{distance}$}.

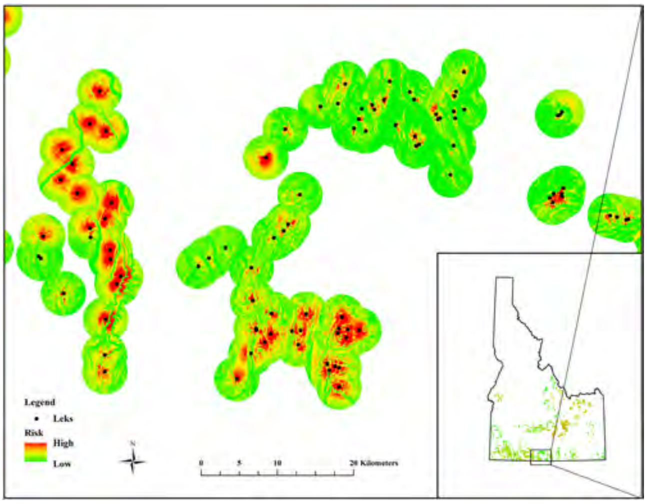

Figure 3. Example of spatially explicit fence-collision-risk maps from greater sage-grouse breeding habitats of southern Idaho, USA. Collision risk was a function of terrain ruggedness (TRI) and distance to the nearest lek. Maximum-likelihood estimates of total collisions (i.e., risk) from the top stochastic-linear-immigration-death model = 78 × 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).

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 (θ) and removal (ψ) 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 (ΔAIC = 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*) power-line 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.

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Viability analyses for conservation of sage-grouse populations:

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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

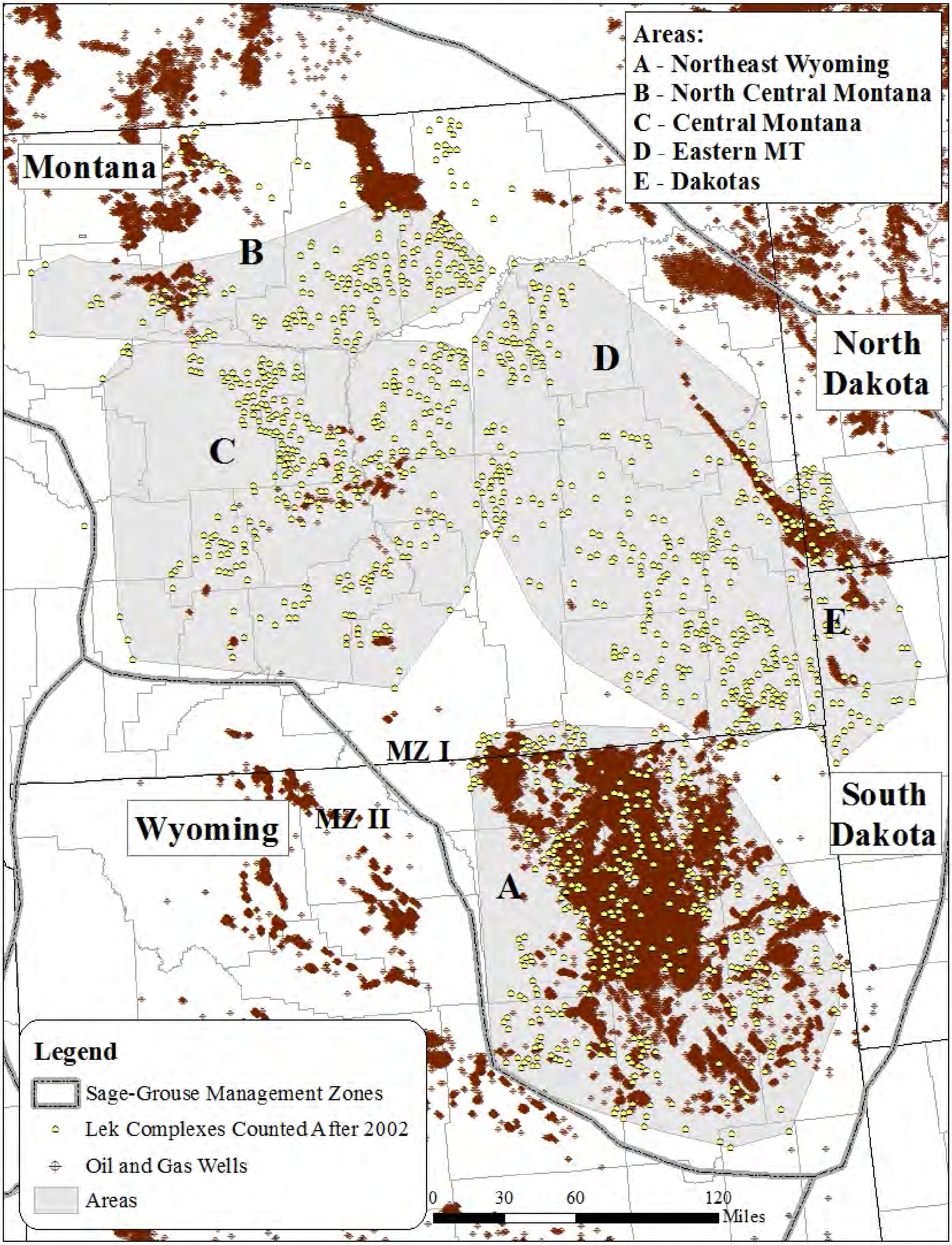


Figure 1. Distribution of oil and gas development and lek complex centers used in analysis with respect to focal and supporting areas.

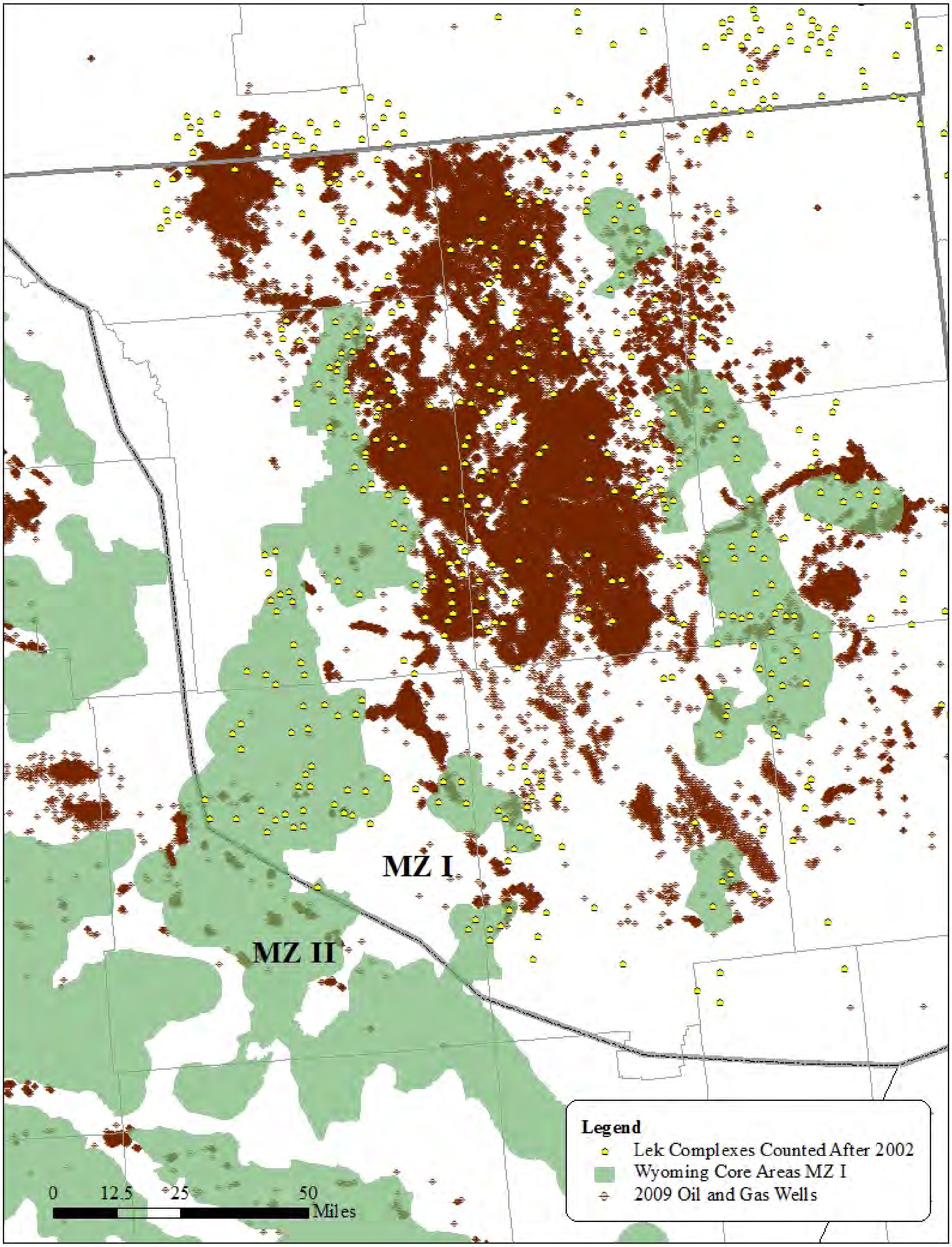


Figure 2. Distribution of oil and gas wells and lek complex centers used in the analysis with respect to northeast Wyoming core areas.

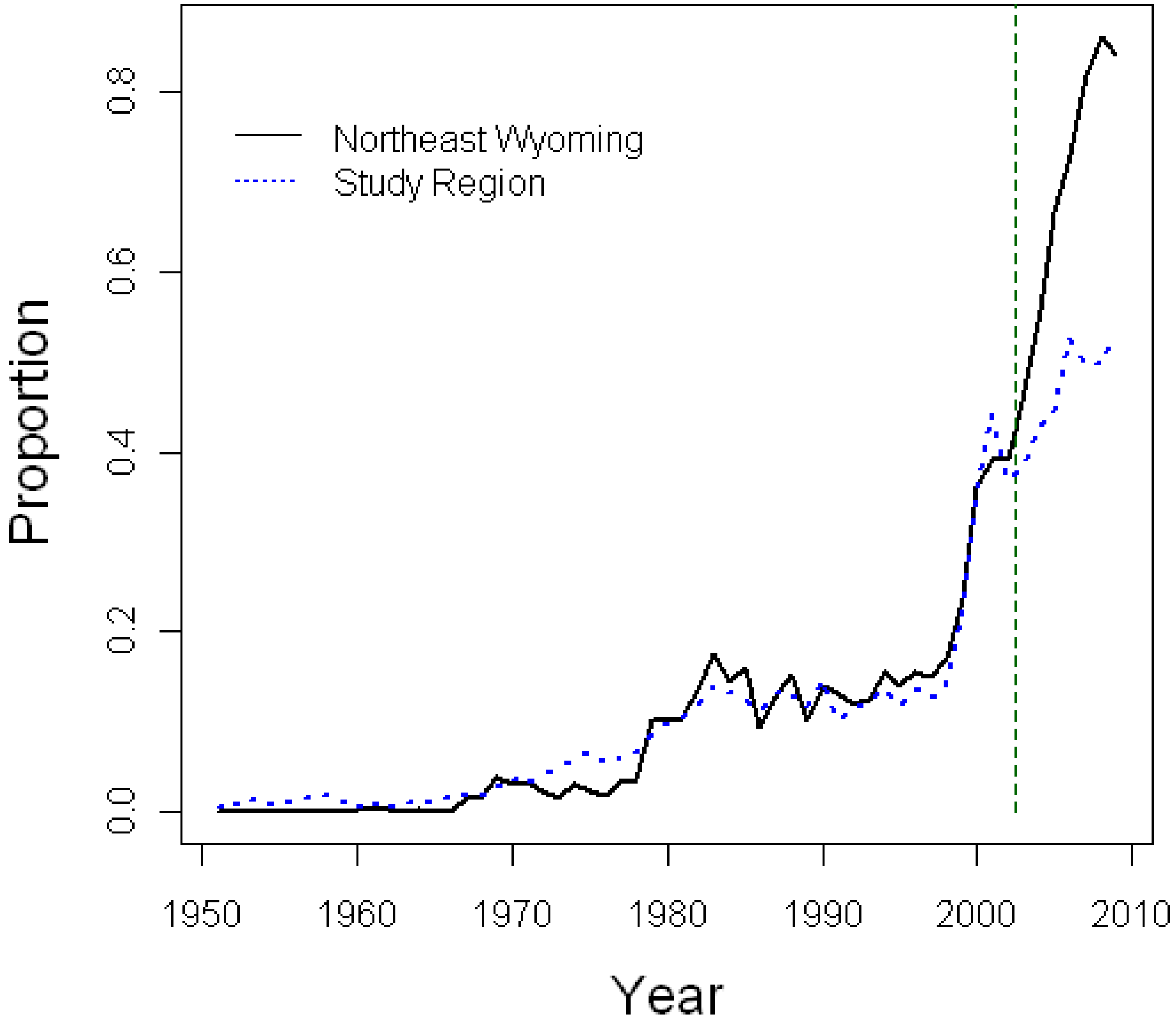


Figure 3. Proportion of lek centers in northeast Wyoming (n=428) and study region (n=1,508) counted during the year. Proportion of northeast Wyoming core area leks counted each year was similar to that in the focal area as a whole (difference < 0.07). Only counts to the right of the dashed line were 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

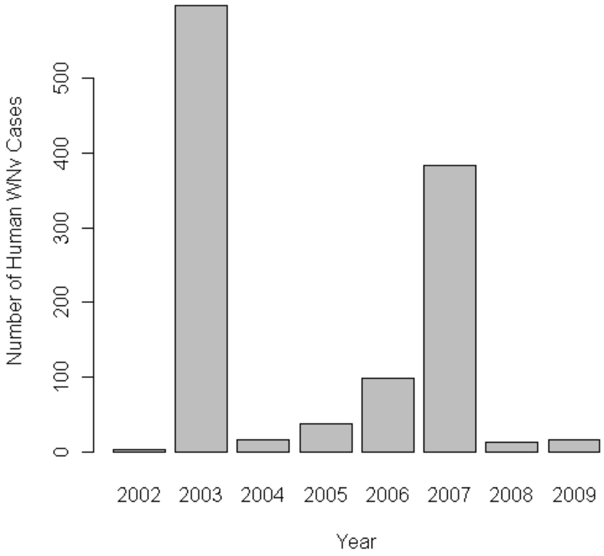


Figure 4. West Nile virus was first detected in the study region in 2002. Outbreaks occurred in 2003 and 2007.

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.

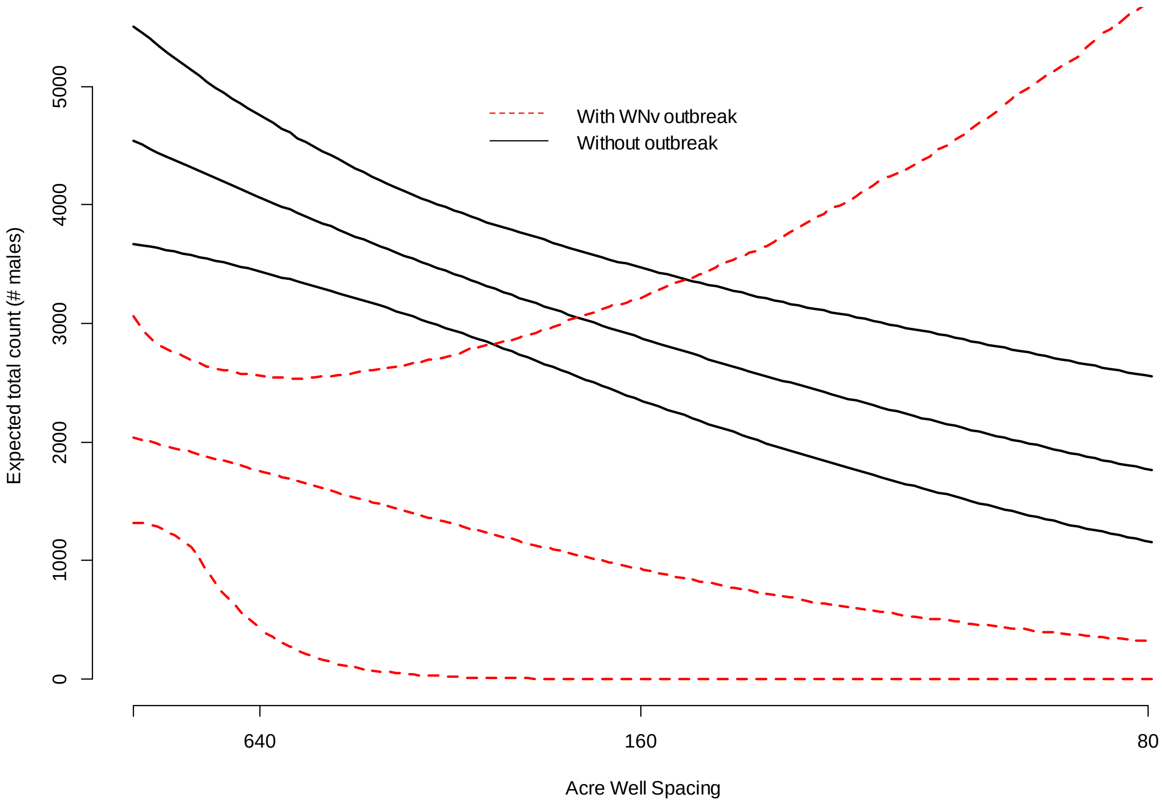
	Total Male Count	
Area	Predicted	Actual
Northeast Wyoming	3,315	3,316
Central Montana	3,661	3,693
Eastern Montana	2,789	2,770
Dakotas	661	659
North-central Montana	3,656	3,681

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



None 640 160 80

Acre Well Spacing

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.

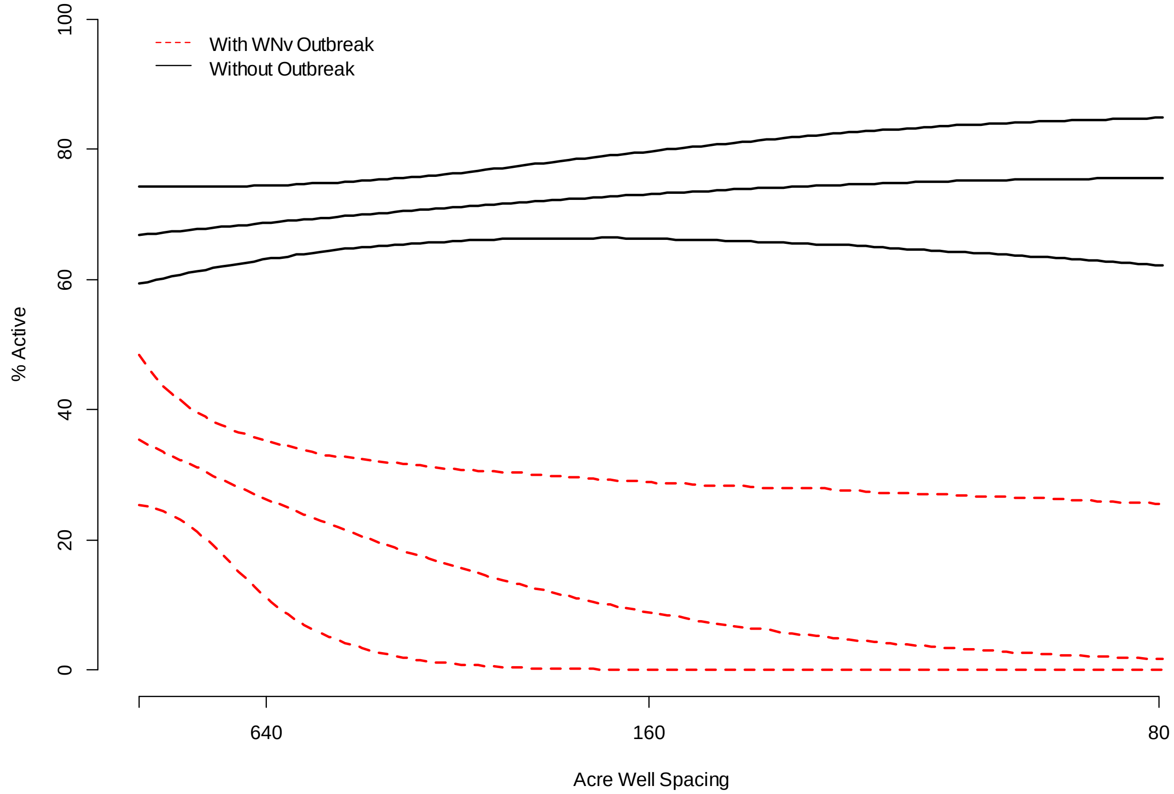


Figure 6. Percent of 370 leks in northeast Wyoming expected to remain active (with 95% confidence bands) versus the average spacing of oil and gas wells within 12.4 mi of each lek.

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]			Number of Leks							
	Total Lek Count		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]			Number of Leks							
	Total Lek Count		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)

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[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.

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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)

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Evaluating efficacy of fence markers in reducing greater sage-grouse collisions with fencing

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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

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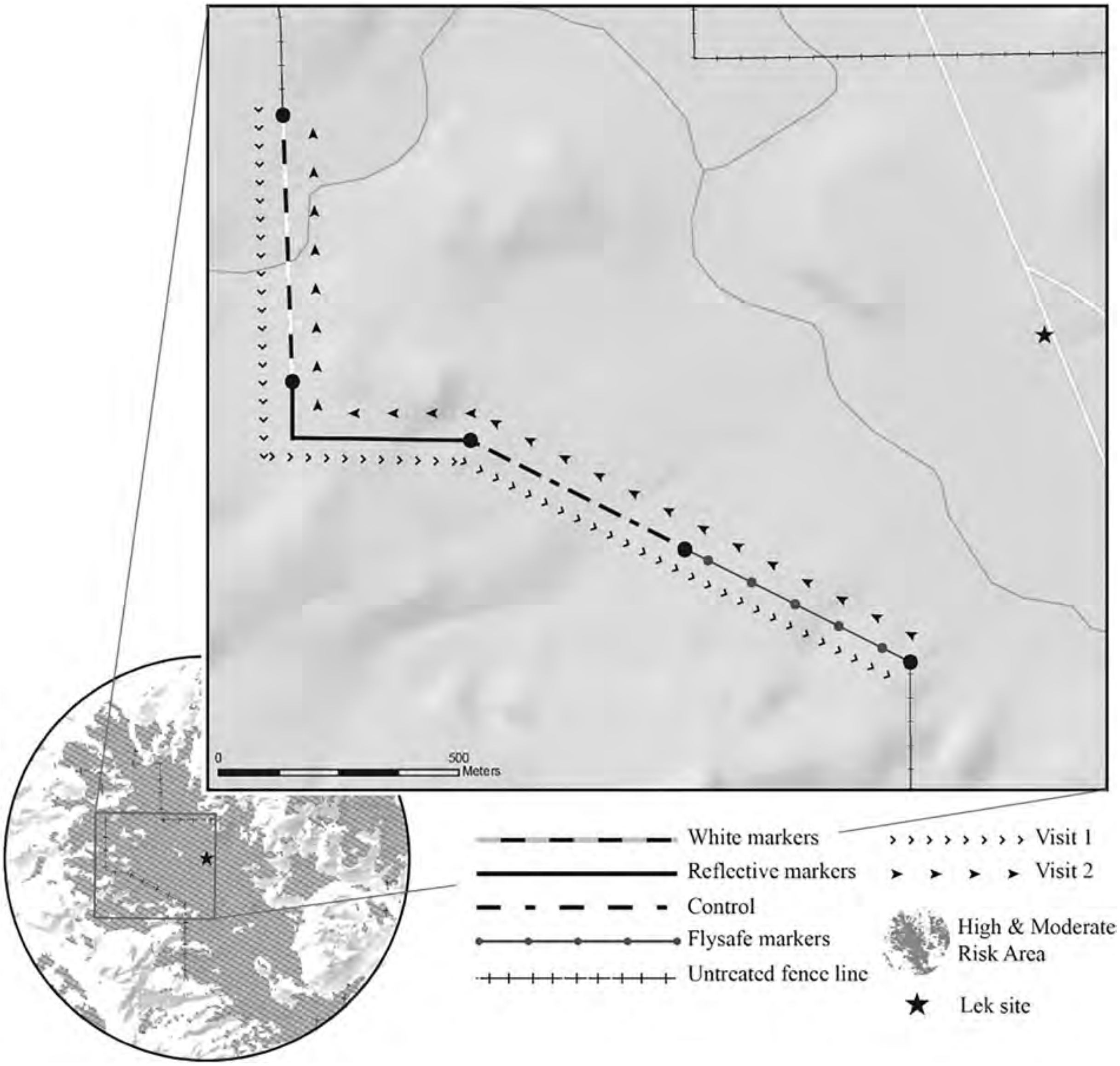

Fig. 1. Illustration of four treated segments of fence-line associated with a focal lek.

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 ≥ 1 new sage-grouse collision was present on ≥ 1 fence segment at site i during any of the surveys, ψ_i, (2) the probability that evidence of ≥ 1 new collision was present at a fence segment during survey j, θ_{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 (ΔAIC$_c$), and AIC$_c$ weights are also shown for models with ΔAIC$_c$ ≤ 10.

ψ	p	npar	AIC$_c$	ΔAIC$_c$	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 ≫ 1 indicate support for the importance of that variable, weights near 1 are inconclusive, and weights ≪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 ≥ 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 ≥ 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 (ΔAIC$_c$), and AIC$_c$ weights.

ψ	npar	AIC$_c$	ΔAIC$_c$	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 $\mathrm{AIC_c}$ 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 $\gg 1$ suggest strong support for that variable, weights near 1 are ambiguous, and weights $\ll 1$ 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 [$\beta = -0.843$,(95% CI = -1.545, -0.141); odds ratio: 0.430, (0.128, 0.732)], with reflective [$\beta = -1.018$,(95% CI = -1.967, -0.068); odds ratio: 0.361, (0.018, 0.705)] and white markers [$\beta = -0.808$, (-1.703, 0.087); odds ratio: 0.446, (0.047, 0.857)] reducing occupancy probabilities slightly more than Fly Safe markers [$\beta = -0.725$, (-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.

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 ($\mathrm{AIC_c}$), difference between a model's AICc value and the minimum AICc value ($\Delta\mathrm{AIC_c}$), and $\mathrm{AIC_c}$ weights are also shown for the top 10 models.

θ	npar	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	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 $\mathrm{AIC_c}$ 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)

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

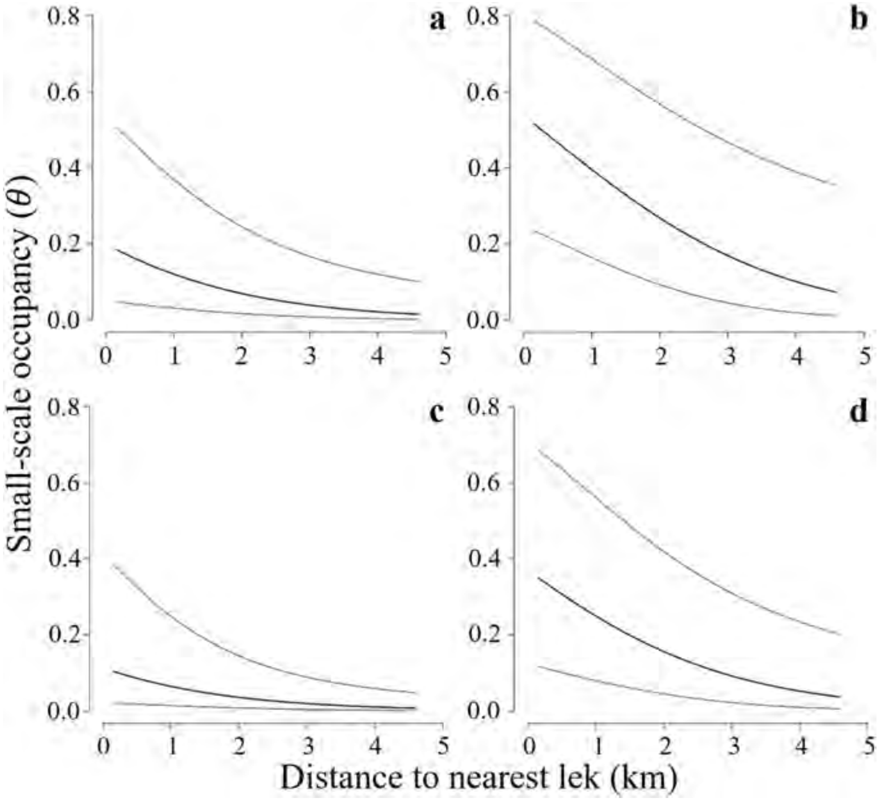

Fig. 3. Small-scale occupancy probability (θ, heavy lines) and associated 95% confidence intervals (light lines) as a function of distance to nearest lek for a) unmarked, wood post, b) unmarked, wood and t-post, c) marked, wood post, and d) marked, wood and t-post fence segments.

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 ≥ 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.

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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 (ΔAIC_c), and AIC_c weights are included.

ψ	p	npar	AIC_c	ΔAIC_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 (ΔAIC_c), and AIC_c weights are included for models with $\Delta\text{AIC}_c < 4$.

θ	npar	AIC_c	ΔAIC_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)

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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, λ) 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, λ), 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, λ) for each of four WNV impact scenarios. We then generated and compared means for λ 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 λ for each year during the 20-yr period.

FINDINGS

The addition of WNV mortality resulted in a projected average estimated reduction in λ 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 λ resulted in wide variation in simulated values for λ 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.

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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	$\Delta\lambda$	$\Delta\lambda$
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, λ) 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, λ, 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.

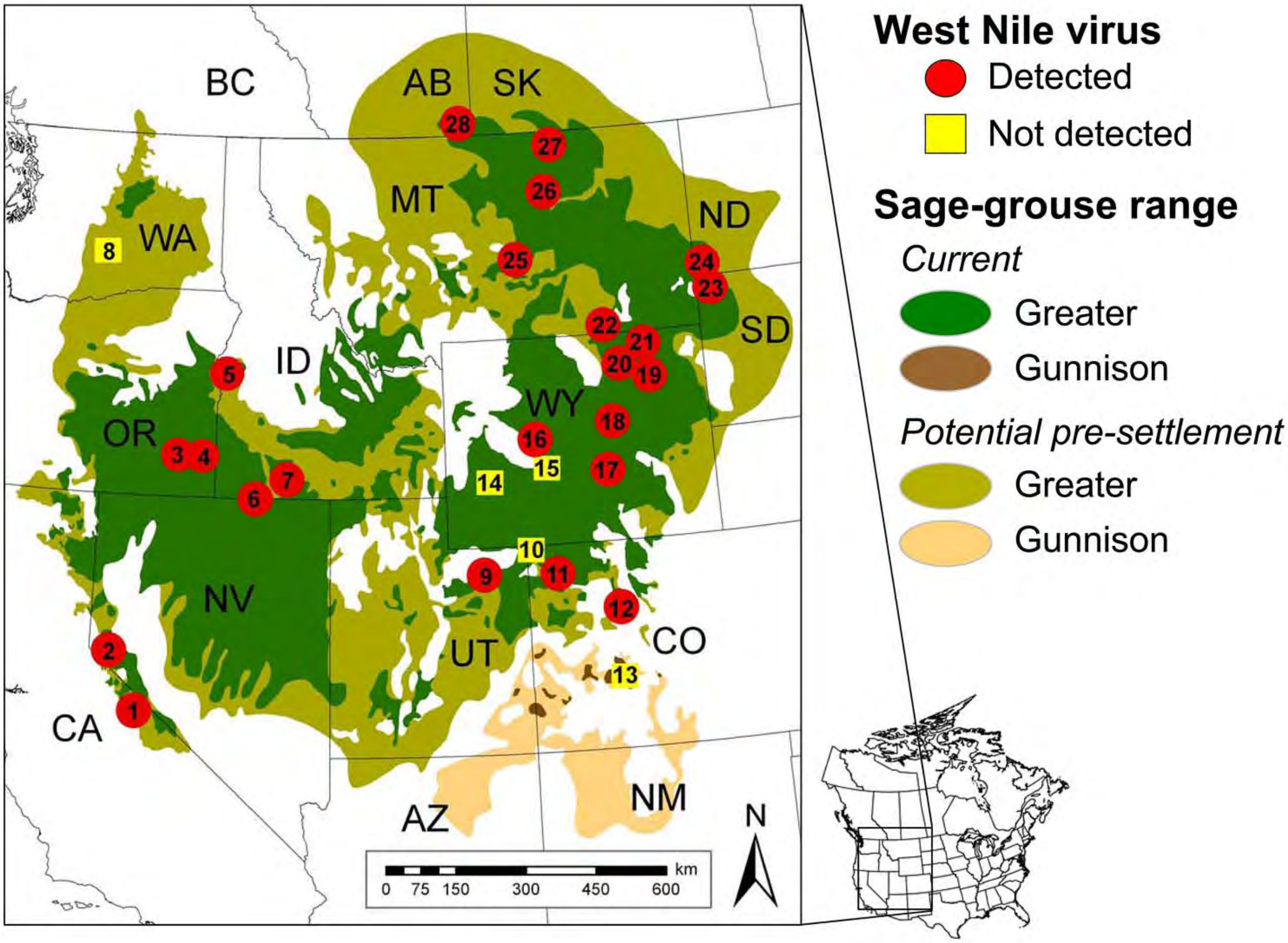
West Nile virus
Detected
Not detected
Sage-grouse range
Current
Greater
Gunnison
Potential pre-settlement
Greater
Gunnison
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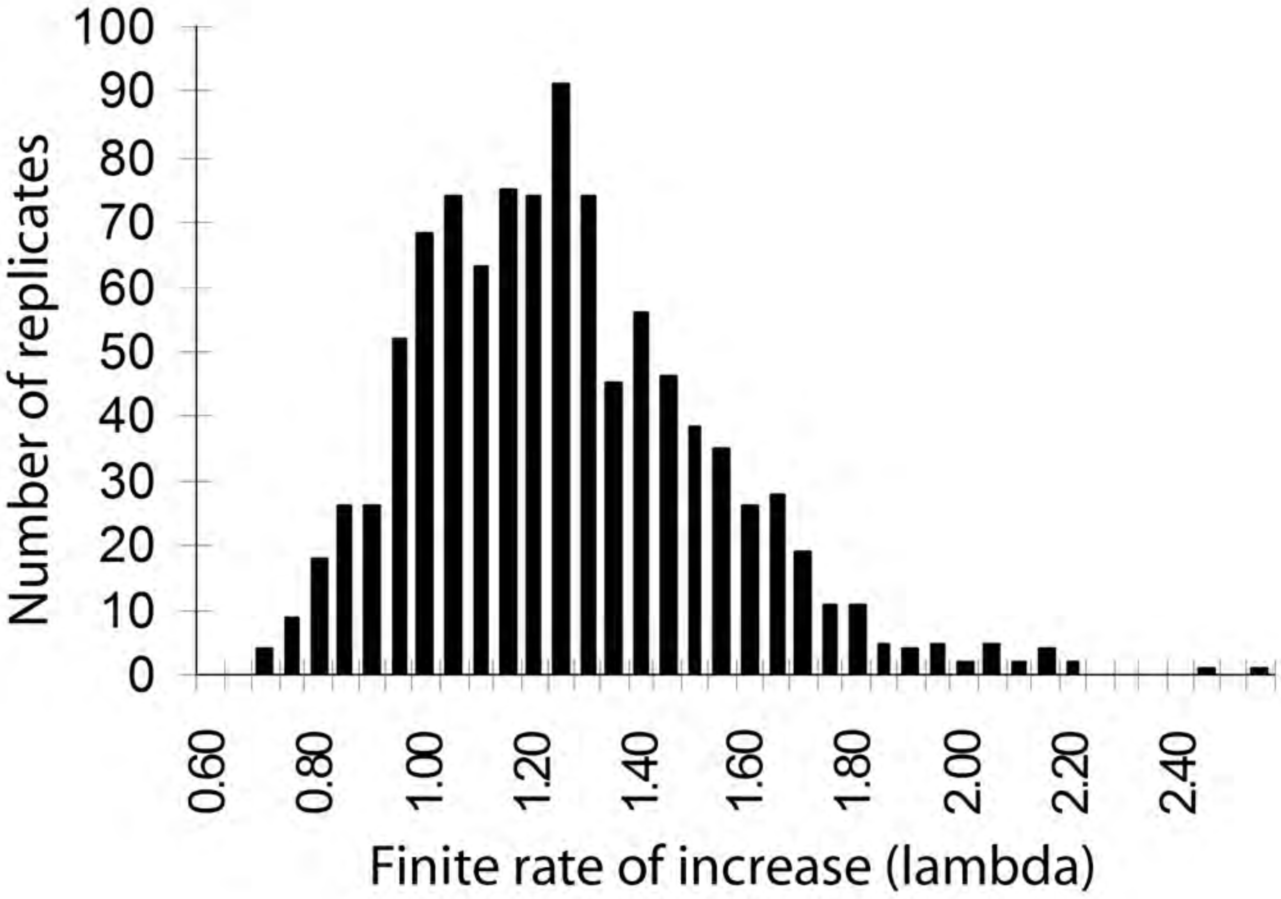
Figure 2.



100
90
80
70
60
50
40
30
20
10
0
Number of replicates
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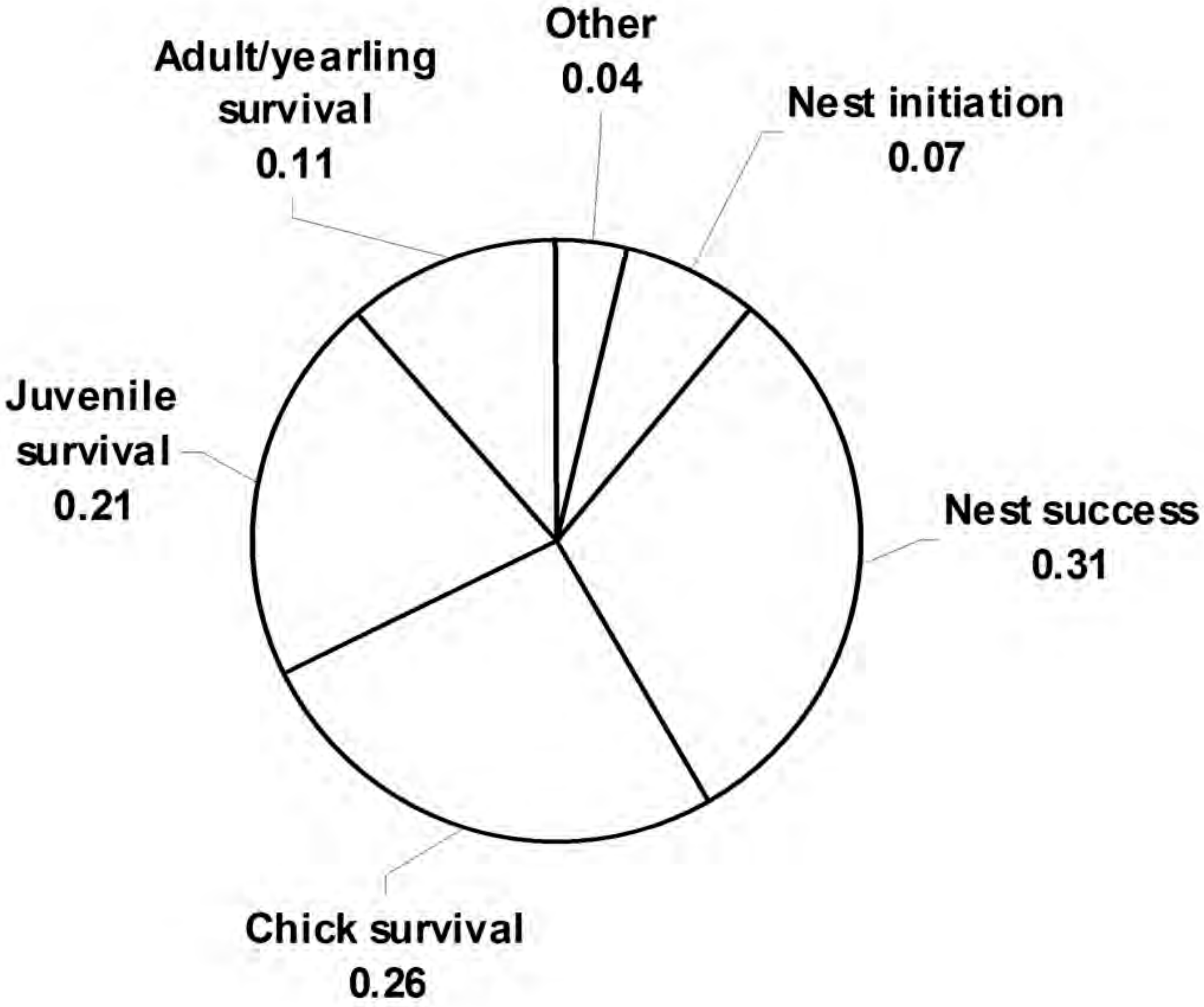
2.40
Finite rate of increase (lambda)

Figure 3.


Other
0.04
Adult/yearling survival
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Juvenile survival
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Nest success
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Chick survival
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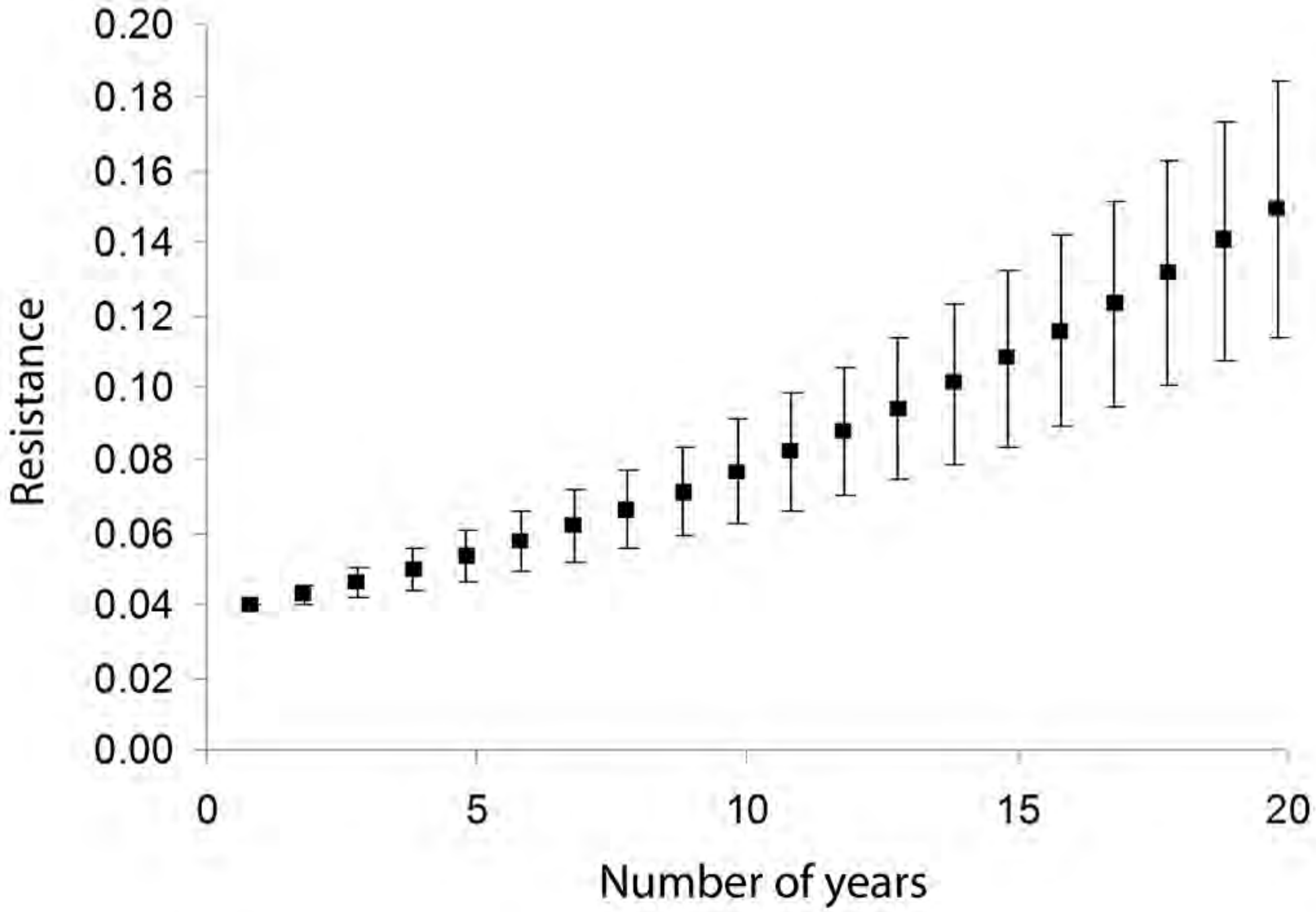
Figure 4.


0.20
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Resistance
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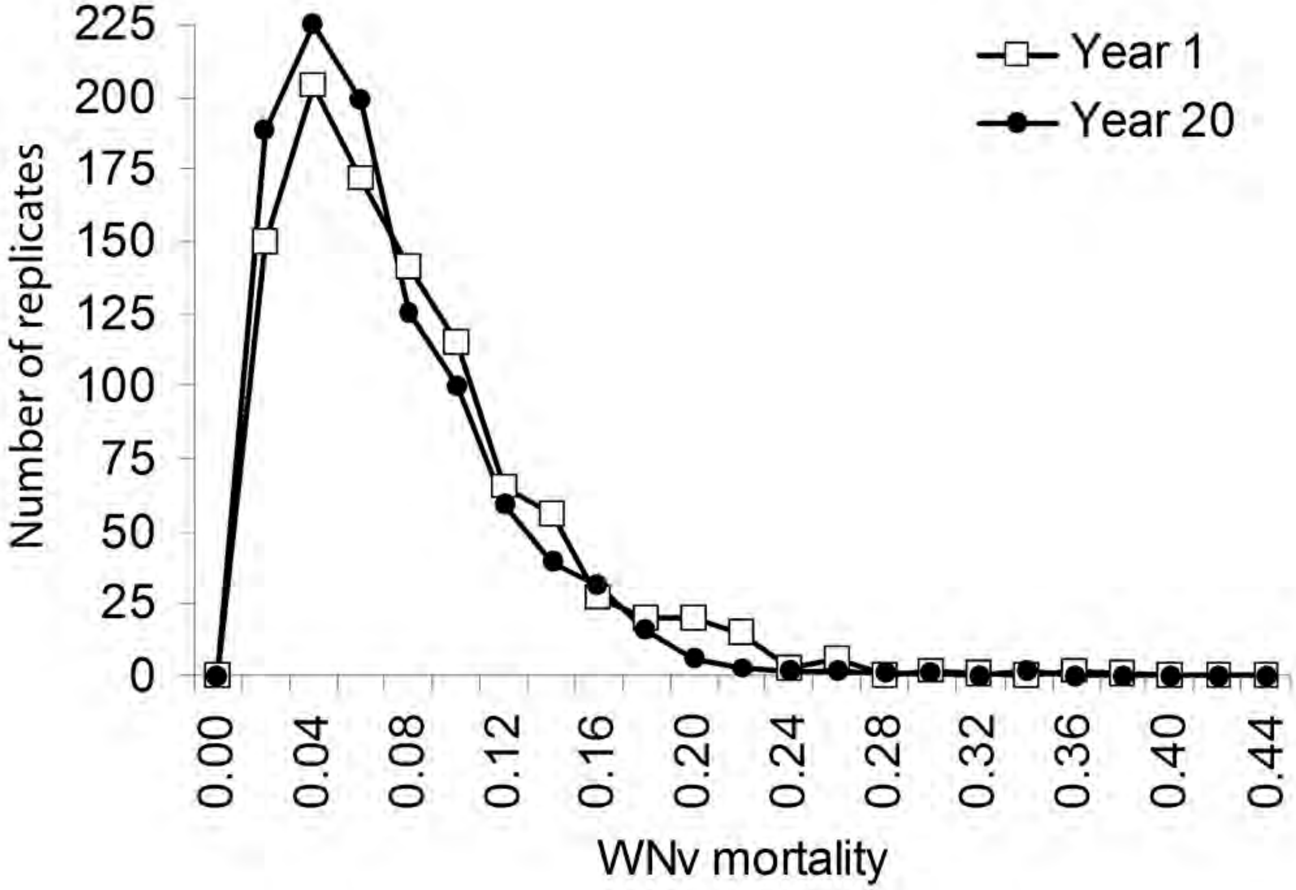
Figure 5.



Year 1
Year 20
Number of replicates
225
200
175
150
125
100
75
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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

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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)

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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

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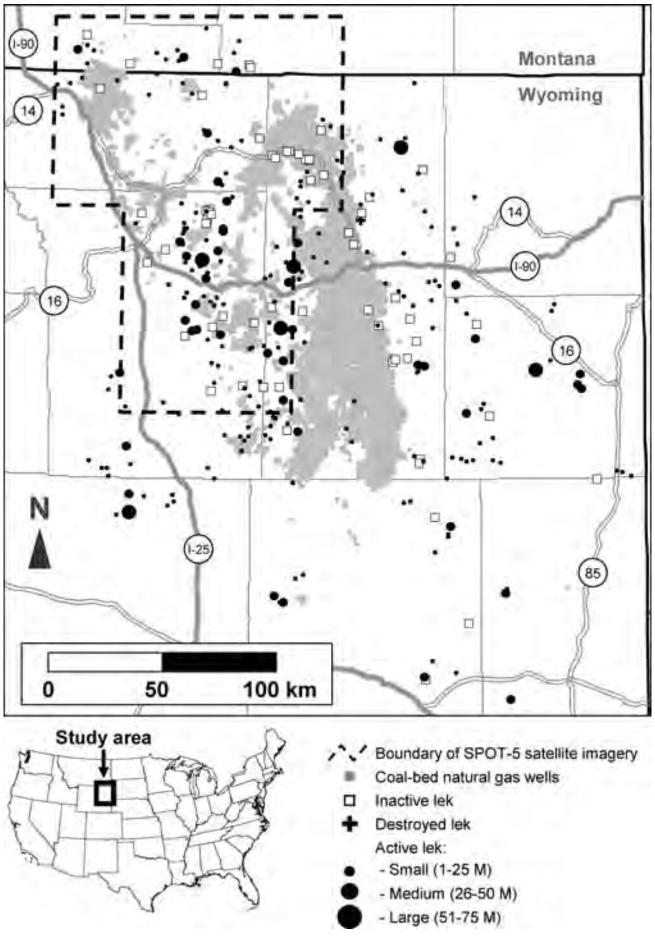

Figure 1. Distribution and status of active, inactive, and destroyed greater sage-grouse leks, coal-bed natural gas wells, and major highways in the Powder River Basin, Montana and Wyoming, USA. The dashed line shows the extent of SPOT-5 satellite imagery. This map excludes leks that became inactive 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.

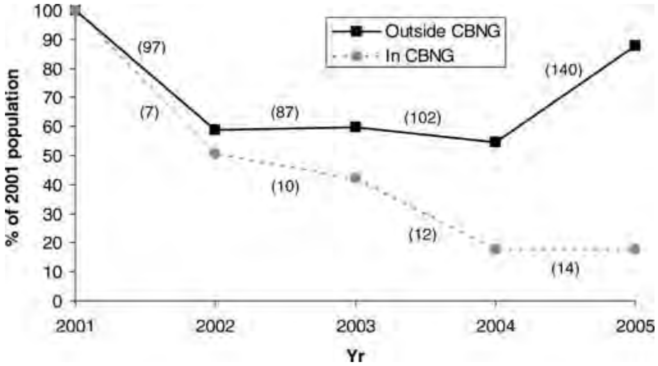

Figure 2. Population indices based on male lek attendance for greater sage-grouse in the Powder River Basin, Montana and Wyoming, USA, 2001–2005 for leks categorized as in coal-bed natural gas fields or outside coal-bed natural gas (CBNG) fields on a year-by-year basis. Sample sizes in parentheses next 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

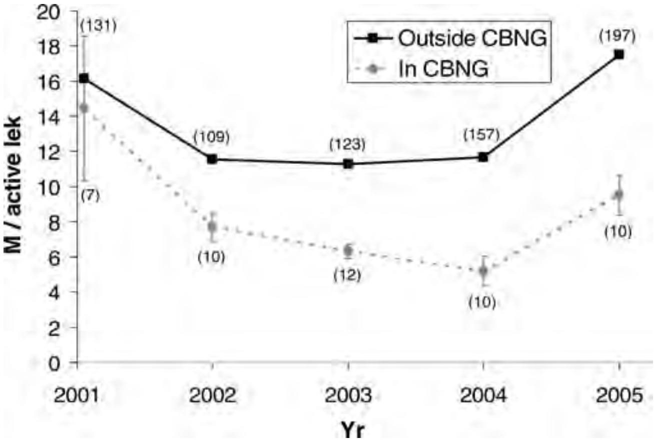

Figure 3. Number of male sage-grouse per active lek in coal-bed natural gas (CBNG) fields (gray) and outside (black) CBNG fields in the Powder River Basin, Montana and Wyoming, USA, 2001–2005. Error bars represent 95% confidence intervals (error bars for leks outside CBNG are too small to be visible). Sample sizes in parentheses above each index indicate the number of active leks available for calculating males per active lek in each year.

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 ($\bar{x} \pm$ 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).

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.

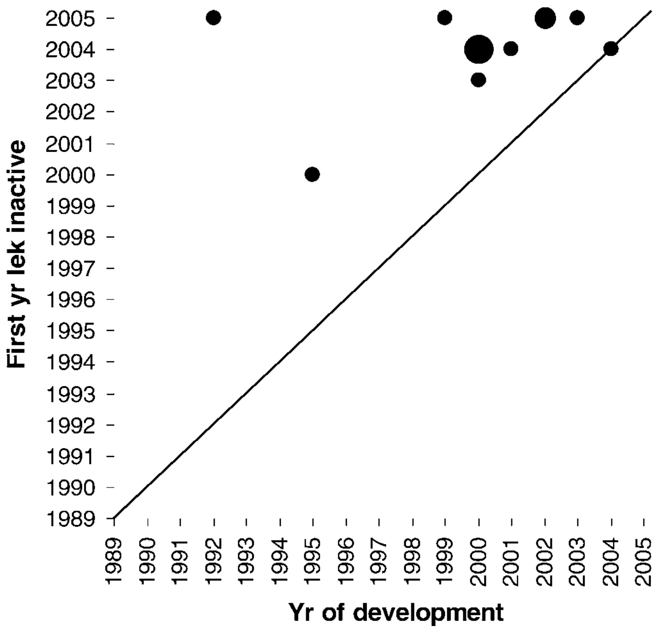

Figure 4. Timing of greater sage-grouse lek disappearance relative to coal-bed natural gas (CBNG) development in the Powder River Basin, Montana and Wyoming, USA, for leks confirmed active in 1997 or later. Leks above the diagonal line became inactive after CBNG development reached ≥40% within 3.2 km (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.

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 ΔAIC$_c$ units of the best approximating model, whereas all habitat-plus-infrastructure and habitat-only models showed considerably less support (>6 ΔAIC$_c$ 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 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	$\Delta \mathrm{AIC}_c$	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 ($\Delta \mathrm{AIC}_c$ 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 $\Delta \mathrm{AIC}_c$ 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 $\Delta \mathrm{AIC}_c$ 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	$\Delta \mathrm{AIC}_c$	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 ($\Delta \mathrm{AIC}_c$ values), and AIC_c wt (w_i) for each model in order of increasing $\Delta \mathrm{AIC}_c$ 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	1.57×10^{-4}	5.81×10^{-12}	4.22×10^{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 ΔAIC_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 ΔAIC_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

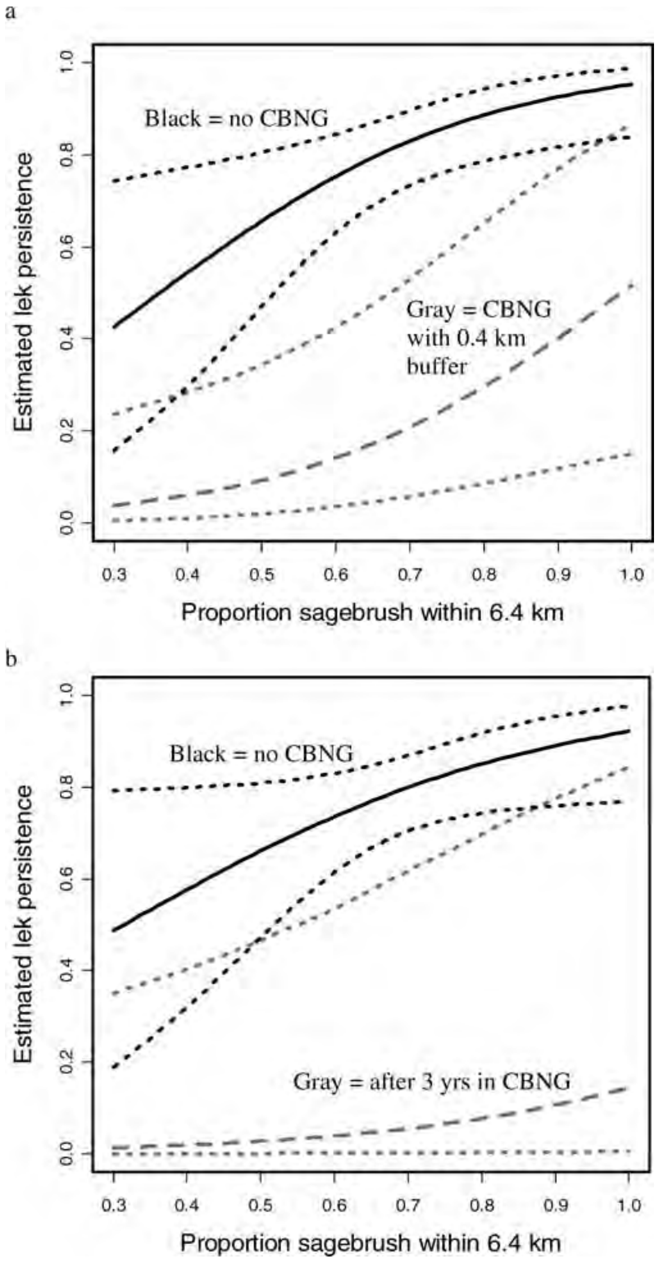

Figure 5. Estimated lek persistence as a function of proportion sagebrush habitat within 6.4 km and either (a) proportion coal-bed natural gas (CBNG) development within 0.8 km or (b) number of years within a CBNG field for greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, USA, 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.

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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 ≥75 and ≥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 ≤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.

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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.

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[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

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[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.

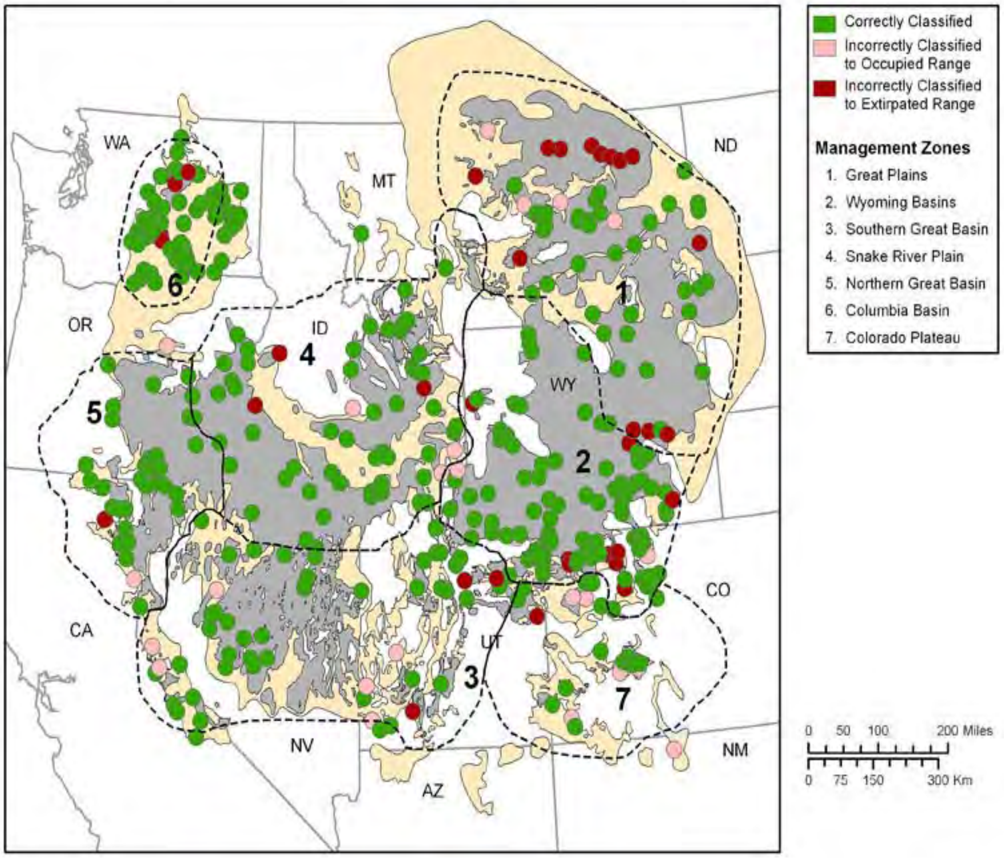

Correctly Classified
Incorrectly Classified to Occupied Range
Incorrectly Classified to Extirpated Range
Management Zones
1. Great Plains
2. Wyoming Basins
3. Southern Great Basin
4. Snake River Plain
5. Northern Great Basin
6. Columbia Basin
7. Colorado Plateau
WA
MT
ND
OR
ID
WY
CA
NV
UT
CO
AZ
NM
1
2
3
4
5
6
7
0 50 100 200 Miles
0 75 150 300 Km

Figure 2.

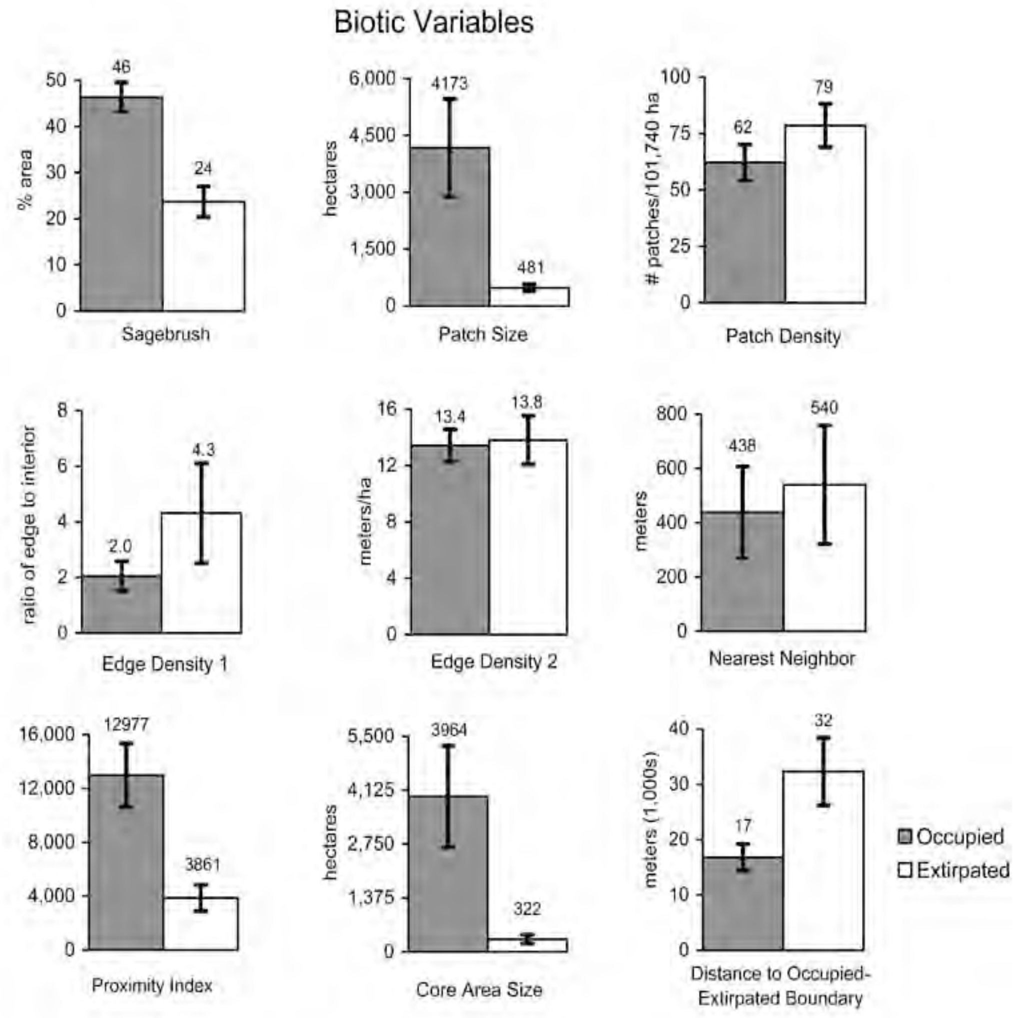

Biotic Variables
% area
50
40
30
20
10
0
46
24
Sagebrush
hectares
6,000
4,500
3,000
1,500
0
4173
481
Patch Size
patches/101,740 ha
100
75
50
25
0
62
79
Patch Density
ratio of edge to interior
8
6
4
2
0
2.0
4.3
Edge Density 1
meters/ha
16
12
8
4
0
13.4
13.8
Edge Density 2
meters
800
600
400
200
0
438
540
Nearest Neighbor
16,000
12,000
8,000
4,000
0
12977
3861
Proximity Index
hectares
5,500
4,125
2,750
1,375
0
3964
322
Core Area Size
meters (1,000s)
40
30
20
10
0
17
32
Distance to Occupied-Extirpated Boundary
▨ Occupied
☐ Extirpated

Figure 3.

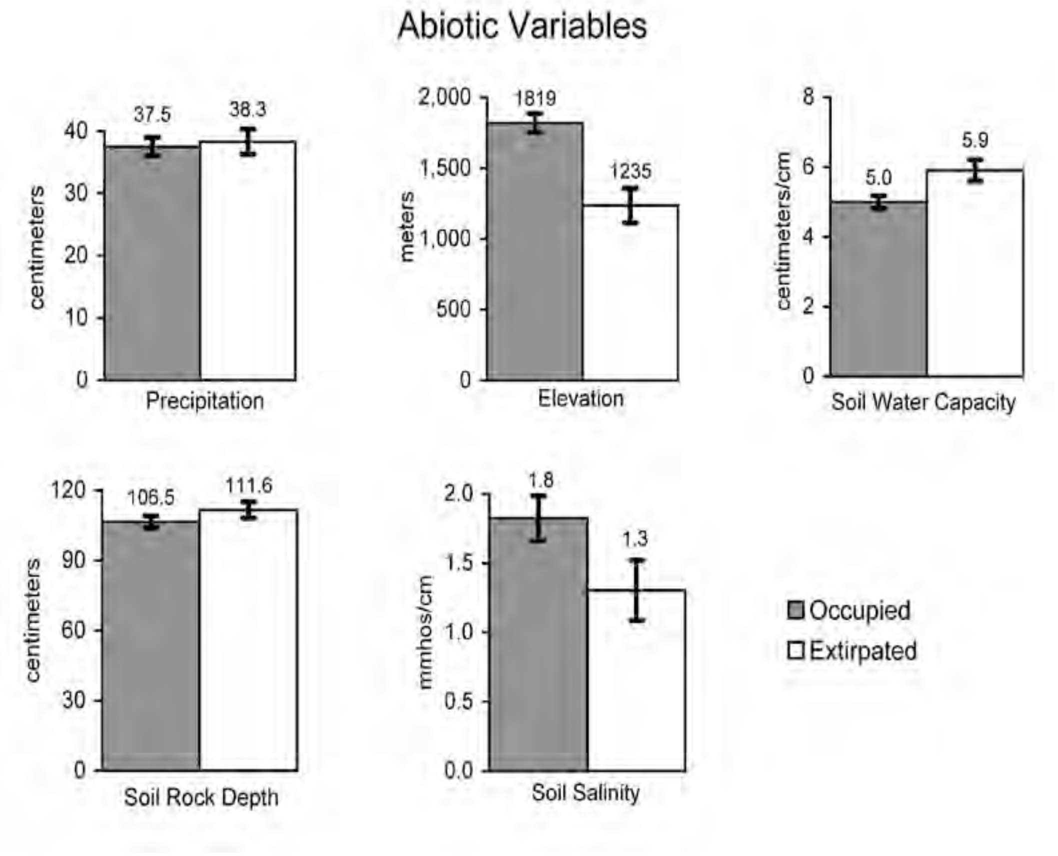

Abiotic Variables
37.5
38.3
40
30
20
10
0
centimeters
Precipitation
2,000
1,500
1,000
500
0
1819
1235
meters
Elevation
8
6
4
2
0
5.0
5.9
centimeters/cm
Soil Water Capacity
120
90
60
30
0
106.5
111.6
centimeters
Soil Rock Depth
2.0
1.5
1.0
0.5
0.0
1.8
1.3
mmhos/cm
Soil Salinity
Occupied
Extirpated

Figure 4.

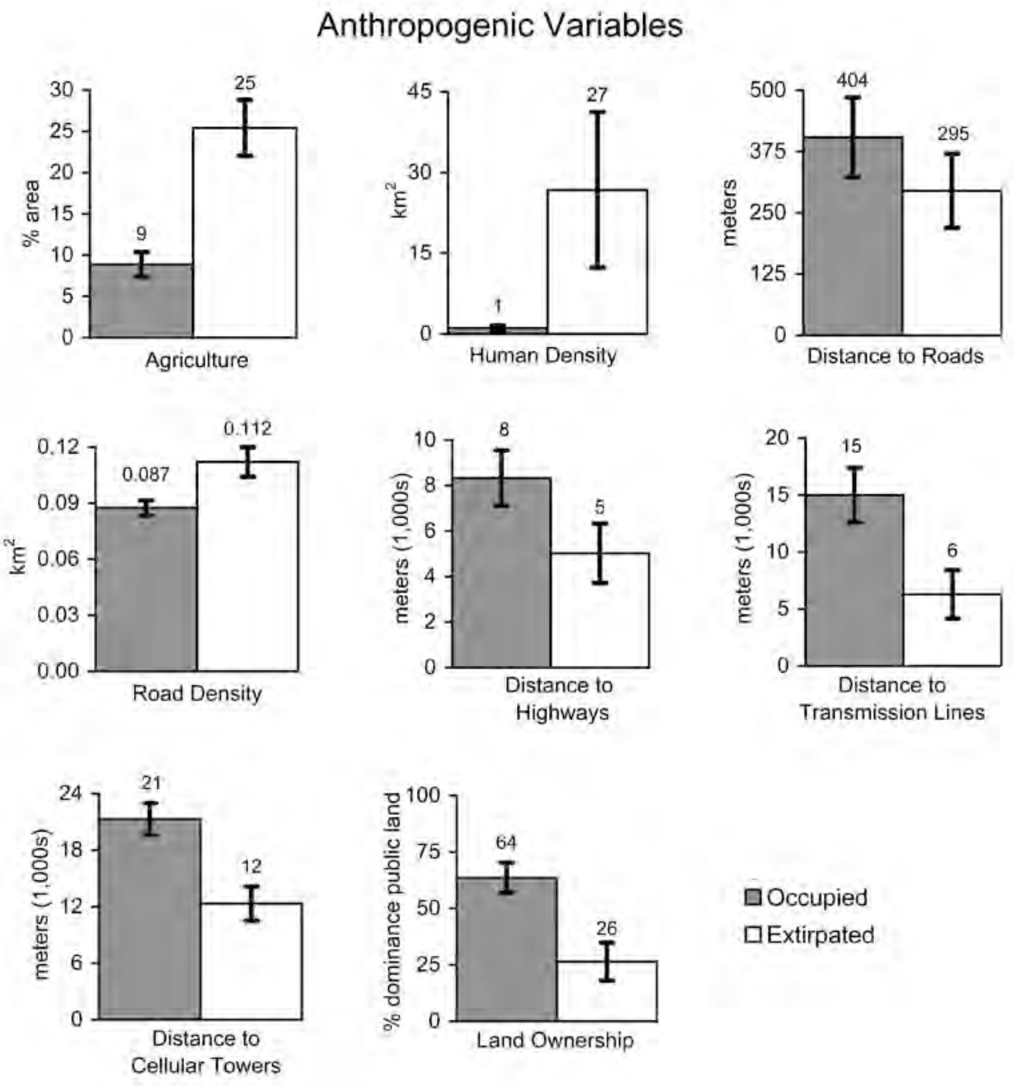
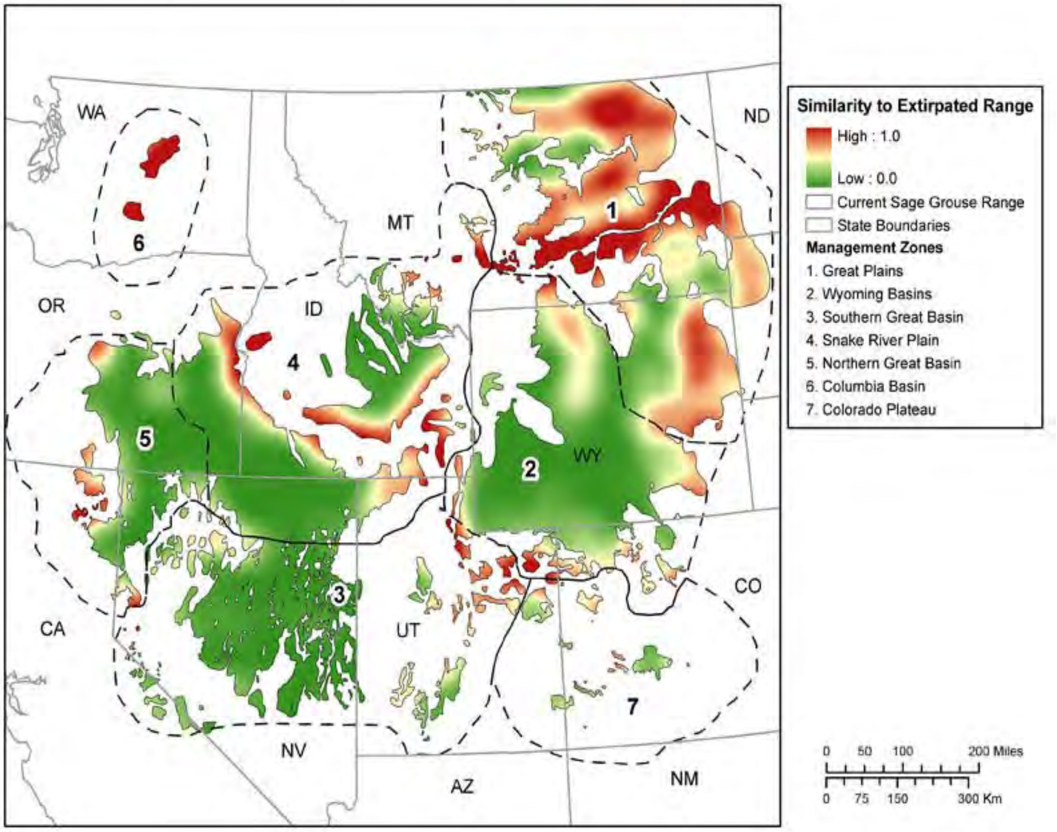

Anthropogenic Variables
% area
30
25
20
15
10
5
0
9
25
Agriculture
km²
45
30
15
0
1
27
Human Density
meters
500
375
250
125
0
404
295
Distance to Roads
km²
0.12
0.09
0.06
0.03
0.00
0.087
0.112
Road Density
meters (1,000s)
10
8
6
4
2
0
8
5
Distance to Highways
meters (1,000s)
20
15
10
5
0
15
6
Distance to Transmission Lines
meters (1,000s)
24
18
12
6
0
21
12
Distance to Cellular Towers
% dominance public land
100
75
50
25
0
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

2008

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The University of Montana

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GREATER SAGE-GROUSE RESPONSE TO COAL-BED NATURAL GAS DEVELOPMENT AND WEST NILE VIRUS IN THE POWDER RIVER BASIN, MONTANA AND WYOMING, USA.

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Dissertation

presented in partial fulfillment of the requirements
for the degree of

Doctor of Philosophy
in Wildlife Biology

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Dept. of Mathematical Sciences

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.

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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).

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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

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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 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 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 ΔAIC_c units of the best approximating model, whereas all habitat-plus-infrastructure and habitat-only models showed considerably less support (> 6 ΔAIC_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 ΔAIC_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 ΔAIC_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, $\beta_{\text{CBNG 0.8 km}} = -3.91 \pm 1.11$ SE) (Table 4). Thus, we illustrate the effects CBNG within 0.8 km on lek persistence using estimates from that model (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 ΔAIC_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 ΔAIC_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 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.

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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	ΔAIC_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), ΔAIC_c values, and AIC_c weights (w_i) listed for each model in order of increasing ΔAIC_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	ΔAIC_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	1.57×10^{-4}	5.81×10^{-12}	4.22×10^{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.

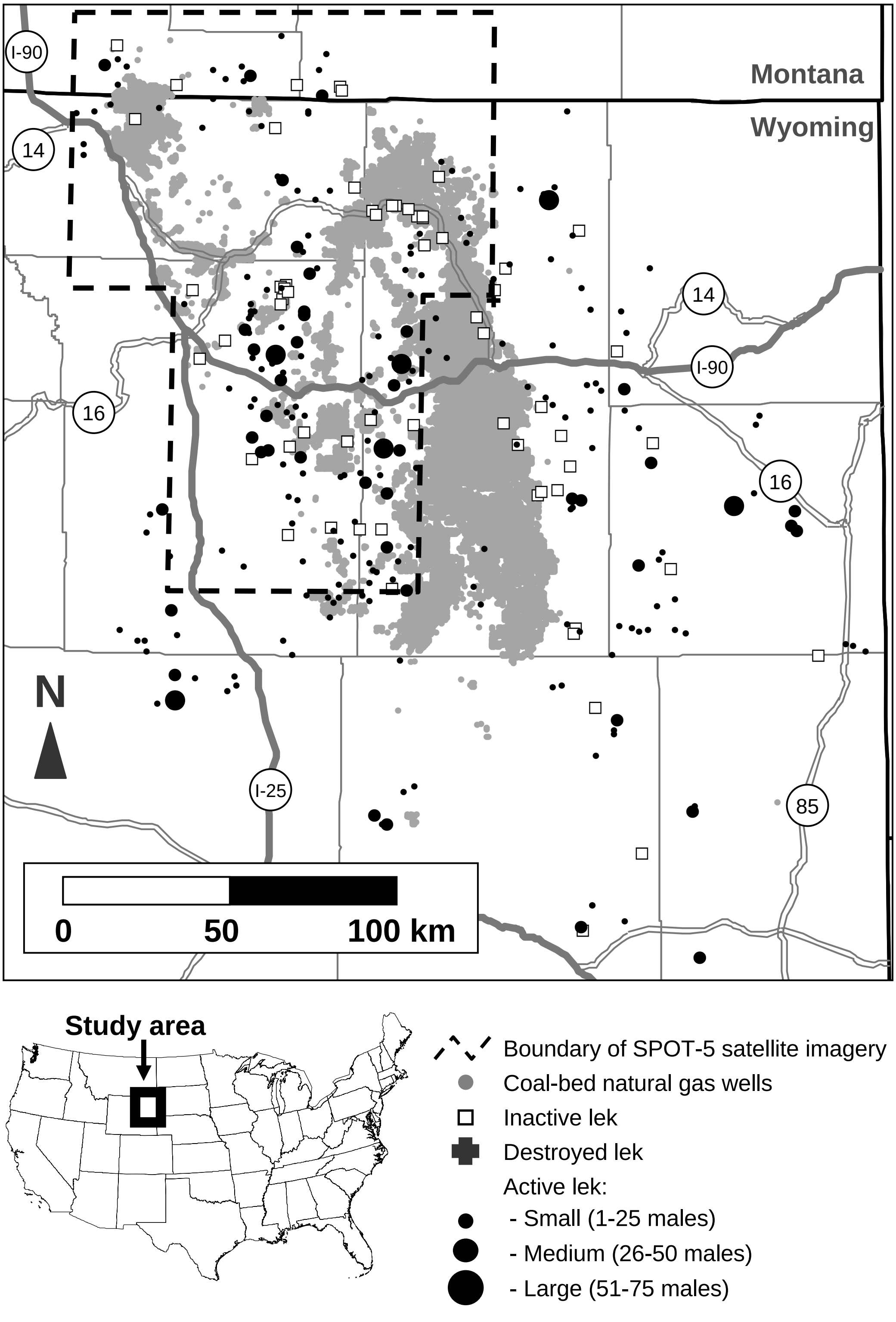

Montana
Wyoming
I-90
14
16
I-25
85
N
0
50
100 km
Study area
Boundary of SPOT-5 satellite imagery
Coal-bed natural gas wells
Inactive lek
Destroyed lek
Active lek:
- Small (1-25 males)
- Medium (26-50 males)
- Large (51-75 males)

Figure 2

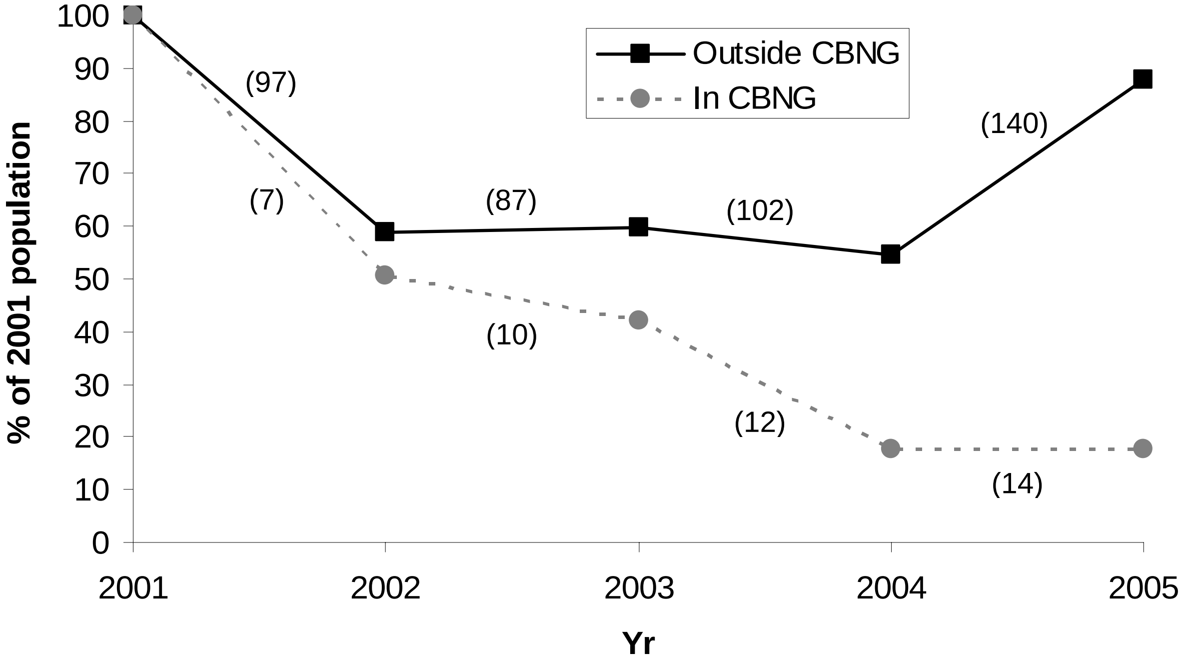

100
90
80
70
60
50
40
30
20
10
0
% of 2001 population
2001
2002
2003
2004
2005
Yr
Outside CBNG
In CBNG
(97)
(7)
(87)
(10)
(102)
(12)
(140)
(14)

Figure 3

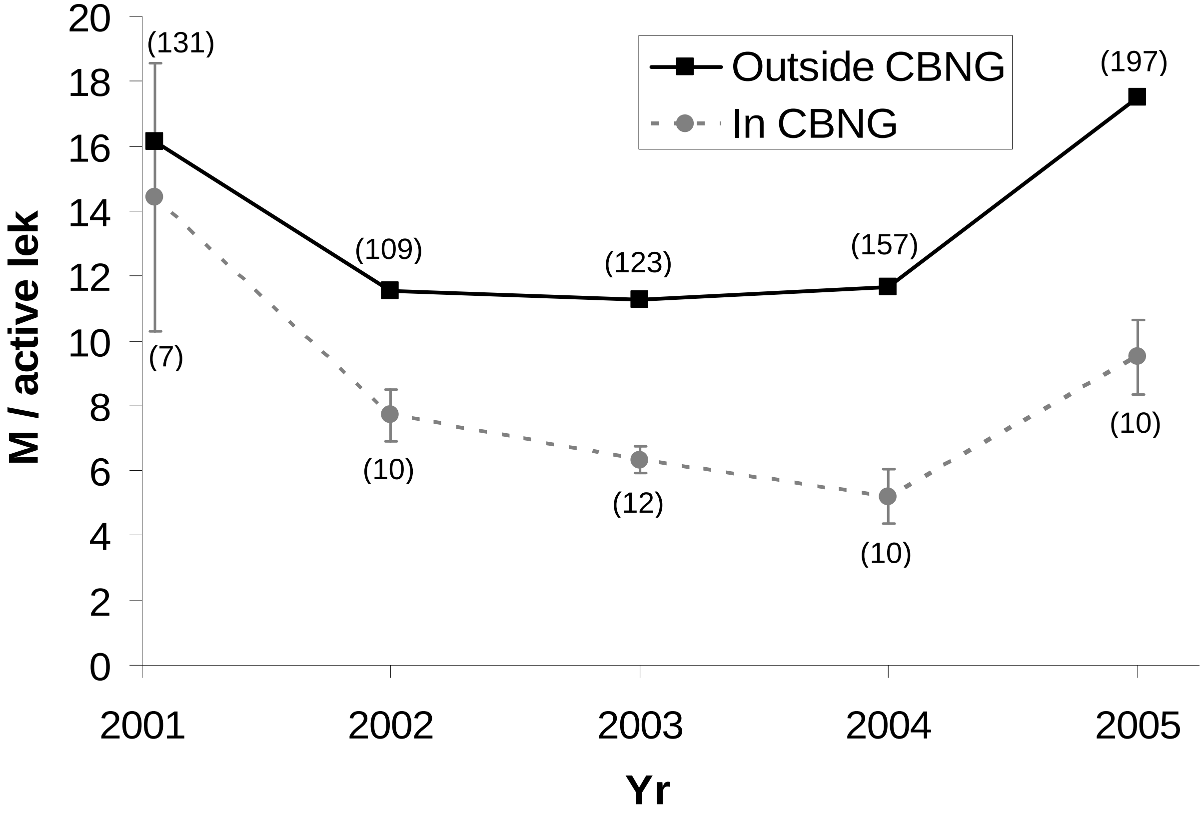

20
18
16
14
12
10
8
6
4
2
0
M / active lek
2001
2002
2003
2004
2005
Yr
Outside CBNG
In CBNG
(131)
(109)
(123)
(157)
(197)
(7)
(10)
(12)
(10)
(10)

Figure 4

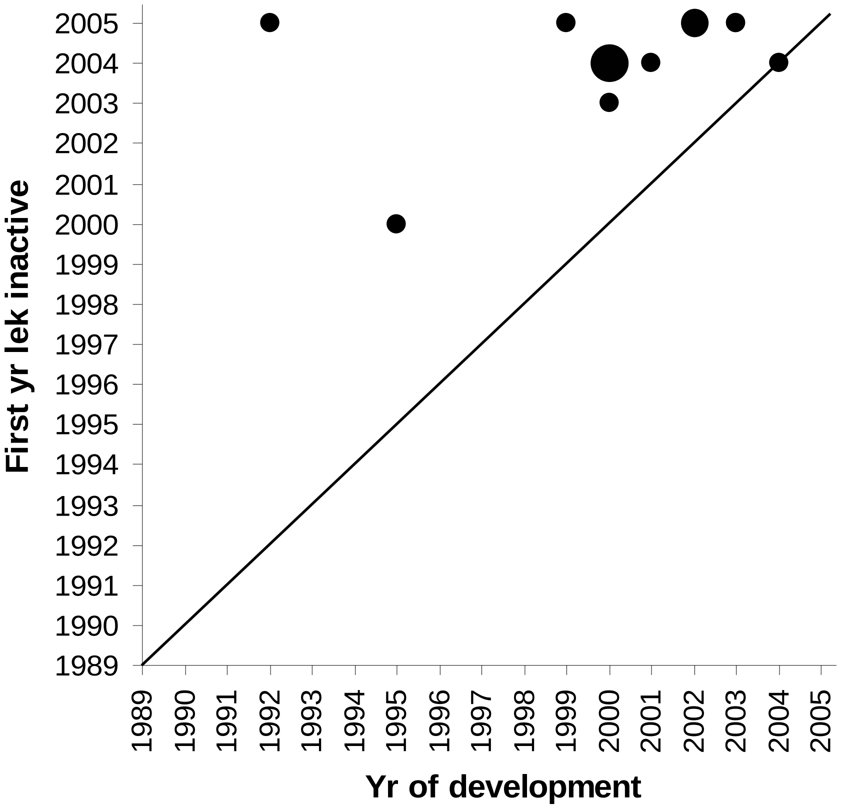
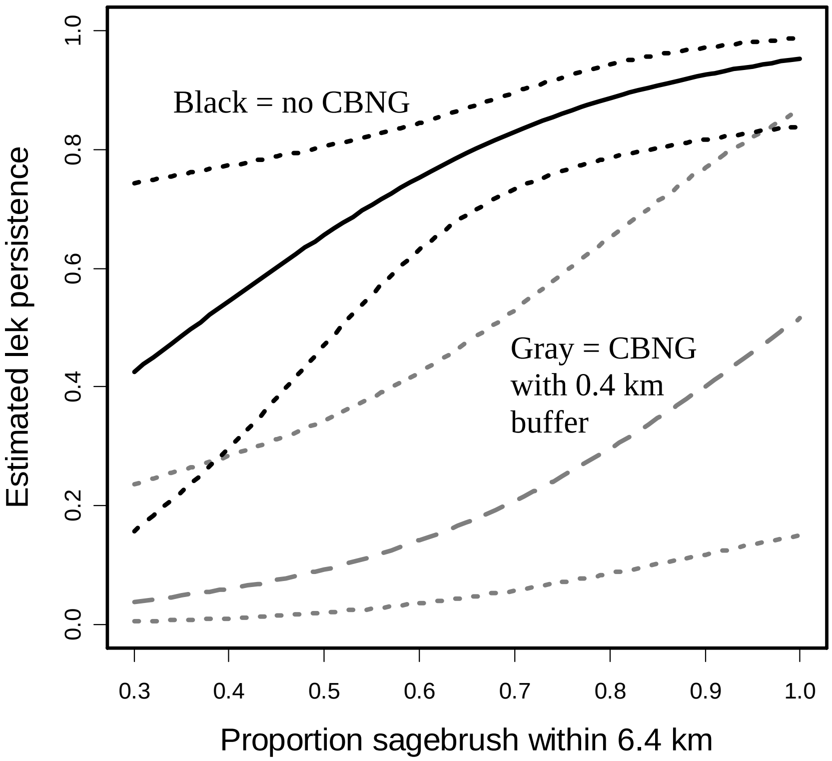

First yr lek inactive
2005
2004
2003
2002
2001
2000
1999
1998
1997
1996
1995
1994
1993
1992
1991
1990
1989
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
Yr of development

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

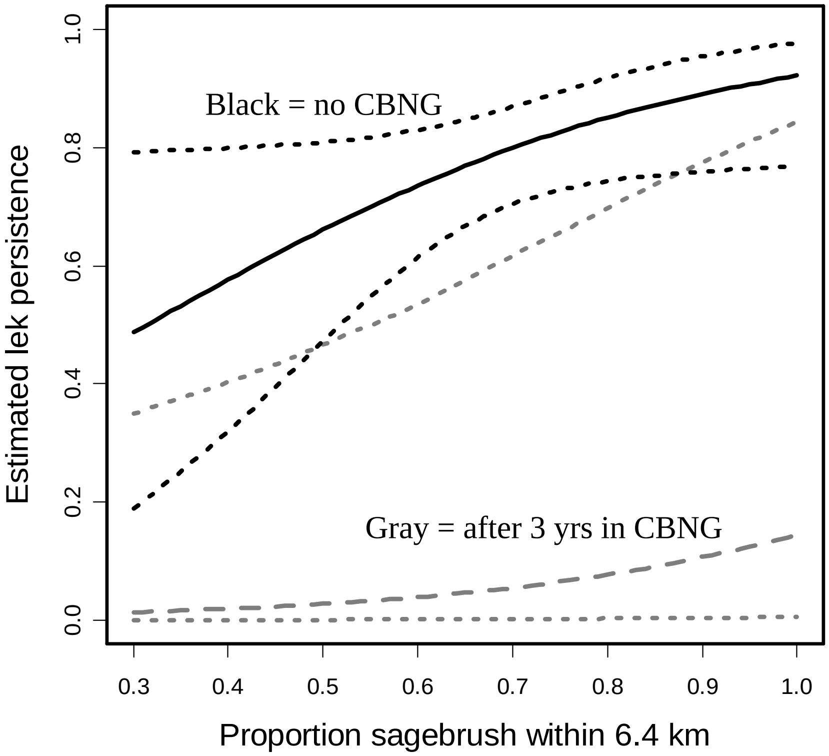
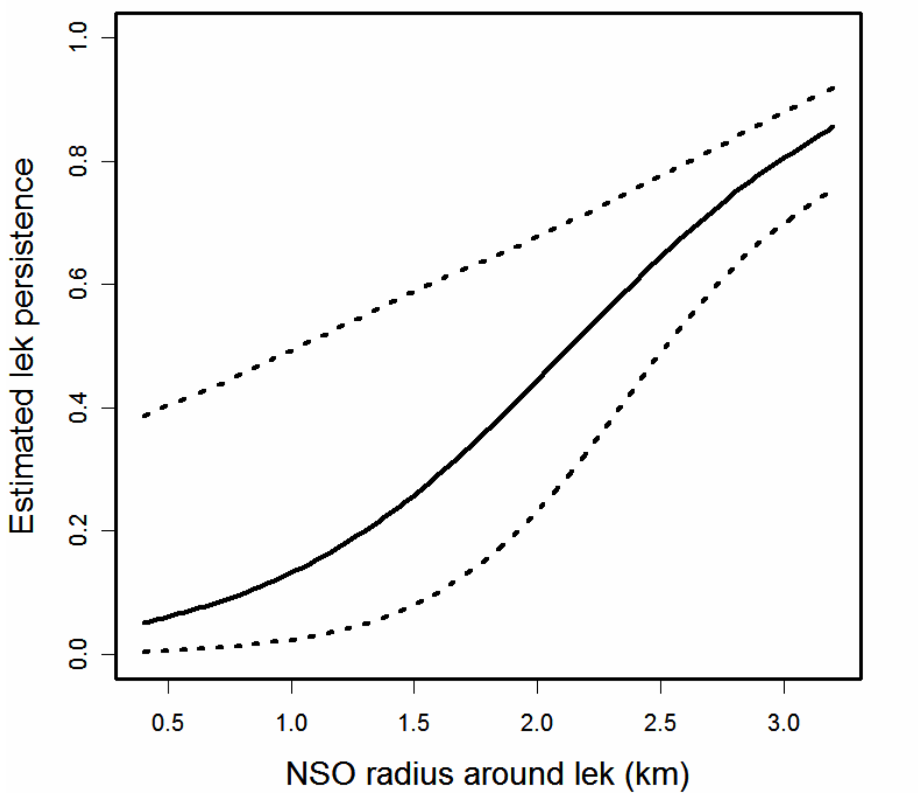

Black = no CBNG
Gray = after 3 yrs in CBNG
Estimated lek persistence
0.0
0.2
0.4
0.6
0.8
1.0
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Proportion sagebrush within 6.4 km

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

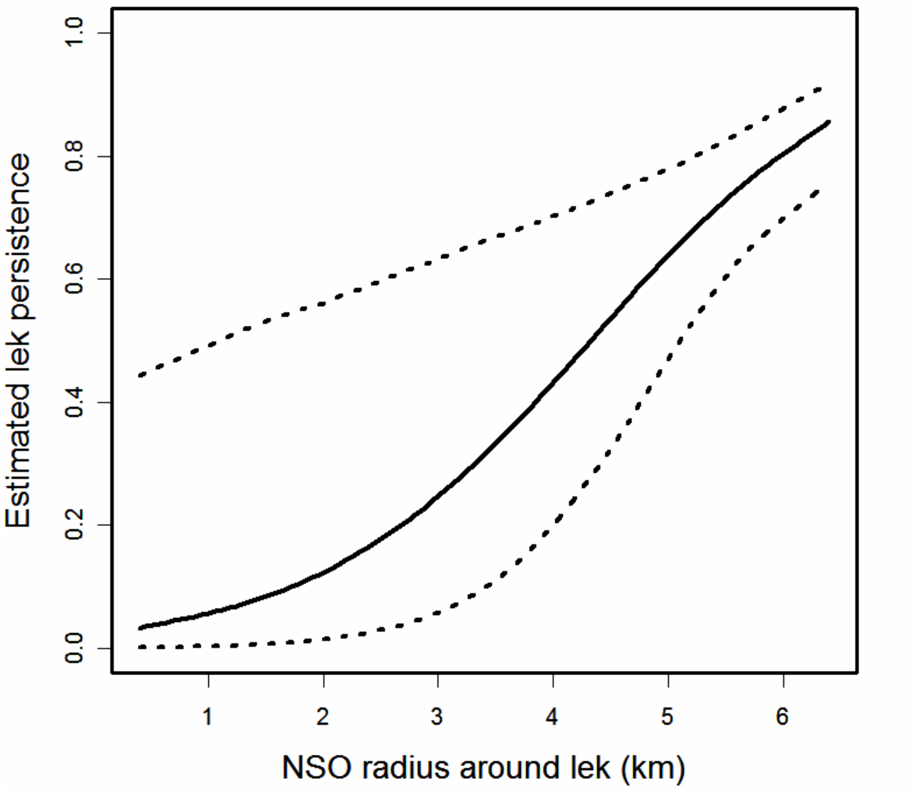
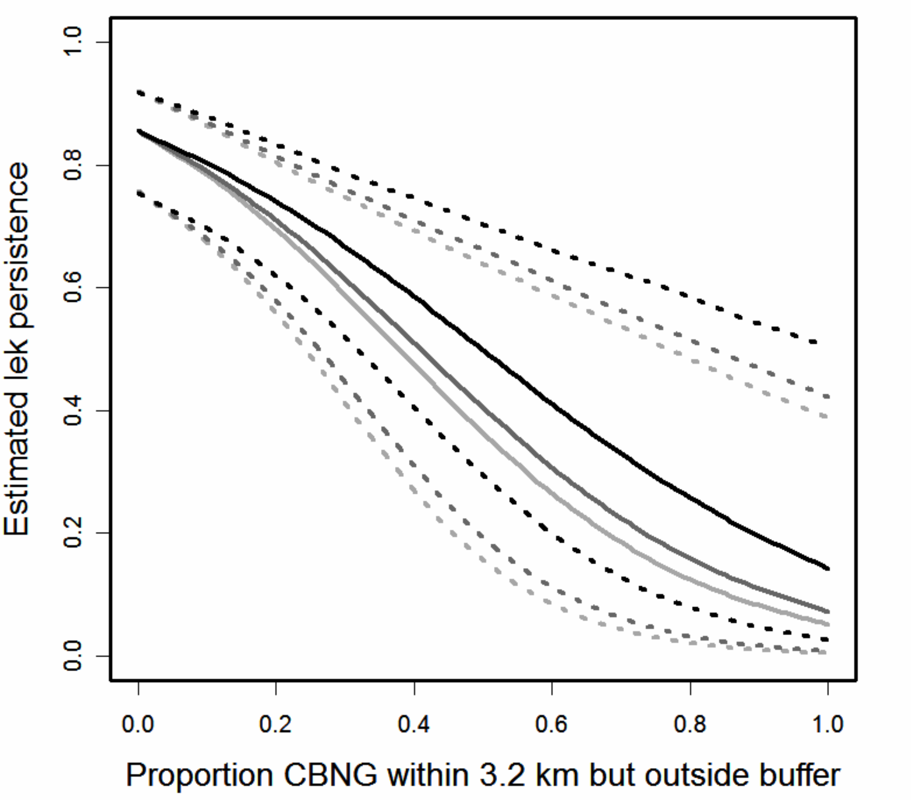
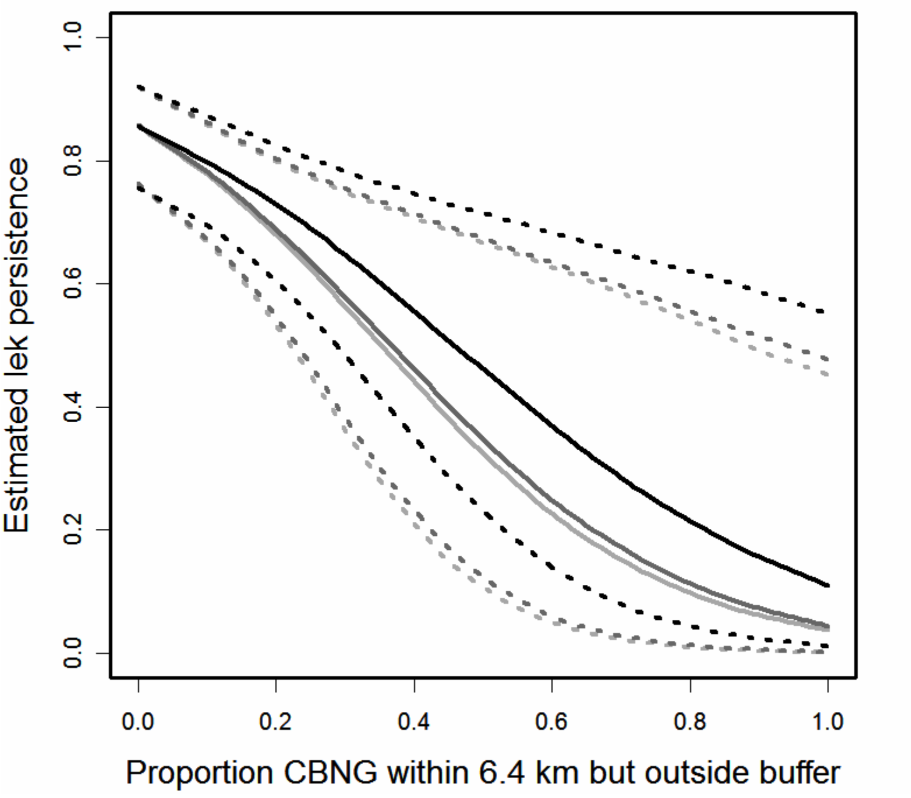

Estimated lek persistence
0.0
0.2
0.4
0.6
0.8
1.0
1
2
3
4
5
6
NSO radius around lek (km)

Figure 7.

a


Estimated lek persistence
0.0
0.2
0.4
0.6
0.8
1.0
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
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:

$$I = S / [1 - M + (S * M)] \qquad (1)$$

Because mortality rate, M, can be expressed as WNv-related mortality, ΔP, 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:

$$I = \Delta P + S - (S * \Delta P) \qquad (2)$$

Because WNv-related mortality reduces post-epizootic population size and inflates the seroprevalence estimate, the S*ΔP 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 6th warmest summer on record in the PRB, than in 2004 and 2005, the 86th and 41st 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.

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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.

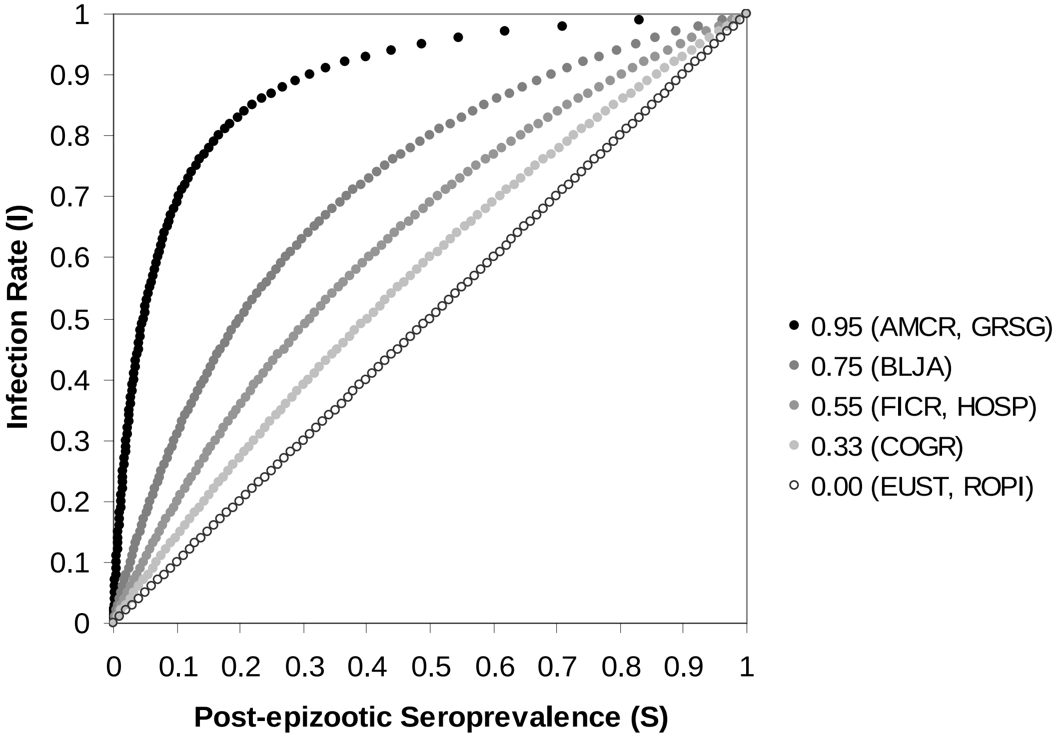
Infection Rate (I)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Post-epizootic Seroprevalence (S)
0.95 (AMCR, GRSG)
0.75 (BLJA)
0.55 (FICR, HOSP)
0.33 (COGR)
0.00 (EUST, ROPI)

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.

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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.

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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.

	Hatching date			Apparent brood success			Apparent chick survival		
Region - Year	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 ΔAIC_c values.

No.	Model[1]	K	AIC_c	ΔAIC_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

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[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 ΔAIC_c values.

No.	Model	K	AIC_c	ΔAIC_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 ΔAIC_c values.

No.	Model	K	AIC_c	ΔAIC_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 ΔAIC_c values.

No.	Model[1]	K	AIC_c	ΔAIC_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

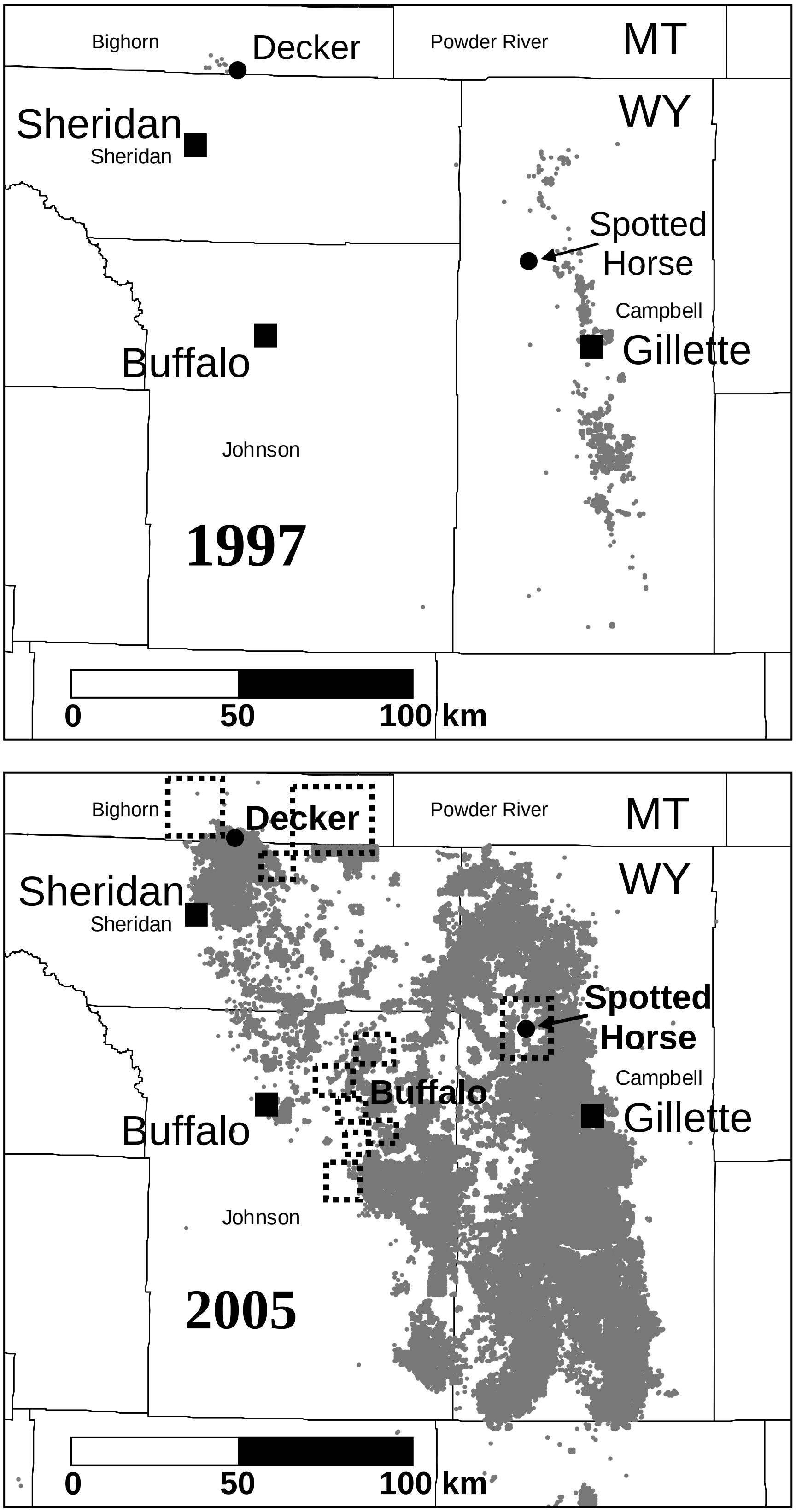
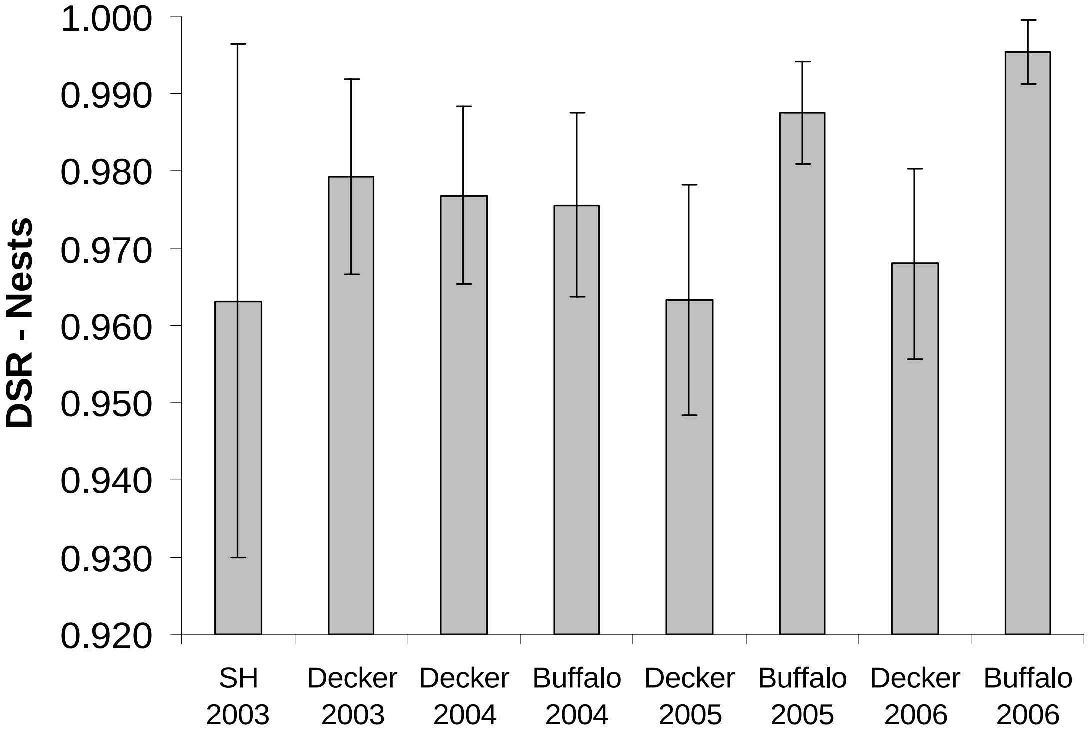

Bighorn
Decker
Powder River
MT
WY
Sheridan
Sheridan
Spotted Horse
Campbell
Gillette
Buffalo
Johnson
1997
0
50
100 km
Bighorn
Decker
Powder River
MT
WY
Sheridan
Sheridan
Spotted Horse
Buffalo
Campbell
Gillette
Buffalo
Johnson
2005
0
50
100 km

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.

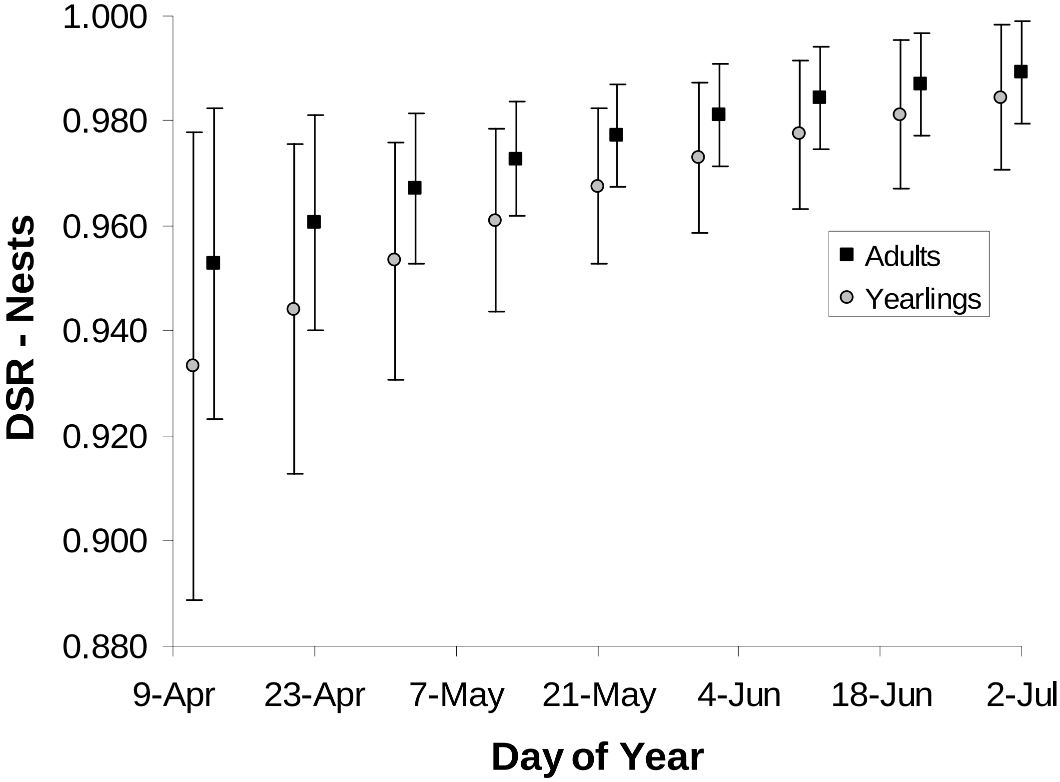

1.000
0.980
0.960
0.940
0.920
0.900
0.880
DSR - Nests
9-Apr
23-Apr
7-May
21-May
4-Jun
18-Jun
2-Jul
Day of Year
■ Adults
● Yearlings

Figure 4.

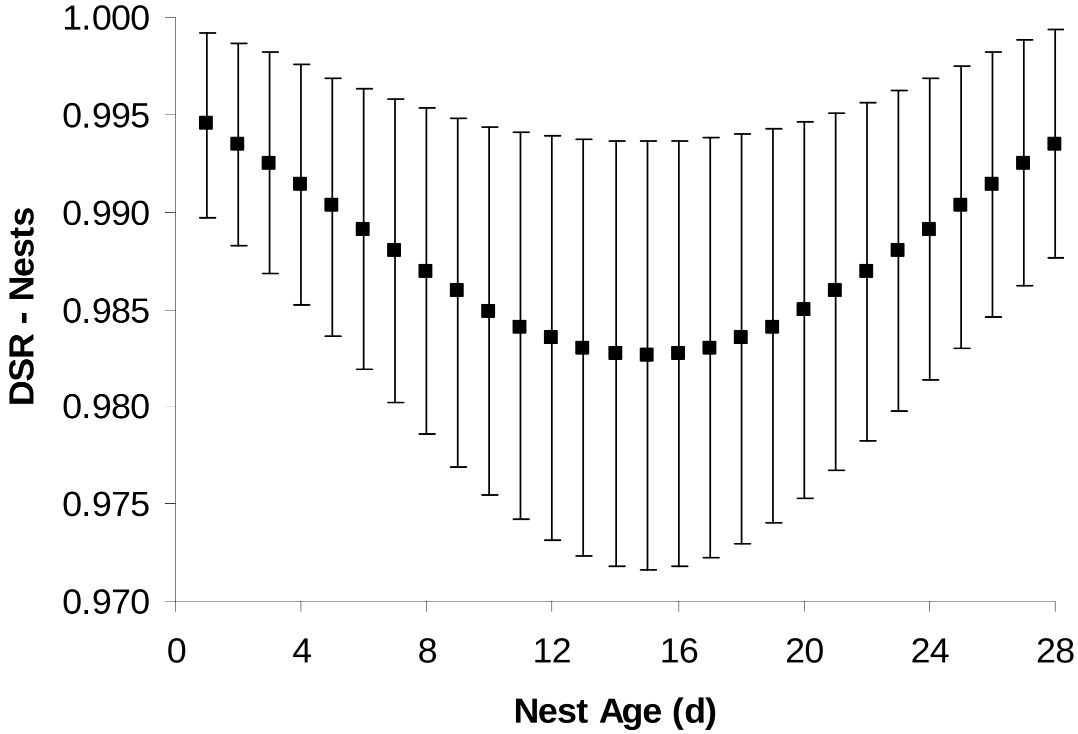
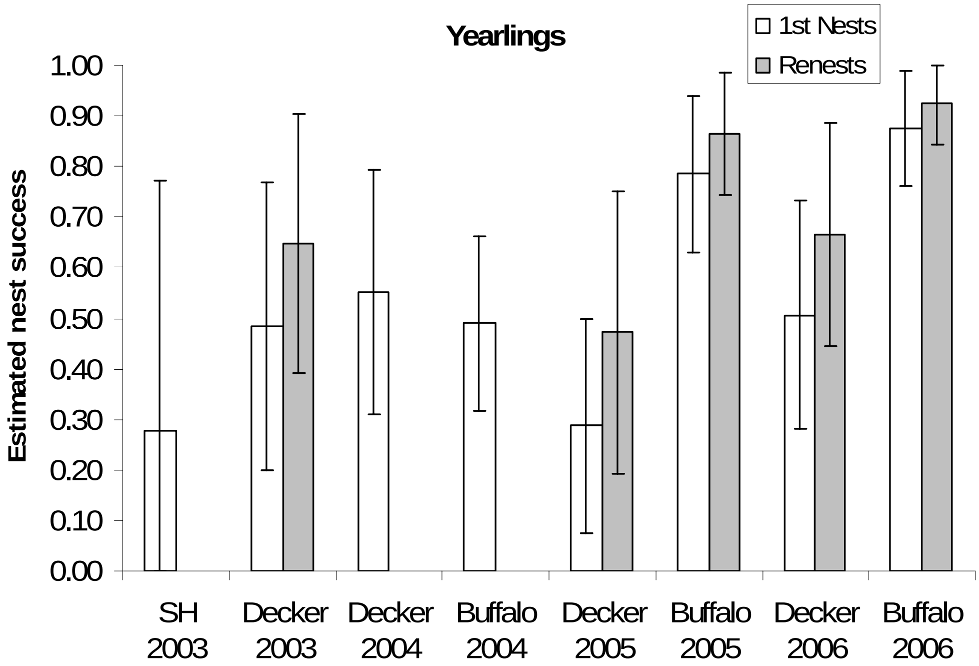

1.000
0.995
0.990
0.985
0.980
0.975
0.970
DSR - Nests
0
4
8
12
16
20
24
28
Nest Age (d)

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)

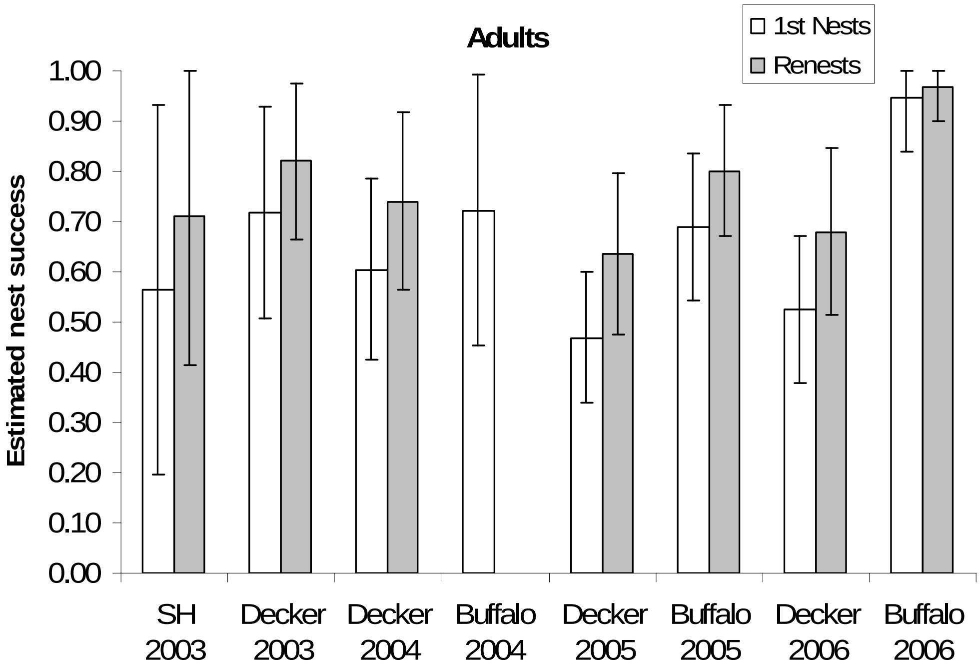

Adults
☐ 1st Nests
▨ Renests
Estimated nest success
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
SH 2003
Decker 2003
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006

Figure 6.

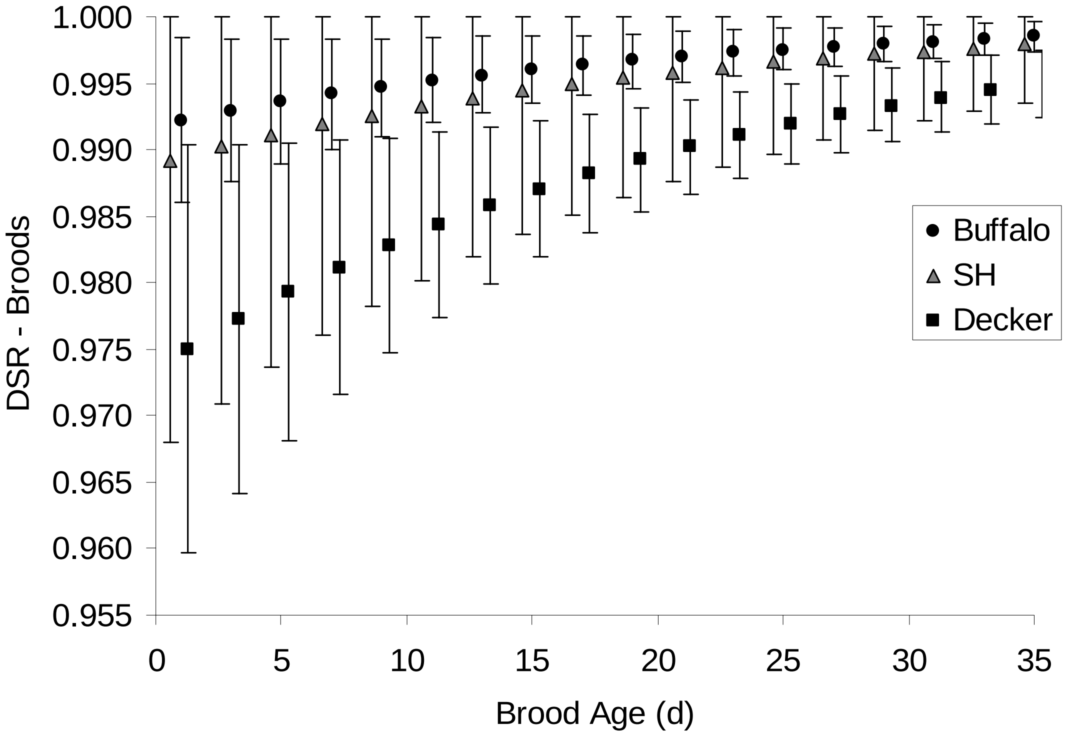

1.000
0.995
0.990
0.985
0.980
0.975
0.970
0.965
0.960
0.955
DSR - Broods
0
5
10
15
20
25
30
35
Brood Age (d)
● Buffalo
▲ SH
■ Decker

Figure 7.

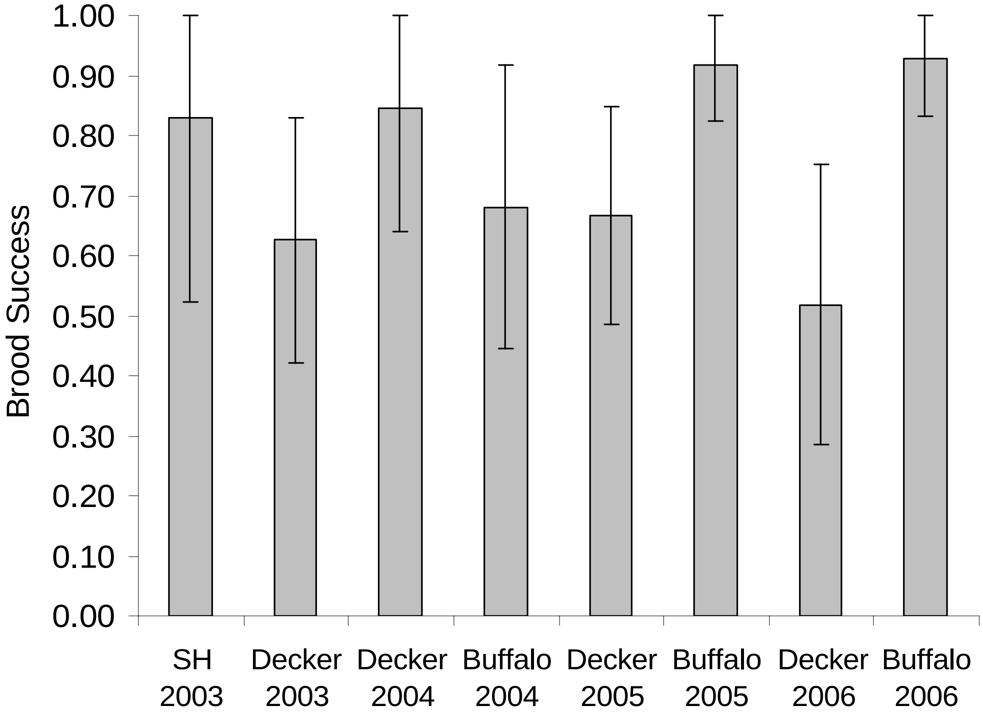

Brood Success
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
SH 2003
Decker 2003
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006

Figure 8.

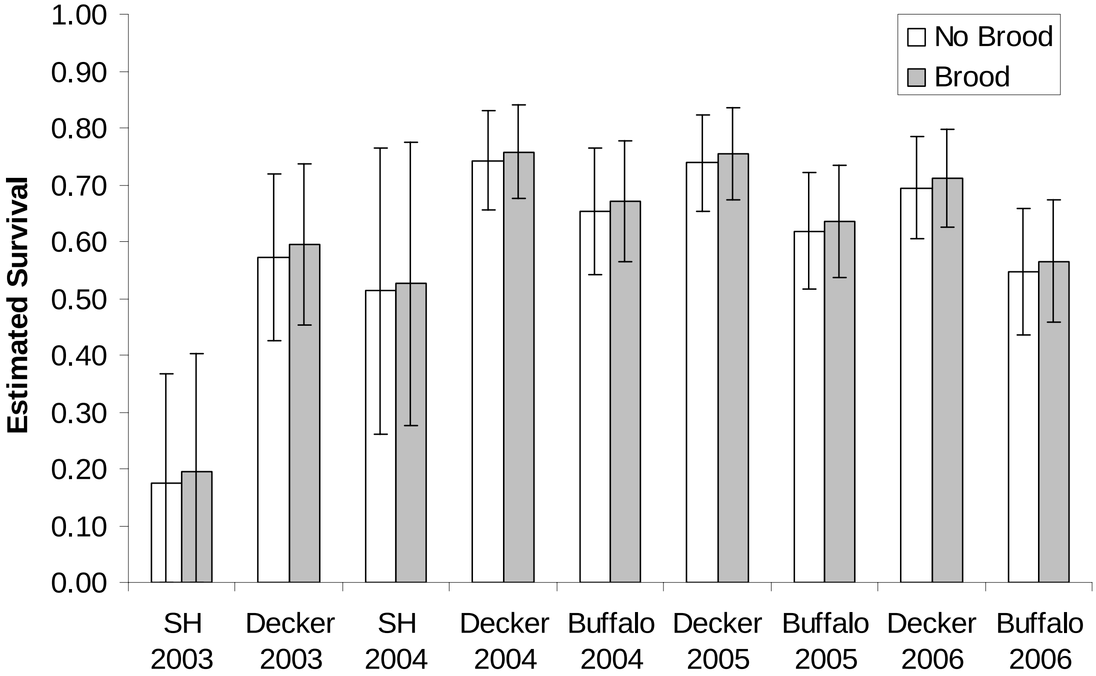
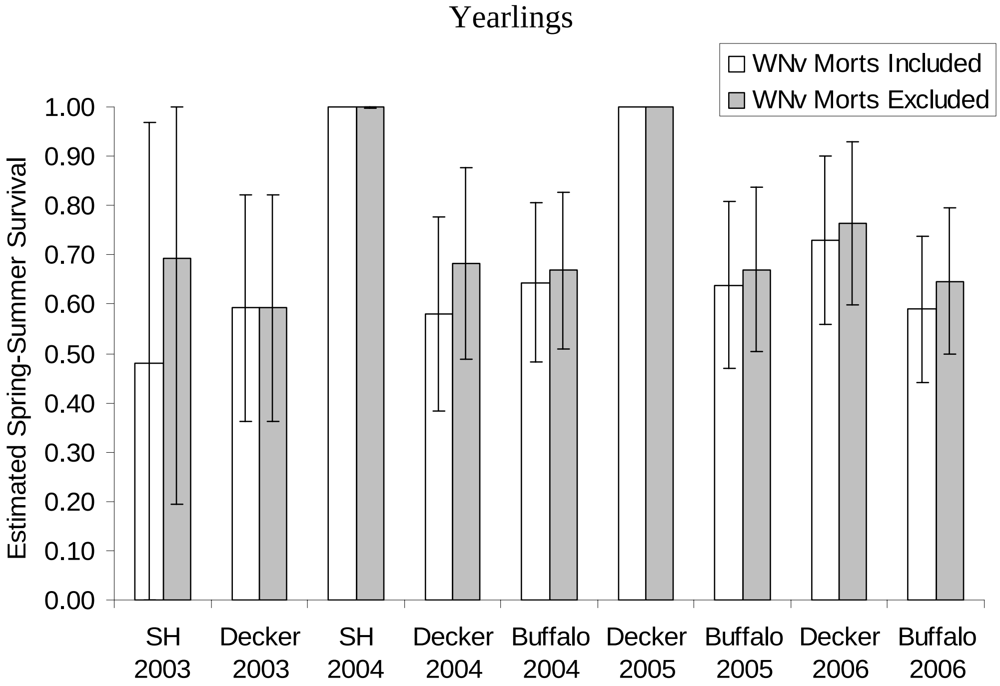

1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Estimated Survival
☐ No Brood
▨ Brood
SH 2003
Decker 2003
SH 2004
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006

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)

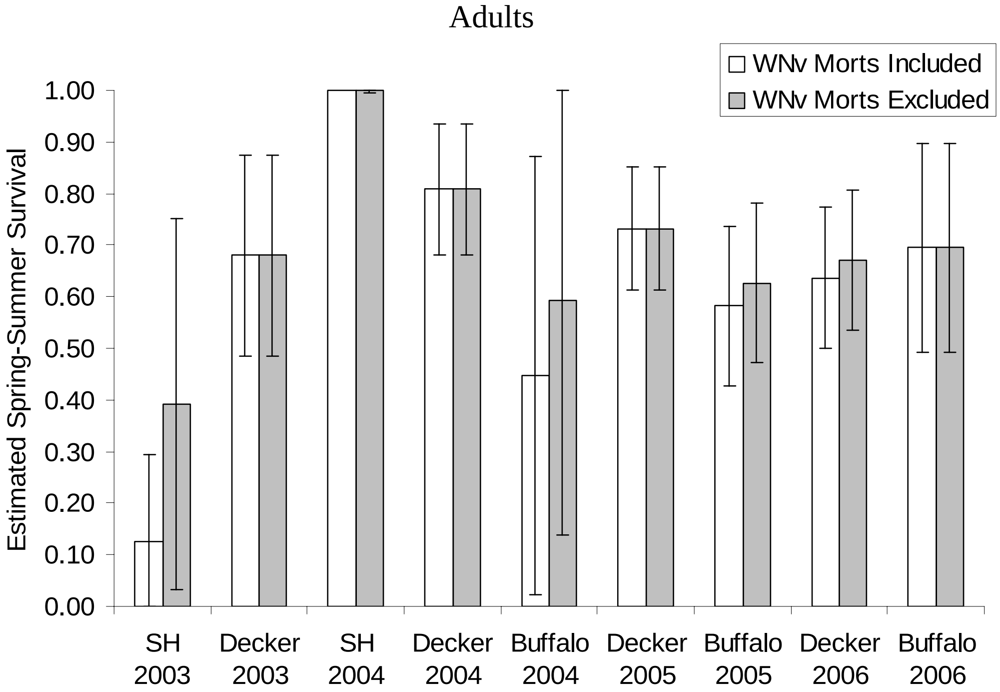

Adults
☐ WNv Morts Included
▨ WNv Morts Excluded
Estimated Spring-Summer Survival
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
SH 2003
Decker 2003
SH 2004
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006

Figure 10.

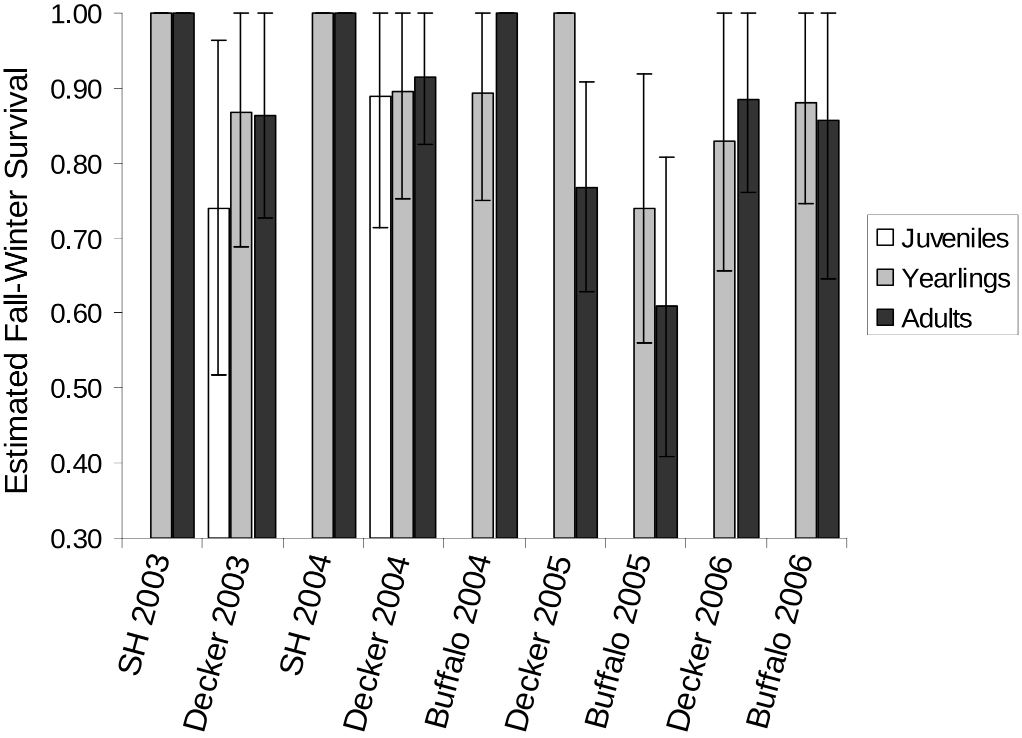
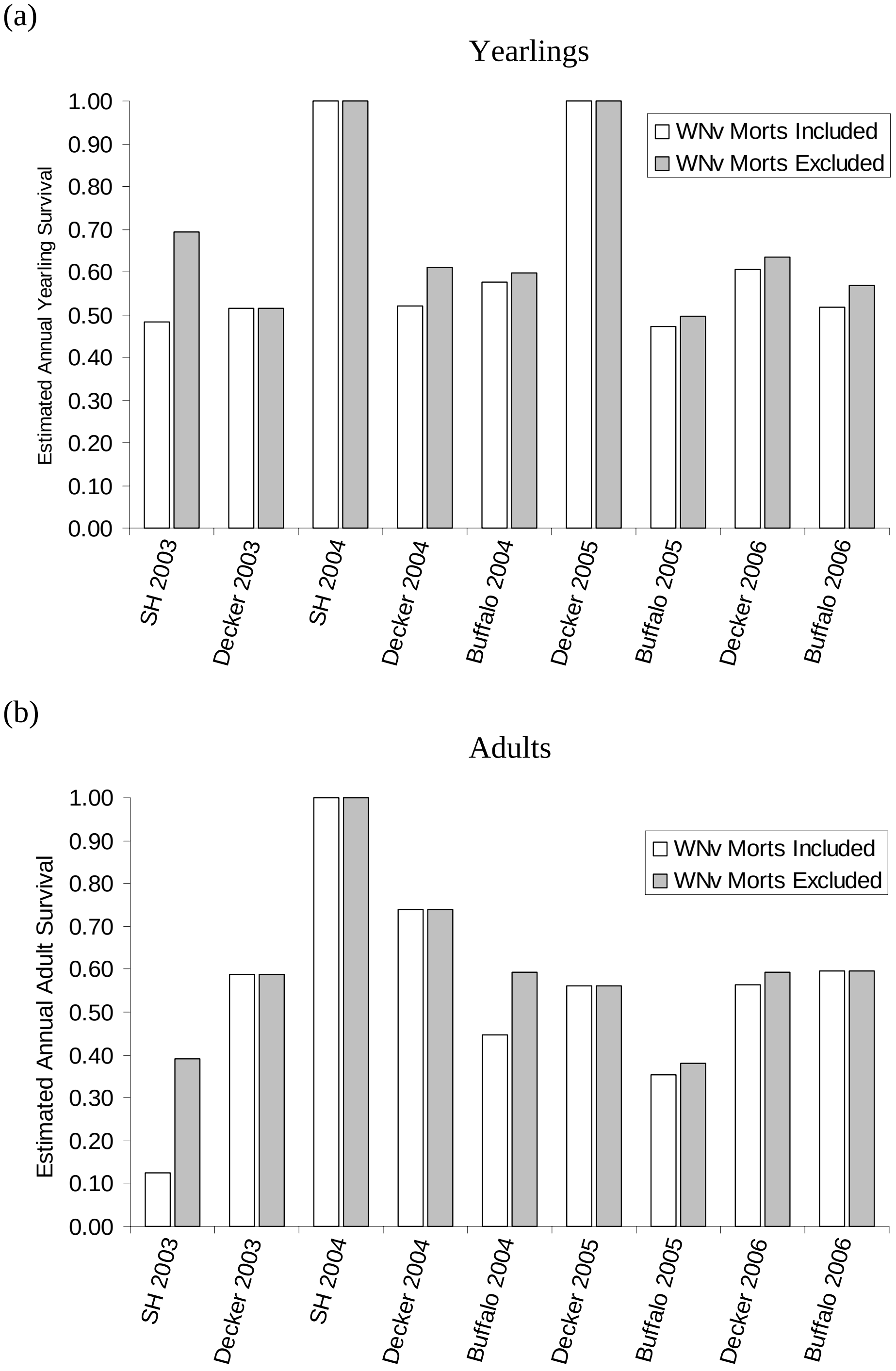

Estimated Fall-Winter Survival
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
SH 2003
Decker 2003
SH 2004
Decker 2004
Buffalo 2004
Decker 2005
Buffalo 2005
Decker 2006
Buffalo 2006
□ Juveniles
▨ Yearlings
■ Adults

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, λ) by -0.073 to -0.103 per year. Simulated impacts based on current estimates of WNv infection rate suggested an average decline in λ 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 λ for the Powder River Basin (Mills et al. 1999, Wisdom et al. 2000,. We then generated and compared means for λ 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:

$$[INIT_{1YR} \text{ x } FCLUTCH_{1YR} \text{ x } SUCC_{1YR} \text{ x } HATCH \text{ x } CHSURV_{YR} \text{ x } JUVSURV_{91}] +$$
$$[INIT_{1YR} \text{ x } (1\text{-}SUCC_{1YR}) \text{ x } INIT_{2YR} \text{ x } FCLUTCH_{2YR} \text{ x } SUCC_{2YR} \text{ x } HATCH \text{ x } CHSURV_{YR} \text{ X } JUVSURV_{83}].$$

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:

$$[INIT_{1AD} \text{ x } FCLUTCH_{1AD} \text{ x } SUCC_{1AD} \text{ x } HATCH \text{ x } CHSURV_{AD} \text{ x } JUVSURV_{91}] +$$

[$INIT_{1AD}$ x (1-$SUCC_{1AD}$) x $INIT_{2AD}$ x $FCLUTCH_{2AD}$ x $SUCC_{2AD}$ x HATCH x $CHSURV_{AD}$ x
JUVSURV83] +

[$INIT_{1AD}$ x (1-$SUCC_{1AD}$) x $INIT_{2AD}$ x (1-$SUCC_{2AD}$) x $INIT_{3AD}$ x $FCLUTCH_{3AD}$ x $SUCC_{2AD}$ x HATCH
x $CHSURV_{AD}$ x $JUVSURV_{83}$].

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:

$$\mathrm{JUVSURV83}_{adj} = (\mathrm{JUVSURV83}^{(0.12)})^{(6.67)} \text{ x } ((\mathrm{JUVSURV83}^{(0.12)})^{(1.63)} \text{ x } (1\text{-WNv mortality rate}))$$

$$\mathrm{JUVSURV91}_{adj} = (\mathrm{JUVSURV91}^{(0.11)})^{(6.67)} \text{ x } ((\mathrm{JUVSURV91}^{(0.12)})^{(2.43)} \text{ x } (1\text{-WNv mortality rate}))$$

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 λ 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 λ. 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.

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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	$\Delta\lambda$	$\Delta\lambda$
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 14.3° 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

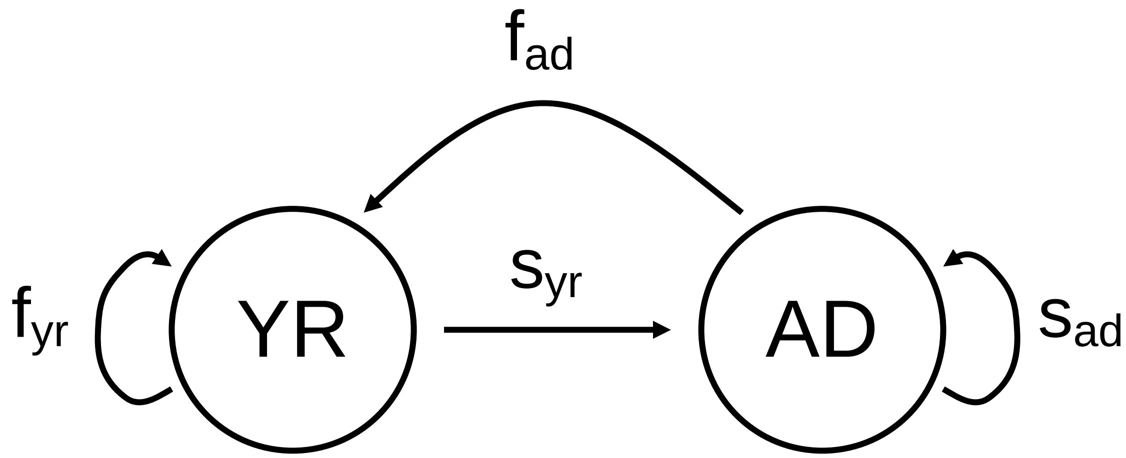
data on vital rates from the Powder River Basin, Montana and Wyoming, USA, 2003-2006, assuming no WNv impacts. Values are based on 1,000 simulation replicates.

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 1st year of the simulation and (b) 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. 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.

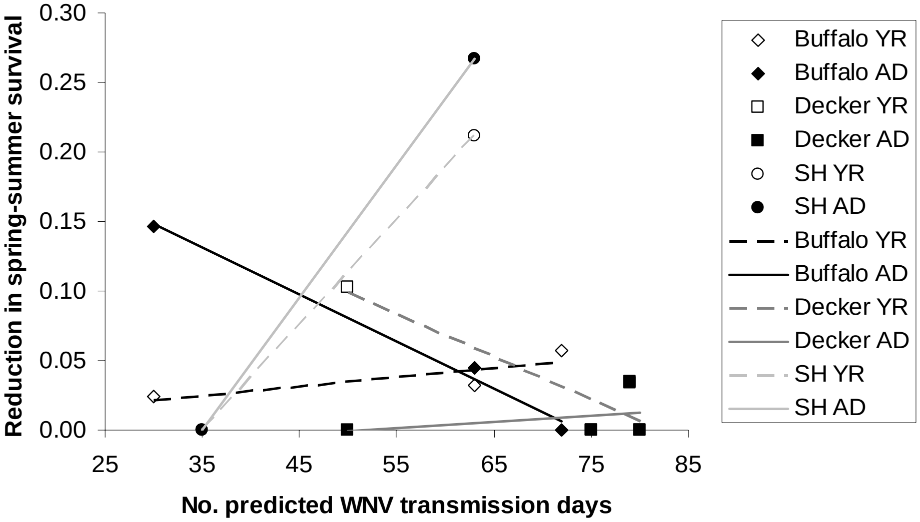
Figure 1.



$$\begin{bmatrix} f_{yr} & f_{ad} \\ s_{yr} & s_{ad} \end{bmatrix}$$

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

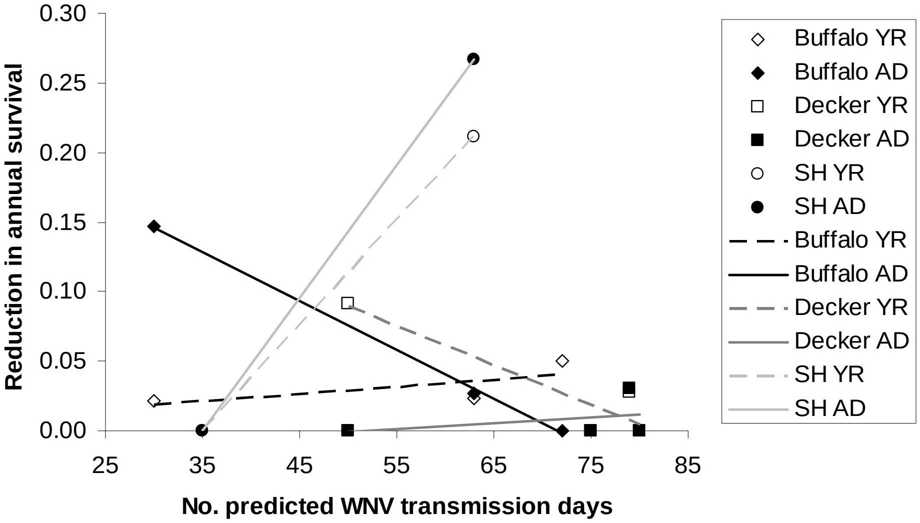

Reduction in annual survival
0.30
0.25
0.20
0.15
0.10
0.05
0.00
25
35
45
55
65
75
85
No. predicted WNV transmission days
Buffalo YR
Buffalo AD
Decker YR
Decker AD
SH YR
SH AD
Buffalo YR
Buffalo AD
Decker YR
Decker AD
SH YR
SH AD

Figure 3.

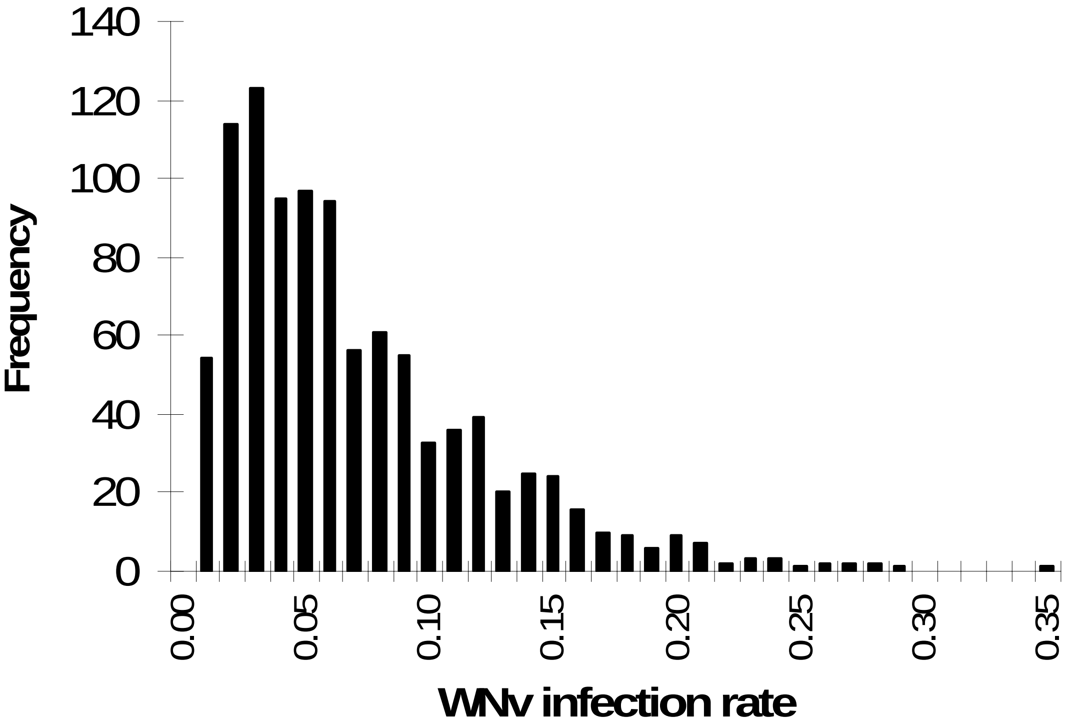
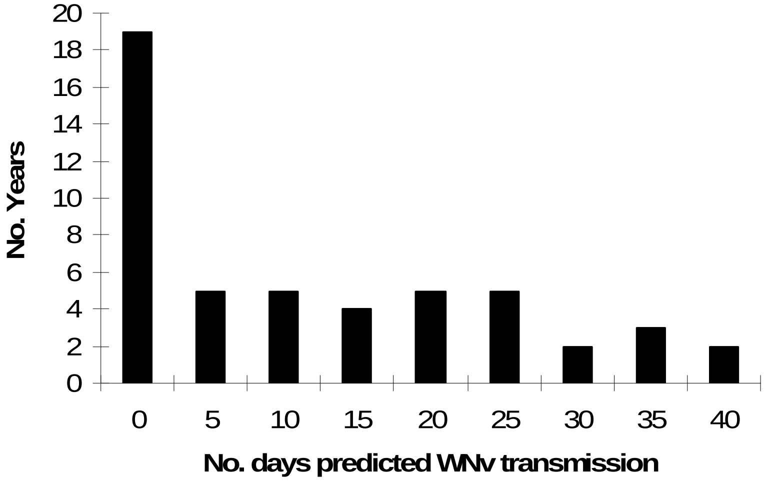

Frequency
140
120
100
80
60
40
20
0
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
WNv infection rate

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

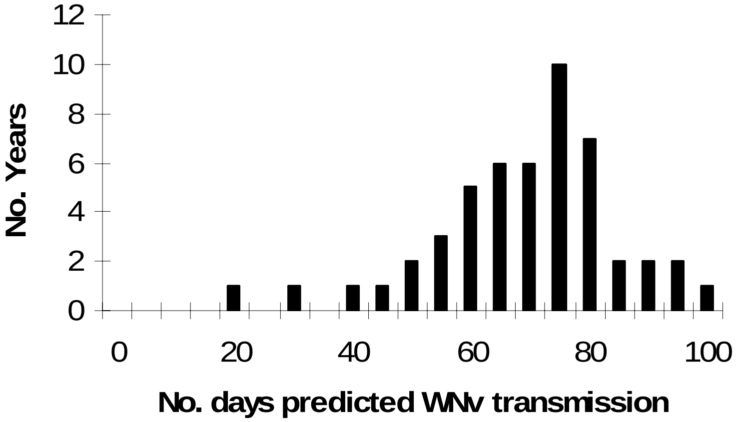

12
10
8
6
4
2
0
No. Years
0
20
40
60
80
100
No. days predicted WNv transmission

Figure 5.

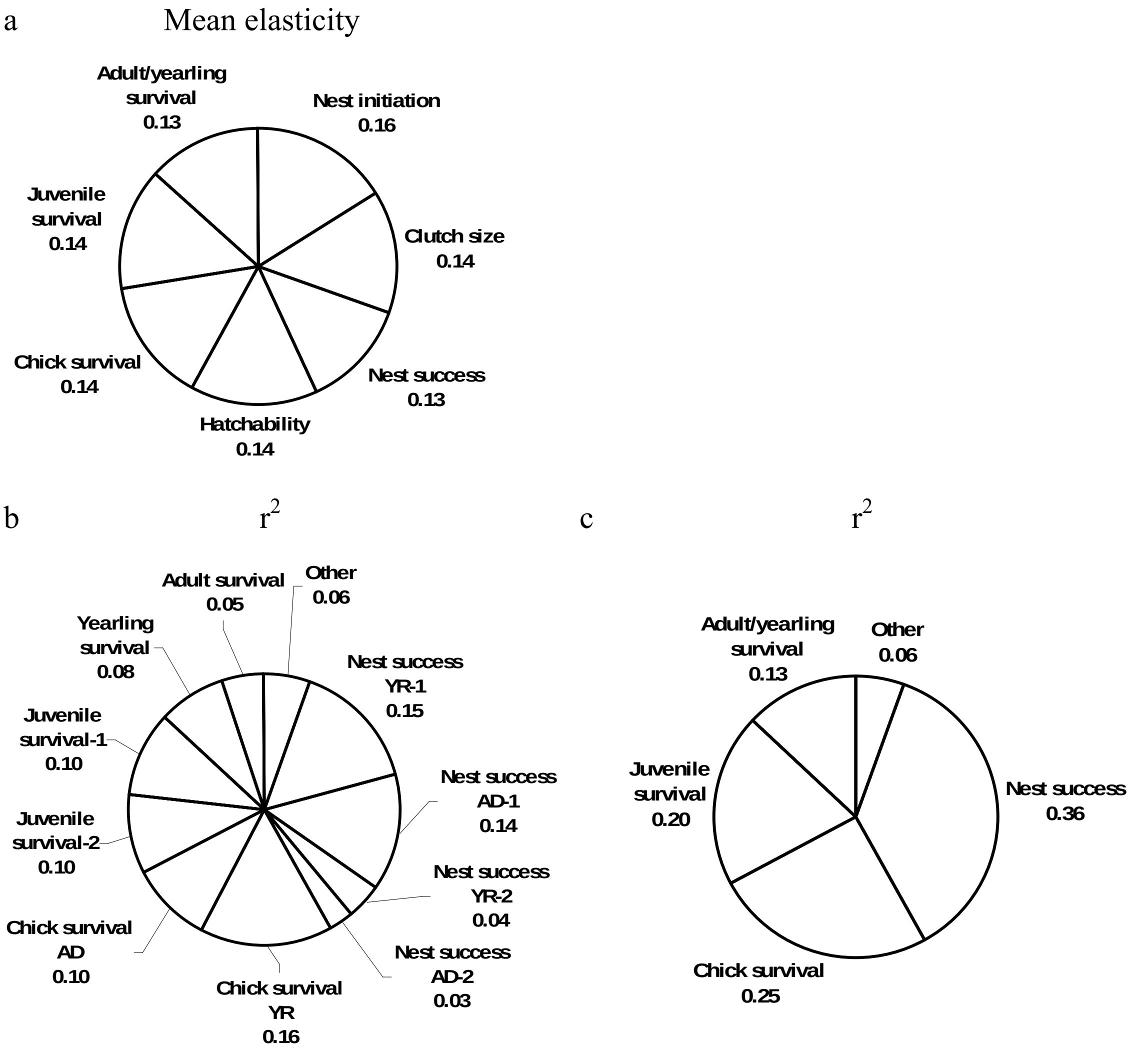

a
Mean elasticity
Adult/yearling survival 0.13
Nest initiation 0.16
Clutch size 0.14
Nest success 0.13
Hatchability 0.14
Chick survival 0.14
Juvenile survival 0.14
b
r^2
Adult survival 0.05
Other 0.06
Nest success YR-1 0.15
Nest success AD-1 0.14
Nest success YR-2 0.04
Nest success AD-2 0.03
Chick survival YR 0.16
Chick survival AD 0.10
Juvenile survival-2 0.10
Juvenile survival-1 0.10
Yearling survival 0.08
c
r^2
Adult/yearling survival 0.13
Other 0.06
Nest success 0.36
Chick survival 0.25
Juvenile survival 0.20

Figure 6.

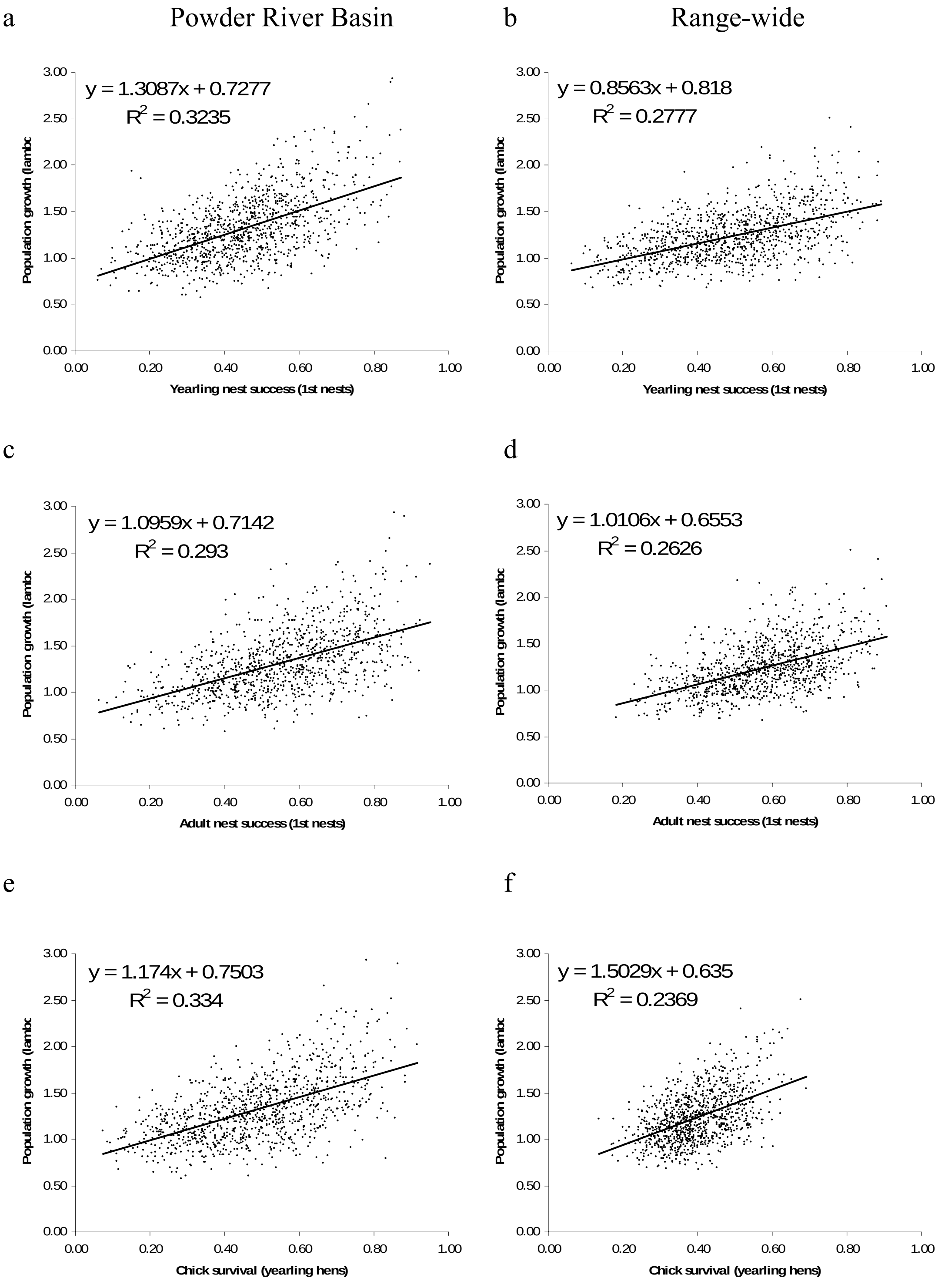

a
Powder River Basin
b
Range-wide
y = 1.3087x + 0.7277
R^2 = 0.3235
y = 0.8563x + 0.818
R^2 = 0.2777
Yearling nest success (1st nests)
c
d
y = 1.0959x + 0.7142
R^2 = 0.293
y = 1.0106x + 0.6553
R^2 = 0.2626
Adult nest success (1st nests)
e
f
y = 1.174x + 0.7503
R^2 = 0.334
y = 1.5029x + 0.635
R^2 = 0.2369
Chick survival (yearling hens)
Population growth (lambc
0.00
0.50
1.00
1.50
2.00
2.50
3.00
0.00
0.20
0.40
0.60
0.80
1.00

Figure 6 (cont.).

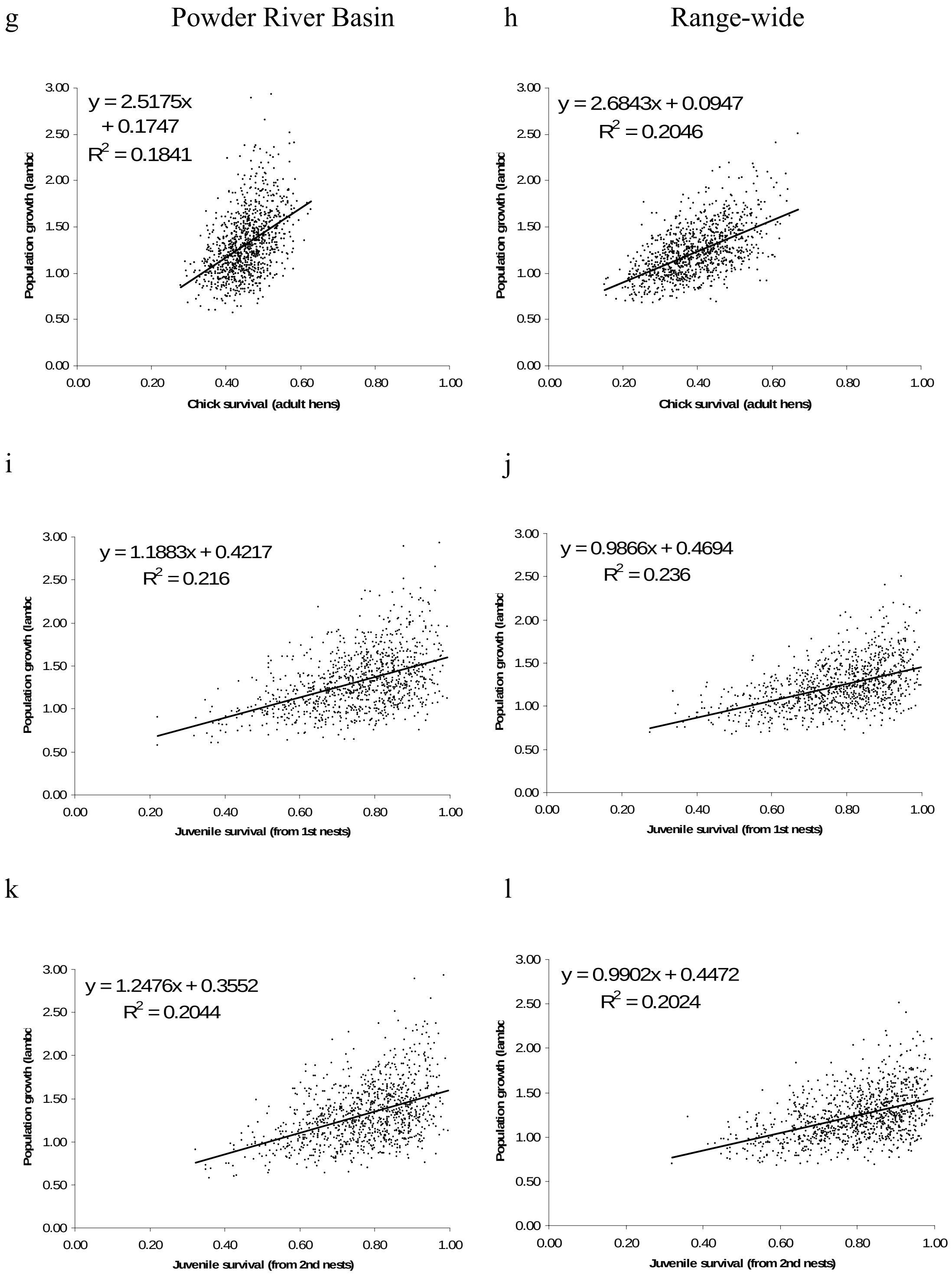


Figure 6 (cont.).

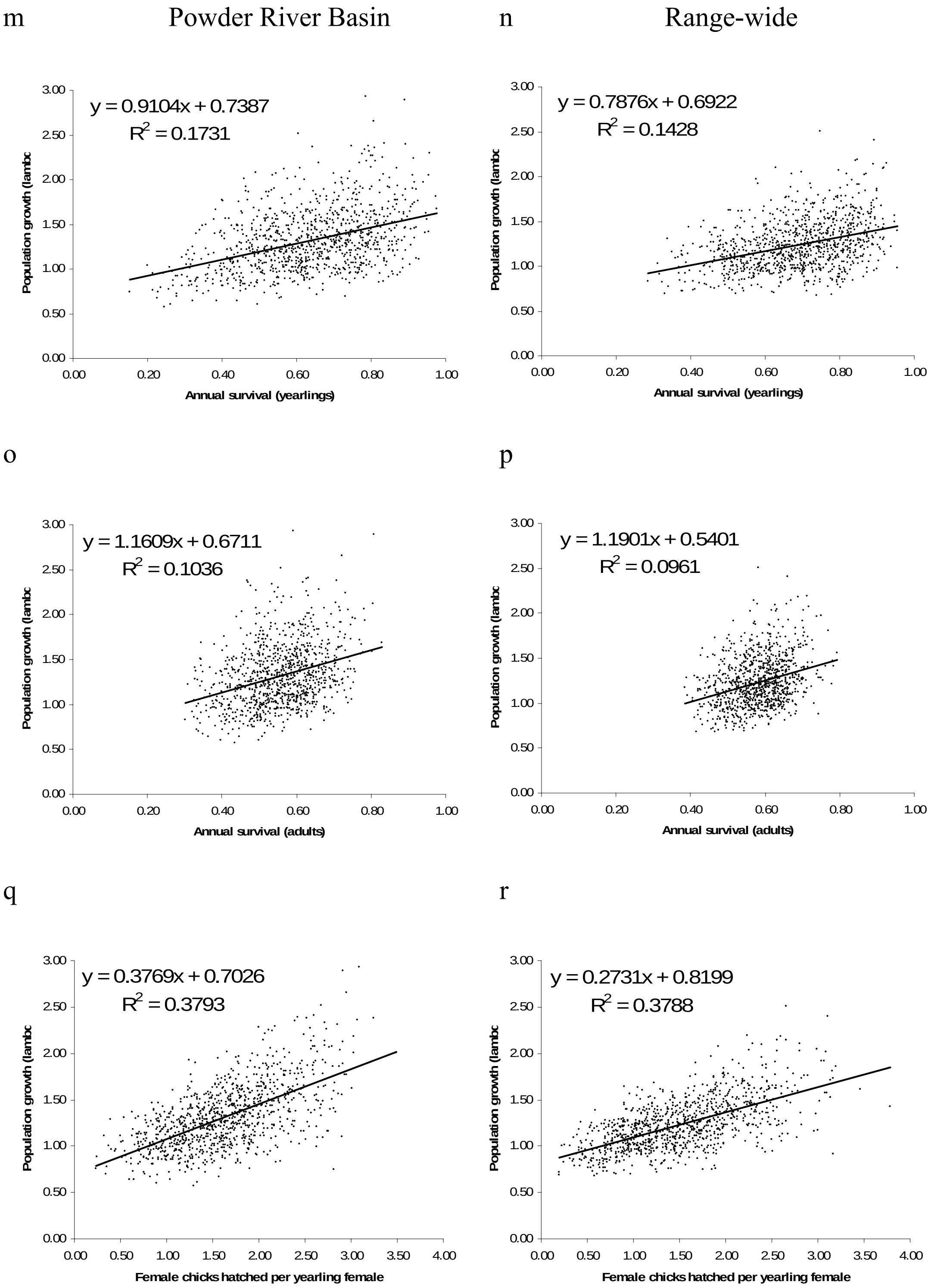
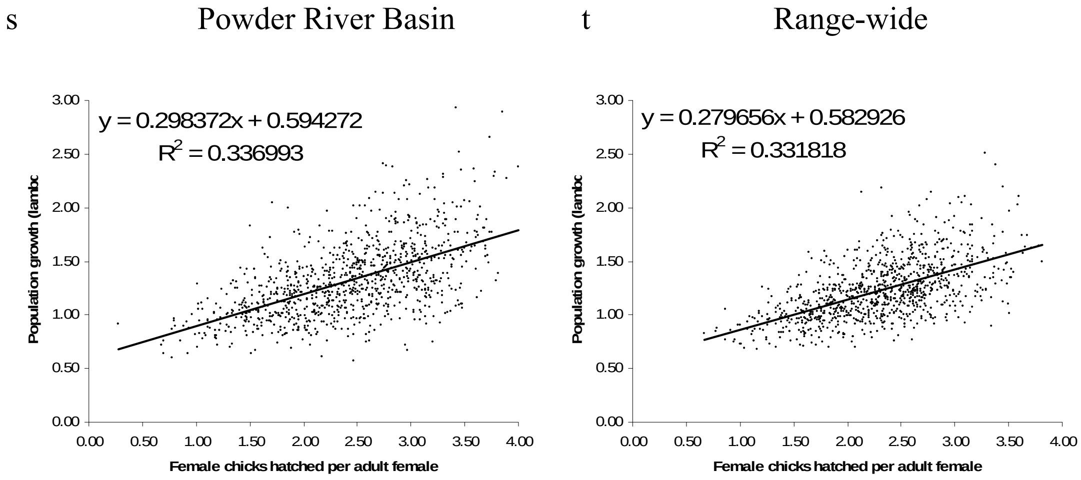


Figure 6 (cont.).



s Powder River Basin

t Range-wide

Figure 7.

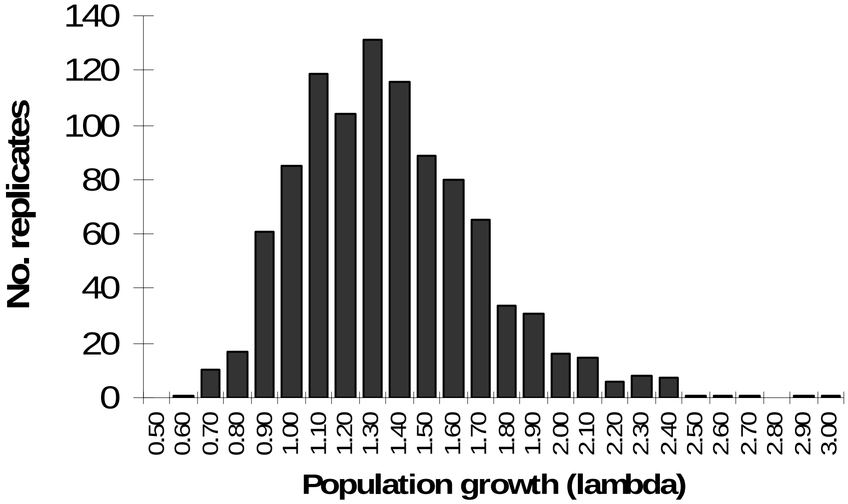
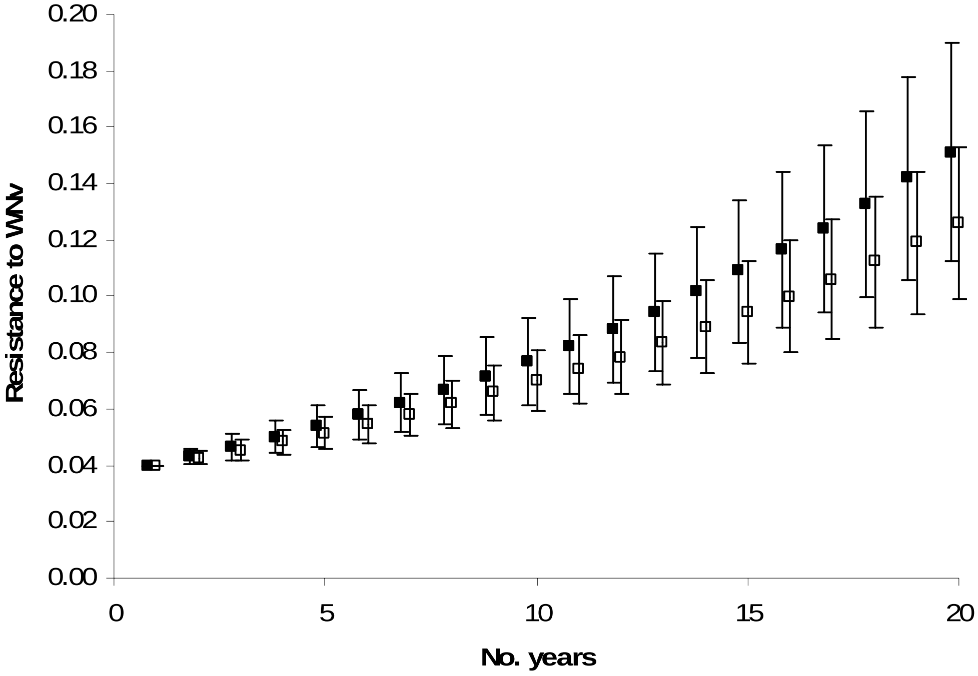

No. replicates
140
120
100
80
60
40
20
0
0.50
0.60
0.70
0.80
0.90
1.00
1.10
1.20
1.30
1.40
1.50
1.60
1.70
1.80
1.90
2.00
2.10
2.20
2.30
2.40
2.50
2.60
2.70
2.80
2.90
3.00
Population growth (lambda)

Figure 8.

a Current WNv infection rates



b Elevated WNv infection rates

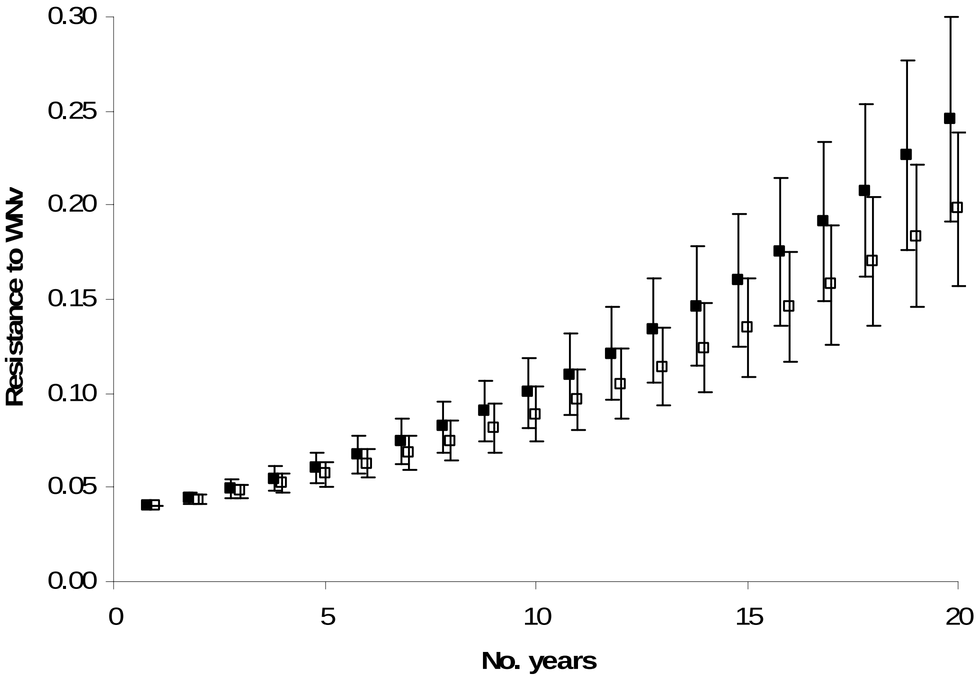


Figure 9.

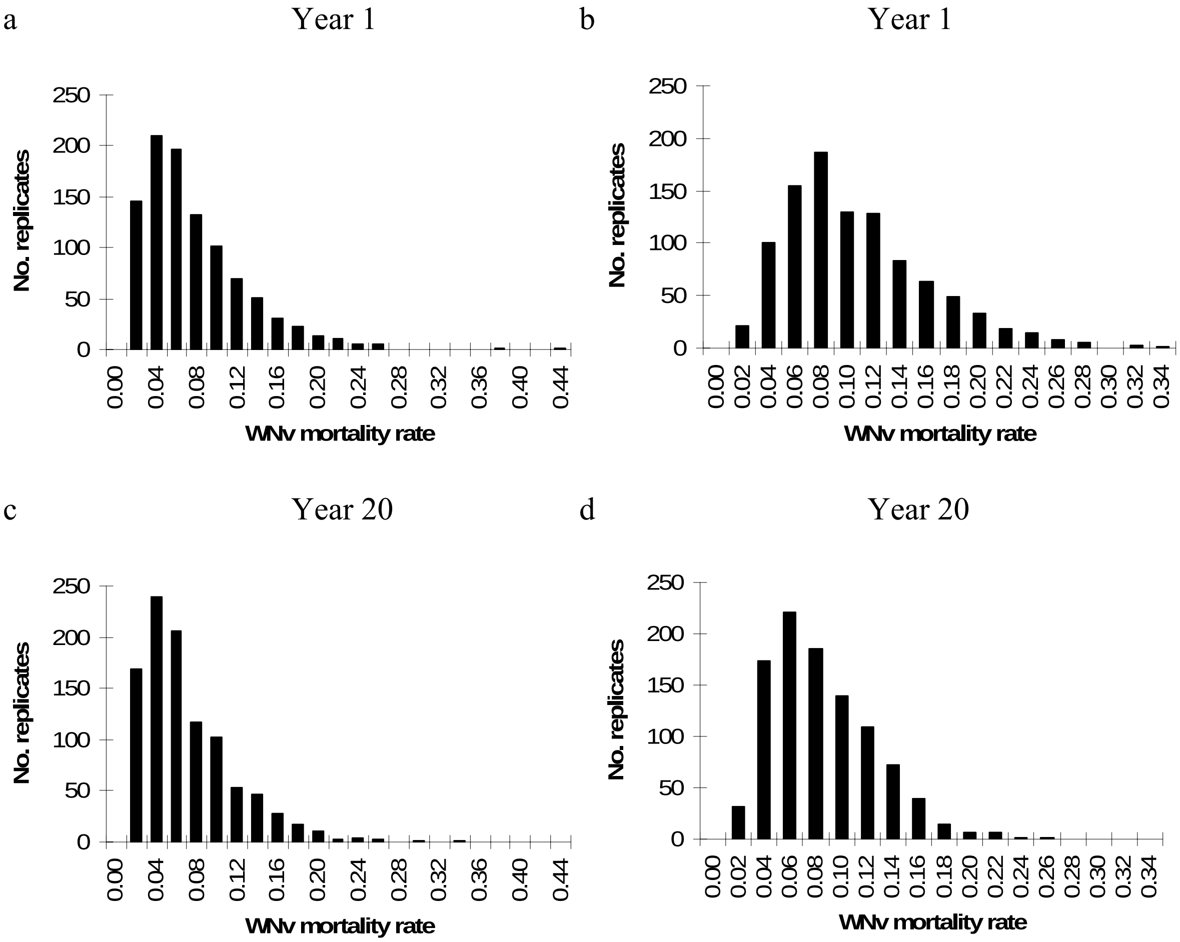
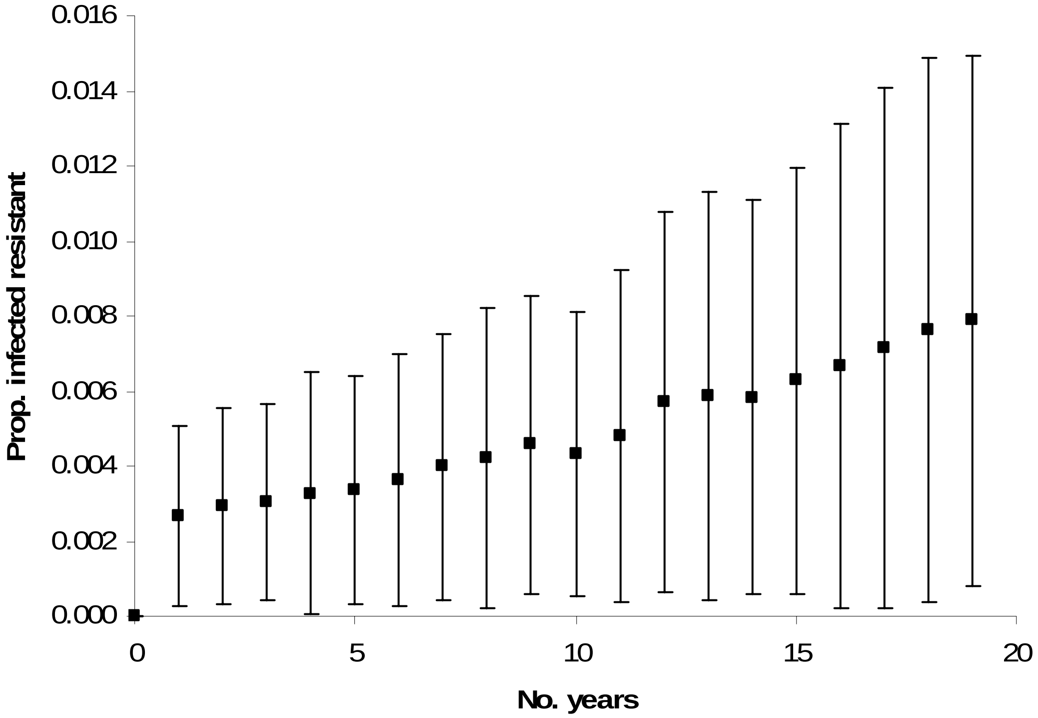

a
Year 1
No. replicates
250
200
150
100
50
0
0.00
0.04
0.08
0.12
0.16
0.20
0.24
0.28
0.32
0.36
0.40
0.44
WNv mortality rate
b
Year 1
No. replicates
250
200
150
100
50
0
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
0.18
0.20
0.22
0.24
0.26
0.28
0.30
0.32
0.34
WNv mortality rate
c
Year 20
No. replicates
250
200
150
100
50
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 rate
d
Year 20
No. replicates
250
200
150
100
50
0
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
0.18
0.20
0.22
0.24
0.26
0.28
0.30
0.32
0.34
WNv mortality rate

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

	Powder River Basin		Range-wide	
Vital Rate[a]	Mean	Variance[b]	Mean	Variance[b]
$\mathrm{INIT}_{\mathrm{YR1}}$	0.982	0.0003	0.829	0.0166
$\mathrm{INIT}_{\mathrm{AD1}}$	0.990	0.0001	0.930	0.0038
$\mathrm{INIT}_{\mathrm{YR2}}$	0.151	0.0284	0.148	0.0368
$\mathrm{INIT}_{\mathrm{AD2}}$	0.460	0.0681	0.395	0.0599
$\mathrm{INIT}_{\mathrm{AD3}}$	0.042	0.0021	0.074	0.0051
$\mathrm{FCLUTCH}_{\mathrm{YR1}}$	3.74	0.0880	3.81	0.118
$\mathrm{FCLUTCH}_{\mathrm{YR2}}$	2.98	0.1460	3.29	0.316
$\mathrm{FCLUTCH}_{\mathrm{AD1}}$	4.10	0.0860	4.16	0.040
$\mathrm{FCLUTCH}_{\mathrm{AD2}}$	3.19	0.1930	3.52	0.200
$\mathrm{FCLUTCH}_{\mathrm{AD3}}$	2.69	0.1500	3.02	0.200[c]
$\mathrm{SUCC}_{\mathrm{YR1}}$	0.453	0.0226	0.481	0.0268
$\mathrm{SUCC}_{\mathrm{AD1}}$	0.555	0.0284	0.569	0.0183
$\mathrm{SUCC}_{\mathrm{YR2}}$	0.521	0.1739	0.540	0.1309
$\mathrm{SUCC}_{\mathrm{AD2}}$	0.618	0.0958	0.553	0.0623
HATCH	0.923	0.0005	0.921	0.0018
$\mathrm{CHSURV}_{\mathrm{YR}}$	0.488	0.0274	0.391[d]	0.0084[d]
$\mathrm{CHSURV}_{\mathrm{AD}}$	0.456	0.0033	0.391[d]	0.0084[d]
$\mathrm{JUVSURV}_{83}$	0.776	0.0154[e]	0.799	0.0154
$\mathrm{JUVSURV}_{91}$	0.757	0.0177[e]	0.782	0.0177
$\mathrm{SURV}_{\mathrm{YR}}$	0.639	0.0239	0.684	0.0182

$\mathrm{SURV}_{\mathrm{AD}}$	0.556	0.0082	0.582	0.0050

---

[a] Variables defined as: $\mathrm{INIT}_{\mathrm{YR1}}$ = nest initiation rate of yearlings; $\mathrm{INIT}_{\mathrm{AD1}}$ = nest initiation rate of adults; $\mathrm{INIT}_{\mathrm{YR2}}$ = renesting rate of yearlings; $\mathrm{INIT}_{\mathrm{AD2}}$ = renesting rate of adults; $\mathrm{INIT}_{\mathrm{AD3}}$ = second renesting rate of adults; $\mathrm{FCLUTCH}_{\mathrm{YR1}}$ = clutch size (female eggs) of yearling first nests; $\mathrm{FCLUTCH}_{\mathrm{YR2}}$ = clutch size (female eggs) of yearling renests; $\mathrm{FCLUTCH}_{\mathrm{AD1}}$ = clutch size (female eggs) of adult first nests; $\mathrm{FCLUTCH}_{\mathrm{AD2}}$ = clutch size (female eggs) of adult renests; $\mathrm{FCLUTCH}_{\mathrm{AD3}}$ = clutch size (female eggs) of adult second renests; $\mathrm{SUCC}_{\mathrm{YR1}}$ = nest success of yearling first nests; $\mathrm{SUCC}_{\mathrm{AD1}}$ = nest success of adult first nests; $\mathrm{SUCC}_{\mathrm{YR2}}$ = nest success of yearling renests; $\mathrm{SUCC}_{\mathrm{AD2}}$ = nest success of adult renests (and second nests); HATCH = hatching success; $\mathrm{CHSURV}_{\mathrm{YR}}$ = survival of chicks from yearling females from hatch to 35 d; $\mathrm{CHSURV}_{\mathrm{AD}}$ = survival of chicks from adult females from hatch to 35 d; $\mathrm{JUVSURV}_{83}$ = survival of juveniles from 35 d of age to 10 September for renests; $\mathrm{JUVSURV}_{91}$ = survival of juveniles from 35 d of age to 10 September for first nests; $\mathrm{SURV}_{\mathrm{YR}}$ = annual survival of yearlings; $\mathrm{SURV}_{\mathrm{AD}}$ = 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.

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August 28th, 2020

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

Dear Commissioners,

PETITION FOR RULEMAKING Submitted pursuant to SDCL 1-26-13.

Nancy Hilding and Prairie Hills Audubon Society of Western SD submit this petition. Nancy Hilding is a resident of Meade County, SD. Prairie Hills Audubon Society is a non-profit corporation registered in SD and as such is a person by SD law and Supreme Court decisions.

RULE TO BE AMENDED - SD beaver trapping-hunting rule(s) - Kotilnek version

Jon Kotilnek has been reviewing GFP's rules for sake of improving clarity. At the July 16-17th Commission meeting, the Commission adopted non-substantive changes to the existing beaver trapping rules, which consolidated several rules about beaver trapping (41:08:01:07 and 41:08:01:08). These rules were consolidated into one rule 41:08:01:07 and amended. On August 18th the Interim Rules Review Committee concurred and this rule will be published by the Secretary of State and become a formal SD rule on about September 7th. We submit this petition as an amendment to the rule that will be in place in a few days and at finalization, rather than the two current rules that are currently in place, but will soon be gone.

Rule we seek to amend:

41:08:01:07. Beaver trapping and hunting season established. *The season is open from sunrise on November 1 through sunset on April 30 to catch, trap, or hunt beaver within the Black Hills Fire Protection District south of Interstate 90 and west of State Highway 79, except U. S. Forest Service lands where the beaver season is open from January 1 through March 31. The season is open year-round to catch, trap, or hunt beaver in the remaining portion of the Black Hills Fire Protection District. In all counties east of the Missouri River the season is open from sunrise on November 1 through sunset on April 30. The season is open year-round to catch, trap, or hunt beaver in all counties west of the Missouri River except the portion of the Black Hills Fire Protection District as described in this section.*

Source: *SL 1975, ch 16, § 1; 1 SDR 26, effective September 11, 1974; 3 SDR 22, effective September 23, 1976; 5 SDR 19, effective September 14, 1978; 6 SDR 14, effective August 23, 1979; 7 SDR 21, effective September 15, 1980; 8 SDR 19, effective August 31, 1981; 9 SDR 30, effective September 13, 1982; 10 SDR 12, effective August 17, 1983; 10 SDR 76, 10 SDR 102, effective July 1, 1984; 11 SDR 30, effective August 30, 1984; 12 SDR 22, effective August 21, 1985; 13 SDR 26, effective September 10, 1986; 14 SDR 40, effective September 23, 1987; 15 SDR 24, effective August 14, 1988; 16 SDR 32, effective August 20, 1989; 17 SDR 23, effective August 16, 1990; 18 SDR 33, effective August 19, 1991; 23 SDR 20, effective August 13, 1996; 32 SDR 31, effective August 29, 2005; 35 SDR 47, effective September 8, 2008.*

General Authority: *SDCL 41-2-18(2)(17), 41-8-20.*
Law Implemented: *SDCL 41-2-18(2)(17), 41-8-20.*

Current rules soon to be replaced, which we are ignoring.

41:08:01:07. Beaver trapping and hunting season established in East River and Black Hills Fire Protection District -- Exception. *The season is open from sunrise on the first Saturday of November to sunset on April 30 to catch, trap, or hunt beaver within the Black Hills Fire Protection District south of Interstate 90 and west of State Highway 79, except U. S. Forest Service lands where the beaver season is open from January 1 to March 31, inclusive. The season is open the year around to catch, trap, or hunt beaver in the remaining portion of the Black Hills Fire Protection District. In all counties east of the Missouri River the season is open from sunrise on the first Saturday of November to sunset on April 30.*

41:08:01:08. Beaver trapping and hunting season established in West River -- Exception. *The season is open the year around to catch, trap, or hunt beaver in all counties west of the Missouri River except that portion of the Black Hills Fire Protection District described in § 41:08:01:07.*

CHANGE REQUESTED

We propose this new rule

41:08:01:07. Beaver trapping and hunting season established. The season is open from sunrise on November 1 through sunset on March 31st to catch, trap or hunt beaver in all of South Dakota, except U. S. Forest Service lands where the beaver season is open from January 1 through March 31.

STATEMENT OF REASONS

1. Crazy division of the Black Hills Fire Protection District

The 41:08:01:07 current rule(s) in both Jon Kotilnek's version and the old versions, creates a crazy subdivision of the Black Hills Fire Protection District. The District is split into four parts. You need to imagine a box, with east-to-west sides as lines drawn horizontally from Rapid City to the Wyoming border and from Hot Springs to the Wyoming border. You need to imagine north-to-south sides of the box created by the Wyoming border and highway 79. In that square the private inholdings have a 6-month trapping season and the Forest Service lands have 3-months. However in the Fire Protection district below the southern box edge at Hot Springs and above the northern box edge at Rapid City, all the private land inholdings in the forest and edge properties around the forest have 360 day season. There is a lot of forest north of Rapid City. We imagine due to homesteading many riparian areas are on private property, not on Forest Service land. We ask what possible rational reason could there be for this weird division?

2. Relationship of beavers to otters

SD otters are recovering from likely past extirpation in SD. Otters are frequently taken incidentally in beaver traps & otters rely on habitat provided by beavers.

The "2018 Game, Fish and Parks Threatened and Endangered Species Status Review" says at pages 123:

> "River otters have a commensal relationship with beavers as beaver dams provide year-round open water and beaver bank dens and lodges are used by river otters as rest and natal sites"

SD 2018 Endangered and Threatened Species Status Review says at page 124

> "Of 117 reported river otters killed in South Dakota from 1979 through 2016, 73% were killed incidental to legal trapping activities.....
>
> A year-round beaver trapping season west of the Missouri River and a focus on non-native trout management in Black Hills streams will impair statewide recovery of river otters."

Melquist in his 2015 report to SDGFP on his 4-year study of SD river otters writes on page 71:

> *"I do not believe current regulations for harvesting and controlling beaver populations in South Dakota are conducive to the expansion of otters in West River and could hinder the rate of growth in East River. In South Dakota, female otters give birth on approximately 1 April. Any lactating female otter trapped and killed will result in the loss of her offspring. To reduce the possibility of trapping female otters with dependent young, beaver trapping seasons should not extend beyond 31 March. The unrestricted 31 March take of beaver that is currently allowed in West River should be replaced with a harvest season not to extend beyond 31 March if SDGFP plans to try and recover otters in that region of the State. Unregulated shooting of beaver should be discouraged or prohibited to avoid accidentally shooting an otter"*
> **(Emphasis added)**

Melquist in his 2015 report to SDGFP on his 4-year study of SD river otters at page 12 - writes:

Features I looked for in evaluating suitability of the different streams for otters included:

> •_*Stream characteristics: Varying water depths and stream velocity, stream meanders, suitable bank cover (trees, shrubs), and presence of bank and in-stream structures.*

> - _*Watershed features: Presence of adjacent wetlands and suitable tributaries, presence of beaver or beaver activity, and the level of human impacts.*
> - _*Prey availability: A diverse prey base (e.g., multiple fish species, crayfish, and frogs) is always preferable to enhance otter habitat. While I always looked for the presence of potential prey at each survey site, prey suitability was based on existing data.*
> - _*Other factors: Not a high traffic area and few or no human establishments.*
>
> **(Emphasis added)**

SDGFP's Draft 2020-2029 SD River Otter Management Plan July Version at page 3

> "Target species was known for 146 of the 216 (67.5%) incidentally trapped river otter (Table 5). Of these, 116 (53.7%) were caught in traps targeting beaver, 19 while targeting raccoon (8.8%), 5 in fish nets or traps (2.3%), and 3 in sets targeting mink (1.4%). "

Here is the chart about that from the draft River Otter Plan::]

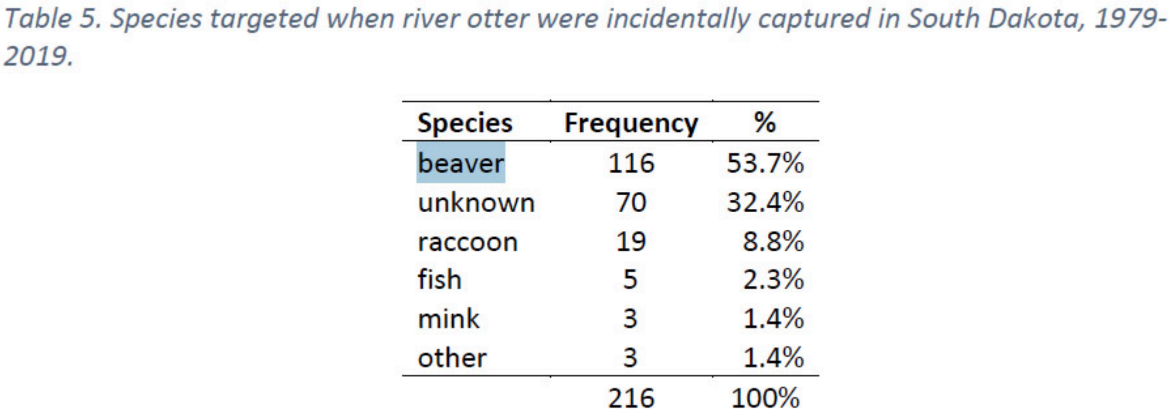

Table 5. Species targeted when river otter were incidentally captured in South Dakota, 1979-2019.

Species	Frequency	%
beaver	116	53.7%
unknown	70	32.4%
raccoon	19	8.8%
fish	5	2.3%
mink	3	1.4%
other	3	1.4%
	216	100%

32.5 percent of the otters were taken in traps for which the purpose was unknown and that set of unknowns likely would have included more beaver traps.

Otters have babies in April and April beaver trapping will harm recovery of otters. The current East & west river trapping seasons overlap time of otters giving birth.

Keith Fisk e-mailed me on 7/24/20 that "Beaver in South Dakota typically breed Feb. – April (most probably breed in March and April) and birth approximately 3 months later or around May -July".

3. Beavers are good for environment.

Beavers serve very valuable help for the South Dakota aquatic and terrestrial habitats that are associated with surface water. Here is a quote from USFWS's "The Beaver Restoration Guidebook *Working with Beaver to Restore Streams, Wetlands, and Floodplains, Version 2.0, June 30, 2017* Please see page iv

> "*Increasingly, restoration practitioners are using beaver to accomplish stream, wetland, and floodplain restoration. This is happening because, by constructing dams that impound water and retain sediment, beaver substantially alter the physical, chemical, and biological characteristics of the surrounding river ecosystem, providing benefits to plants, fish, and wildlife. The possible results are many, inclusive of: higher water tables; reconnected and expanded floodplains; more hyporheic exchange; higher summer base flows; expanded wetlands; improved water quality; greater habitat complexity; more diversity and richness in the populations of plants, birds, fish, amphibians, reptiles, and mammals; and overall increased complexity of the riverine ecosystems.*
>
> *In many cases these effects are the very same outcomes that have been identified for river restoration projects. Thus, by creating new and more complex habitat in degraded systems, beaver dams (and their human-facilitated analogues) have the potential to help restoration practitioners achieve their objectives. Beaver have become our new partner in habitat restoration.*"

Beavers (*Castor canadensis*) are a management indicator species (MIS) on the Black Hills National Forest. (see the 2006 Black Hills National Forest Land and Resource Management Plan page II-32). Management Indicators (MI) are defined in Forest Service Manual (FSM) 2620.5-1 as

> *"(P)lant and animal species, communities, or special habitats selected for emphasis in planning, and which are monitored during forest plan implementation in order to assess the effects of management activities on their populations and the populations of other species with similar habitat needs which they may represent."*

It makes no sense for beaver trapping/hunting on the Black Hills National Forest to not to be monitored and inventoried. The Forest Service needs to know if fluctuations in beaver populations are due to Forest Service forest management choices or private beaver hunting/trapping.

4. SDCL 41-8-23 provides for private people who have conflict beavers on their land to ask GFP Secretary for permission to kill conflict beaver

Keith Fisk has suggested to me that the reason for a more aggressive hunting beaver season west River is that the West River landowners are more vocal with GFP about beaver conflict issues than East River. SD has this law about killing conflict beaver:

> *41-8-23. Killing of mink, muskrats, and beavers causing damage.*
> *Mink may be killed at any time if doing damage around buildings but all such mink killed are the property of the state, if taken during the closed season. If muskrat or beaver are injuring irrigation ditches, dams, embankments, or public highways, or causing any other damage to property, the secretary of game, fish and parks may issue a permit to trap or kill such animals at any time. The Game, Fish and Parks Commission may authorize the killing or trapping of beaver upon public lands and game preserves at any time the commission deems necessary.*
>
> *Source: SDC 1939, § 25.0801; SL 1941, ch 121; SL 1947, ch 113; SL 1951, ch 125; SL 1955, ch 86;*
>
> *SL 1959, ch 122; SL 1959, ch 123; SL 1961, ch 122; SL 2009, ch 206, § 53.*

This law allows private landowners concerned about conflict beavers to apply to the Secretary of GFP for permission to kill conflict beavers. We don't think this is such a hardship.

It allows that land management agencies with conflict beavers may rely on the Commission to authorize beaver killing or trapping. We are not sure that the federal government needs the states permission to manage conflict wildlife in federal jurisdiction, but it seems state and local public land managers would need to.

Our proposed rule change, if finalized, won't take effect till later November 2020 after the Interim Rules Review Committee November meeting, when the 5-month beaver hunting/trapping season will be ongoing. If the Commission wants to use its' power to create a new rule authorizing trapping of conflict beaver on public lands in SD, it has till the end of March to do so. If adopted after October Commission meeting, there may be a short delay for the rule to become effective, while waiting for 20 days after the first Interim Rules Review Committee meeting in March or April 2021.

We could propose a rule for conflict beavers on public land, but you might want to consult with state and local land-managing agencies to see what they would want such a rule to look like and consider what issues there are with it.

However if you don't want to delay so as to study the issue, in addition to the above rule proposal, you could also consider moving forward a new rule proposal for **41:08:01** saying -- "Public land managers have 365 days a year to kill or translocate conflict beavers from the properties or public right of-ways they manage. If a beaver is injuring irrigation ditches, dams, embankments, or public highways, or causing any other damage to property, it may be considered a conflict beaver "

Trapping when beavers have dependent young.

Changing from a year round trapping season to shorter season will reduce the killing of mother beavers with dependent young. This is a conservation issue to help maximize beaver populations, once you acknowledge that beaver are valuable to SD. It is also an animal welfare issue as it reduces suffering of dependent young who may die of starvation.

Otters have babies in April so incidental take in beaver traps in April can orphan otter young. Keith Fisk e-mailed me on 7/24/20 that : "*Beaver in South Dakota typically breed Feb. – April (most probably breed in March and April) and birth approximately 3 months later or around May -July.*" So beaver trapping in May-July will orphan dependent young.

Citations:

Pollock, M.M., G.M. Lewallen, K. Woodruff, C.E. Jordan and J.M. Castro (Editors) 2017. The Beaver Restoration Guidebook: Working with Beaver to Restore Streams, Wetlands, and Floodplains. Version 2.0. United States Fish and Wildlife Service, Portland, Oregon. 219 pp. Online at: https://www.fws.gov/oregonfwo/promo.cfm?id=177175812

SD Department of Game, Fish and Parks, SOUTH DAKOTA RIVER OTTER MANAGEMENT PLAN, 2020-2029, Wildlife Division Report, 2020-02, Pierre, South Dakota, July 2020

SD Department of Game, Fish and Parks, STATE T&E SPECIES STATUS REVIEWS APPROVED BY SDGFP COMMISSION, 5 APRIL 2018 https://gfp.sd.gov/UserDocs/nav/status-reviews.pdf

United States Department of Agriculture Forest Service,mRocky Mountain Region Black Hills National Forest, Black Hills National Forest Land and Resource Management Plan, Custer South Dakota, March 2006 https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd592921.pdf

Wayne E. Melquist, Ph.D., FINAL REPORT, Determination of river otter (*Lontra canadensis*) distribution and evaluation of potential sites for population expansion in South Dakota , 1 October 2011 - 30 January 2015, Prepared for: Wildlife Diversity Program South Dakota Game, Fish and Parks , May 2015 https://gfp.sd.gov/images/WebMaps/Viewer/WAP/Website/SWGSummaries/FINAL REPORT Melquist River Otters T-55.pdf

Sincerely,

Nancy Hilding

Nancy Hilding
President
Prairie Hills Audubon Society
and for Self

Christine Sandvik

Christine Sandvick

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August 28th, 2020

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

Dear Commissioners,

PETITION FOR RULEMAKING Submitted pursuant to SDCL 1-26-13.

Nancy Hilding and Prairie Hills Audubon Society of Western SD submit this petition. Nancy Hilding is a resident of Meade County, SD. Prairie Hills Audubon Society is a non-profit corporation registered in SD and as such is a person by SD law and Supreme Court decisions.

RULE TO BE AMENDED - 41:10:02:05. Endangered fish - Kotilnek version

Jon Kotilnek has been reviewing GFP's rules for sake of improving clarity. At the July 16-17th Commission meeting, the Commission adopted non-substantive changes to the existing endangered fish rule. On August 18th the Interim Rules Review Committee concurred and this rule will be published by the Secretary of State and become a formal SD rule on about September 7th. We submit this petition as an amendment to the rule that will be in place in a few days and at finalization, rather than the rule currently in place, which will soon be gone. They have the same number. Jon just changed the wording of the title a bit.

Exact Rule we seek to amend:

> **41:10:02:05. Endangered fish.** The following fish are classified as endangered in the state:
> (1) Finescale dace, ***Chrosomus neogaeus***;
> (2) Banded killifish, ***Fundulus diaphanus***;
> (3) Pallid sturgeon, ***Scaphirhynchus albus***;

(4) Blacknose shiner, ***Notropis heterolepis***; and
(5) Sicklefin chub, ***Macrhybopsis meeki***.

Source: 4 SDR 57, effective March 16, 1978; 10 SDR 76, 10 SDR 102, effective July 1, 1984; 17 SDR 139, effective March 21, 1991; 22 SDR 155, effective May 22, 1996; 33 SDR 125, effective January 29, 2007; 34 SDR 242, effective April 7, 2008; 44 SDR 93, effective December 4, 2017.
General Authority: SDCL 41-2-18(1)(3).
Law Implemented: SDCL 34A-8-3, 41-2-18(1)(3).
41:10:02:06. List of threatened Threatened fish. Fish The following fish are classified

CHANGE REQUESTED

_We wish to add the Lake Chub to the list

We would add the name of the species of lake chub in the row after Sicklefin chub.

41:10:02:05. Endangered fish. The following fish are classified as endangered in the state:

(1) Finescale dace, ***Chrosomus neogaeus***;
(2) Banded killifish, ***Fundulus diaphanus***;
(3) Pallid sturgeon, ***Scaphirhynchus albus***;
(4) Blacknose shiner, ***Notropis heterolepis***; and
(5) Sicklefin chub, ***Macrhybopsis meeki***.
(6) Lake Chub ***(Couesius plumbeus)***

STATEMENT OF REASONS

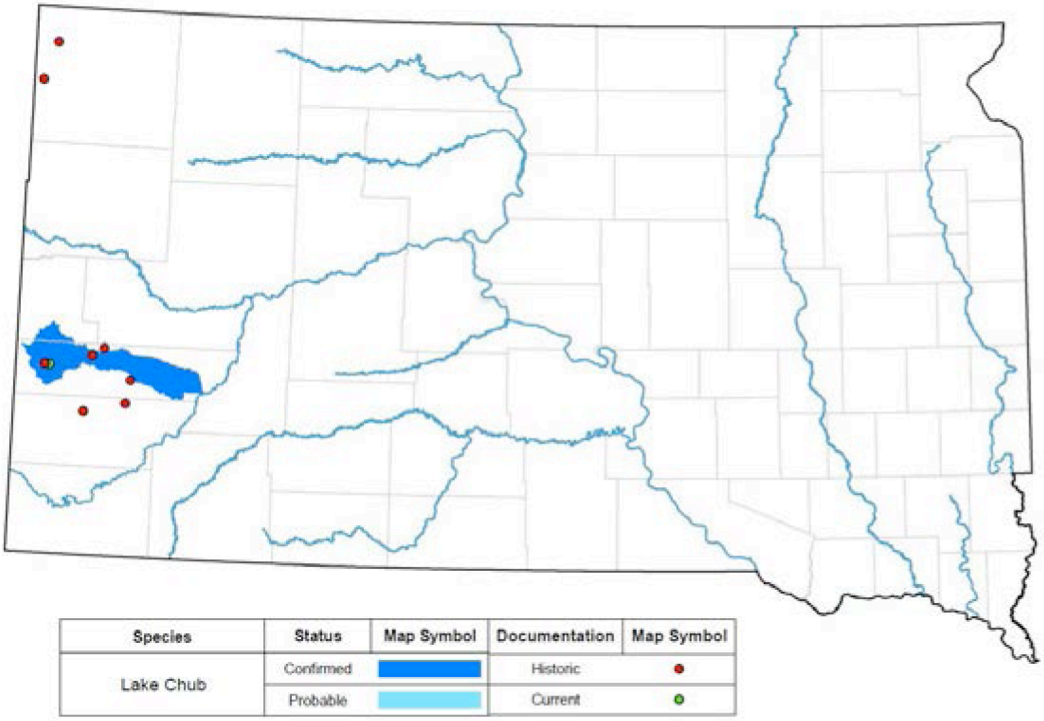
The lake chub is a species of greatest conservation need and is considered critically imperiled in SD

On page 294 SD Wildlife Action Plan Appendix's, SDGFP identifies Lake Chub's challenges as:

"**Conservation Challenges:** • _Modified/suppressed fire regimes • _Exotic/introduced species impacts •

> _Ecosystem alteration/habitat degradation ○ Mining • _Pollution/pesticides/herbicides • _Grazing/Agricultural practices ○ Heavy grazing • _Forest Management Practices ○ Logging"

Scroll down to the next page for a map from the SD Wildlife Action Plan's Appendix's showing historic sightings of lake chub (no current sightings).

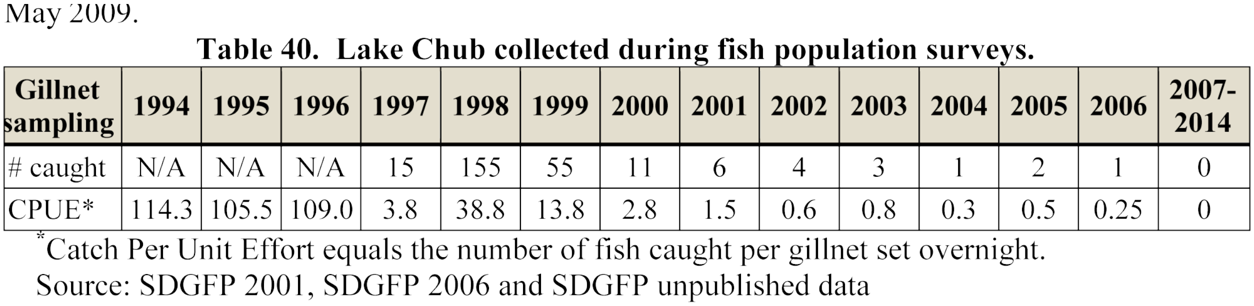


The Lake Chub used to exist in some streams in the Black Hills. Scroll down for a map of past locations on page 7 of this letter. It disappeared from these streams and only remained in Deerfield Lake about 2006.

Lake Chub lost from Deerfield Lake

The below chart and text is from the "Black Hills National Forest's 2013-2014 Monitoring and Evaluation Report" published August 2015 on page 73:

> "The table below shows the number of lake chub collected during fish population surveys done by the South Dakota Department of Game, Fish and Parks (SDGFP) on Deerfield Reservoir. One lake chub was captured incidental to white sucker removal efforts conducted by the SDGFP in May 2009."



May 2009.

Table 40. Lake Chub collected during fish population surveys.

Gillnet sampling	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007-2014
# caught	N/A	N/A	N/A	15	155	55	11	6	4	3	1	2	1	0
CPUE*	114.3	105.5	109.0	3.8	38.8	13.8	2.8	1.5	0.6	0.8	0.3	0.5	0.25	0

*Catch Per Unit Effort equals the number of fish caught per gillnet set overnight.
Source: SDGFP 2001, SDGFP 2006 and SDGFP unpublished data

SD GFP poisoned Deerfield Lake to get rid of an invasive fish species and in the process may have killed all the Lake Chub.

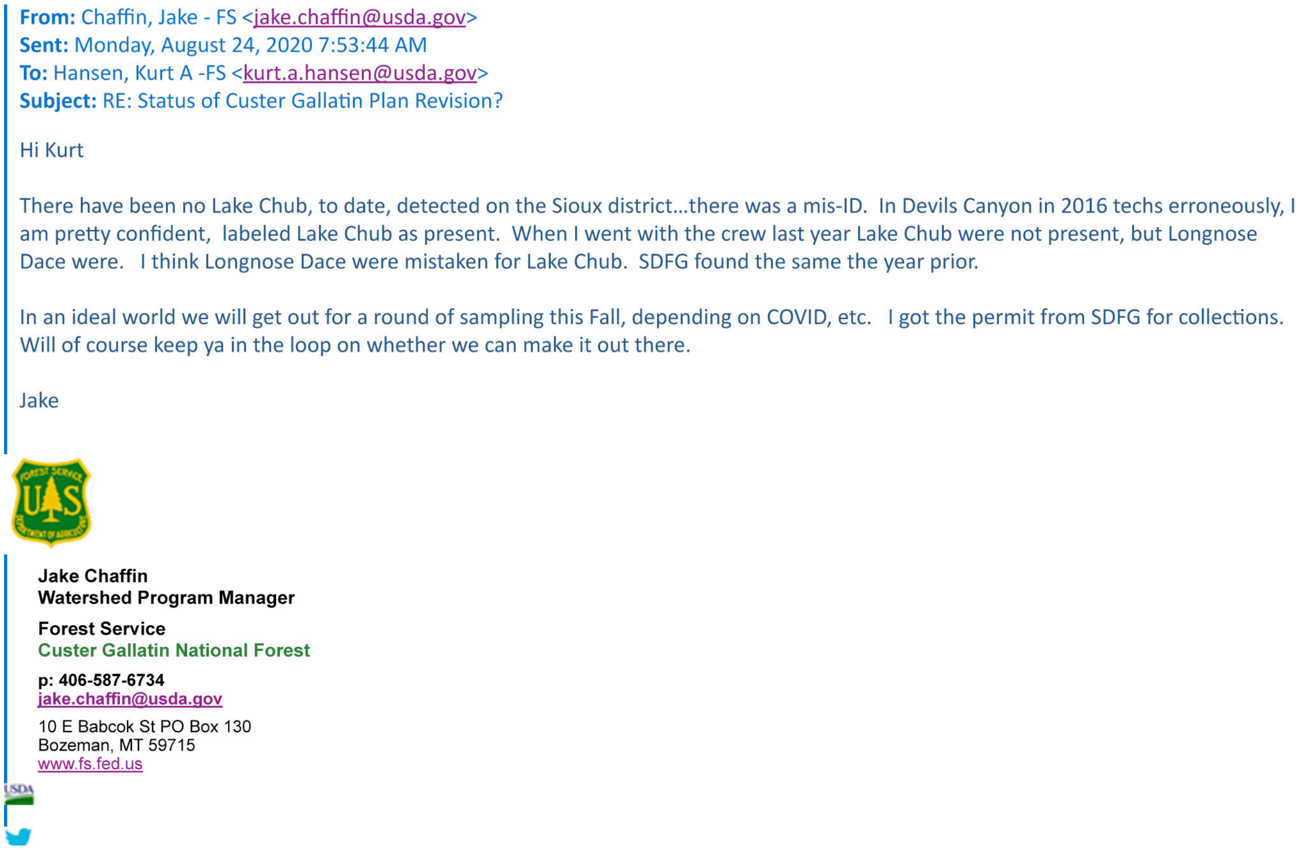
Then about 2016 the Custer Gallatin National Forest found Lake Chubs at a location in the Grand River and another drainage. This quote about Lake Chubs is from a chart that occurs in the Draft Environmental Impact Statement for the Draft Revised Forest Plan - Custer Gallatin National Forest at page 77:

> *" Confirmed in SD - Grand River tributary on Forest; also present downstream of Forest Boundary in several Montane HUCs "*

On June 11th Eileen Dowd Stukel sent me this text in e-mail as update on Lake Chubs:

> "Chelsey Pasbrig provided this answer to your question about the Lake Chub:
>
> *"Lake Chub were sampled in the USFS Custer Gallatin National Forest in 2016 from Devil's Canyon in Harding County, however no voucher specimens were taken. The same area was sampled in 2017 and didn't find any. 2017 was a drought year, however it is difficult to confirm or deny this occurrence.*
>
> *In 2019, the SDGFP stream survey crew sampled Lake Chub in Boxelder Creek in Lawrence County, this was a new tributary that I had not previously sampled Lake Chub. They took a voucher specimen which confirmed the occurrence.*
>
> *Lake Chub are listed as a SGCN but not T/E species. I would say the justification for this is that the state of SD is on the periphery of its range and we have never had a strong Lake Chub population in South Dakota."*

In subsequent years when GFP sampled the streams around Custer Gallatin National Forest and no lake Chub were found. The Custer Gallatin National Forest has since decided the identification in the Grand River drainage was a mistaken ID. I am not sure about their opinion of the ID in the other drainage (Montane HUC downstream of Forest Bounday).



From: Chaffin, Jake - FS <jake.chaffin@usda.gov>
Sent: Monday, August 24, 2020 7:53:44 AM
To: Hansen, Kurt A -FS <kurt.a.hansen@usda.gov>
Subject: RE: Status of Custer Gallatin Plan Revision?

Hi Kurt

There have been no Lake Chub, to date, detected on the Sioux district…there was a mis-ID. In Devils Canyon in 2016 techs erroneously, I am pretty confident, labeled Lake Chub as present. When I went with the crew last year Lake Chub were not present, but Longnose Dace were. I think Longnose Dace were mistaken for Lake Chub. SDFG found the same the year prior.

In an ideal world we will get out for a round of sampling this Fall, depending on COVID, etc. I got the permit from SDFG for collections. Will of course keep ya in the loop on whether we can make it out there.

Jake

Jake Chaffin
Watershed Program Manager

Forest Service
Custer Gallatin National Forest

p: 406-587-6734
jake.chaffin@usda.gov
10 E Babcok St PO Box 130
Bozeman, MT 59715
www.fs.fed.us

However this year Jake Davis August 20, 2020 reported to me by e-mail, that they found lake Chub in Box Elder Creek for the second time:

> *"Lake chub (N=10) were sampled a second time in Box Elder Creek near Steamboat Rock picnic area on July 21st of this year by SDGFP and USFS BHNF staff. We are now working with USFS on continued monitoring and possible reintroduction plans. "*

We believe that there is currently only one current confirmed known location for Lake Chub in SD - Box Elder Creek and the Chub has disappeared from streams in the Black Hills it used to occupy, and warrants listing as an endangered species.

The below chart is from Forest Service document published in 2006, showing SD population conservation status relative to it's conservation status in other areas.

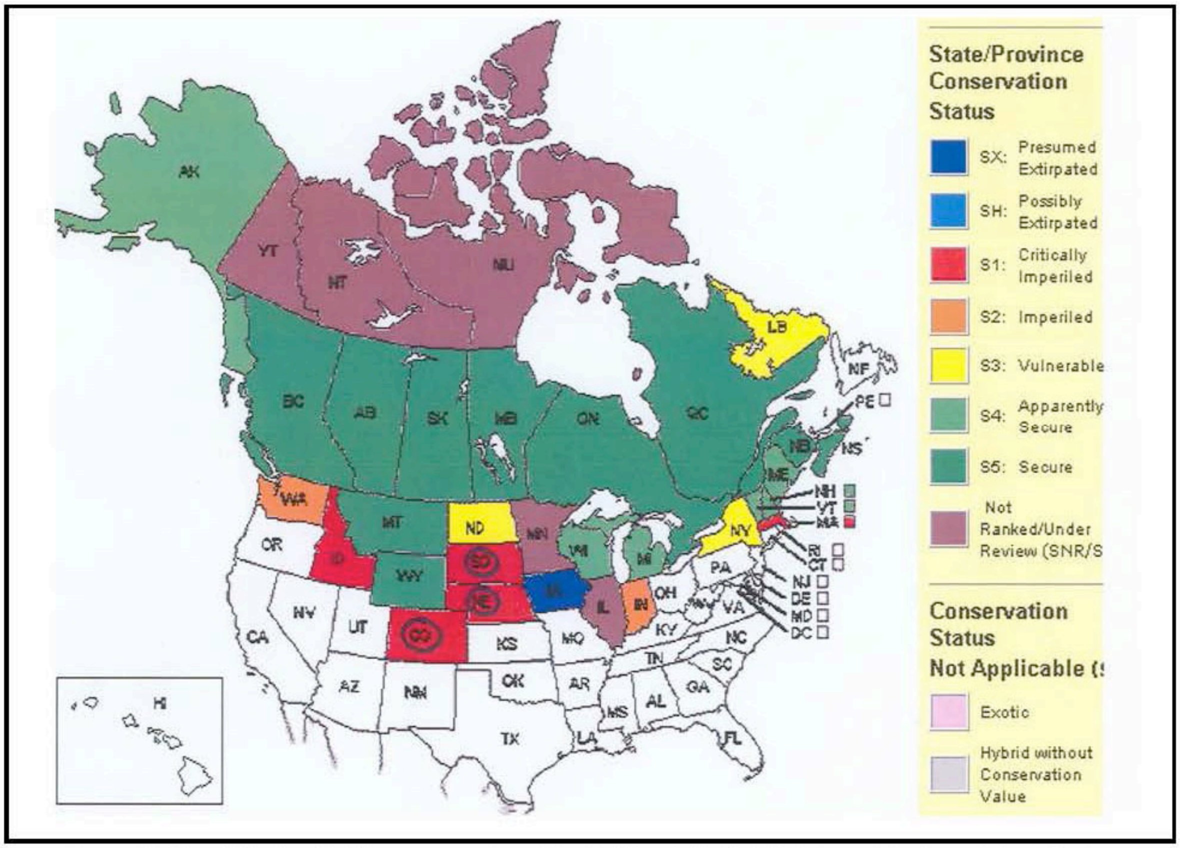


Figure 5. Natural Heritage Database conservation status for lake chub. Note that three of the four states in Region 2 (CO, NE, and SD) are listed as critically imperiled. Nebraska could possibly be considered light blue (possibly extirpated). Modified from NatureServe/explorer.org.

Below (page 7) is a map of historic lake chub sightings in the Black Hills from Forest Service Lake Chub Conservation Technical Assessment from 2006. This lets you know the confirmed locations of the Lake Chub in the Black Hills in history. Please scroll down to the next page

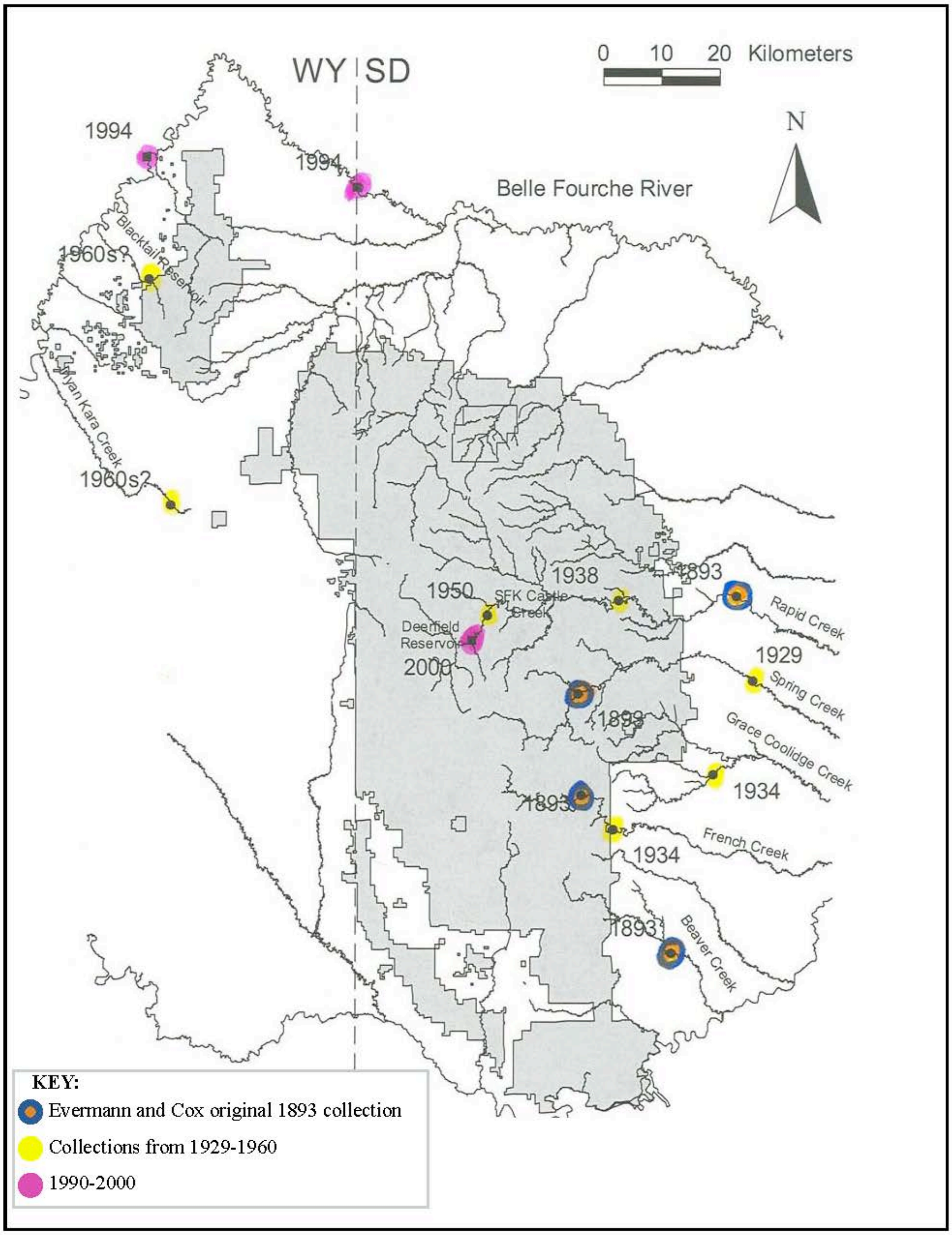


Figure 4. Historic records for lake chub in the Black Hills region of South Dakota and Wyoming. Based on collection data from Evermann and Cox (1896), Bailey and Allum (1962), Eiserman (1966), Patton (1997), Meester (2000), and Wyoming Game and Fish Database. Modified from Isaak et al. 2003.

Eileen Dowd Stukel and/or Chelsey Pasbrig have objected to a threatened or endangered listing for the Lake Chub, as it is in the periphery of it's range in SD. However other SD listed species such as the American Dipper or Fine Scale Dace are also just in the Black Hills in SD. The Black Hills are on the western edge of SD and have some habitat from the Rocky Mountains. Is SDGFP going to refuse to list any more species located in the Black Hills claiming they are all peripheral?

Scroll down for a map from the Forest Services 2006 Lake Chub Conservation Assessment:

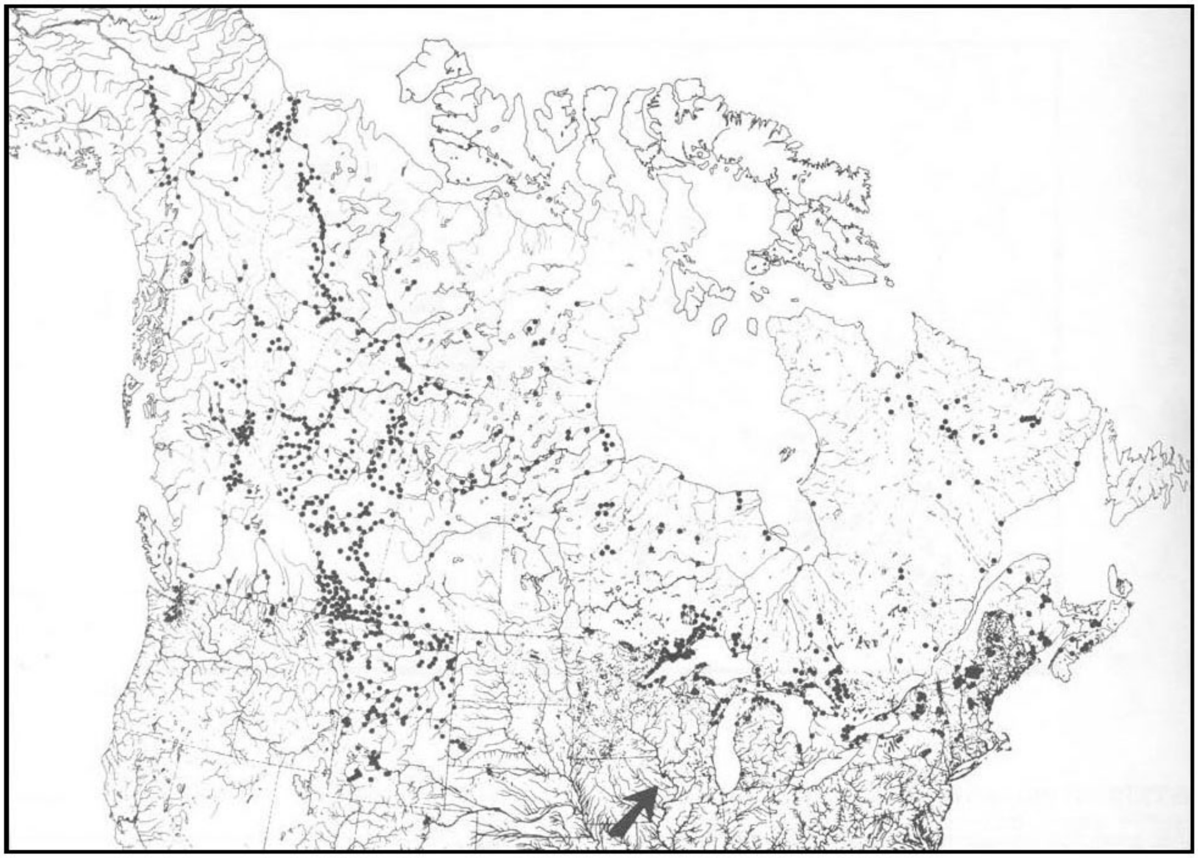


Figure 2. Lake chub distribution in North America. Taken from Wells (1980).

Citations

South Dakota Department of Game and Fish, Wildlife Action Plan, Appendix
https://gfp.sd.gov/wildlife-action-plan/

United States Department of Agriculture, Forest Service,Rocky Mountain Region Black Hills National Forest, "Black Hills National Forest, 2013-2014 Monitoring and

Evaluation Report" published August 2015

Isaak, Daniel J. Ph.D., Hubert, Wayne A. Ph.D.,. Berry, Charles R Jr., Ph.D.U.S. , Conservation Assessment for Lake Chub (Couesius plumbeus), "Mountain Sucker (Catostomus platyrhynchus), and Finescale Dace (Phoxinus neogaeus) in the Black Hills National Forest of South Dakota and Wyoming," Geological Survey Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071
https://www.fs.fed.us/rm/boise/AWAE/scientists/profiles/Isaak/FishConservationAssessmentForBlackHillsNF.pdf

Stasiak, R. (2006, May 4). Lake Chub (*Couesius plumbeus*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/lakechub.pdf
or
https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5200373.pdf

United States Department of Agriculture (USDA) Forest Service, Draft Environmental Impact Statement for the Revised Forest Plan , Custer Gallatin National Forest , Volume 1: Chapters 1 through 4, Forest Service Northern Region Publication No. R1-19-08, March 2019

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Sincerely,

Nancy Hilding

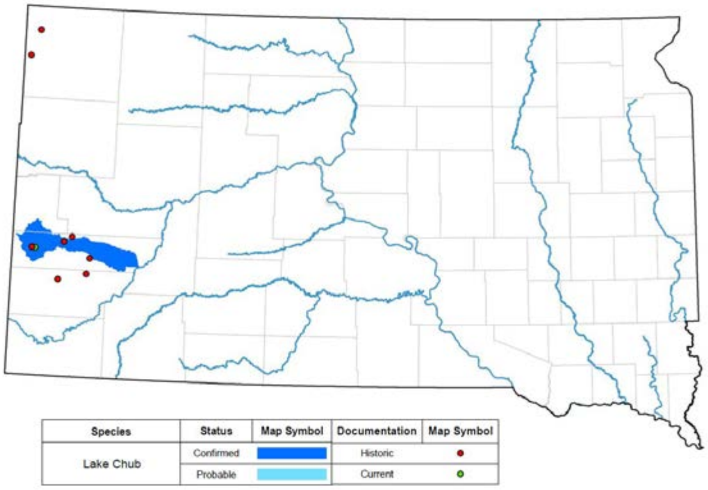
Nancy Hilding
President
Prairie Hills Audubon Society
and for Self

1 Attachment, Excerpt from the SD Wildlife Action Plan on Lake Chb

Lake Chub LACH *Couesius plumbeus*

Description:

- Silver-gray color with light belly
- Lead colored mid lateral stripe is present but not conspicuous
- Scattered dark scales give a speckled appearance
- Well-developed barbel located at corners of mouth



Protection Status:

- Federal: None
- State: None
- Global Rank: G5 (Secure)
- State Rank: S1 (Critically imperiled)

Distribution:

- Western SD-tributaries to the Cheyenne & Belle Fourche River basins
- SD is on the southern periphery of the range for this species

Key Habitat:

- Occurs in varied habitats, both large/small water bodies & standing/flowing waters
- Prefer gravel bottomed pools & runs of streams & along rocky lake margins

Conservation Challenges:

- Modified/suppressed fire regimes
- Exotic/introduced species impacts
- Ecosystem alteration/habitat degradation
  - Mining
- Pollution/pesticides/herbicides
- Grazing/Agricultural practices
  - Heavy grazing
- Forest Management Practices
  - Logging

Conservation Actions:

- Increase partnerships & cooperative arrangements
- Increase educational efforts
- Promote management practices that reduce/limit soil erosion & nutrient/pesticide runoff
- Develop programs to reduce or eliminate the treat non-native species on Lake Chub
- Develop captive breeding and reintroduction programs for Lake Chub into suitable habitats

Current Monitoring & Inventory Programs (Appendix E):

- Western prairie streams and rivers inventory survey

SWG Accomplishments (Appendix F):

- An aquatic invasive species risk assessment for South Dakota – T-36

Priority Research & Monitoring Needs (Appendices G-K):

- Determine distribution & current status through monitoring efforts
- Assess population dynamics & genetic variation
- Identify critical habitats & limiting factors
- Research seasonal movements & recolonization capabilities
- Investigate captive breeding capabilities for future reintroductions

Existing Recovery Plan/Conservation Strategies:

Isaak, D.J., W.A. Hubert, and C.R. Berry. Jr. 2002. Conservation Assessment for Lake Chub, Mountain Sucker, and Finescale Dace in the Black Hills National Forest, South Dakota and Wyoming. USDA Forest Service, Rocky Mountain Region

GAME, FISH AND PARKS COMMISSION ACTION
PROPOSAL

Camping permits and rules
Chapters 41:03:04

Commission Meeting Dates:	**Proposal**	September 3, 2020	Teleconference
	Public Hearing	October 1, 2020	Fort Pierre
	Finalization	October 1-2, 2020	Fort Pierre

DEPARTMENT RECOMMENDATION

Recommended changes:

41:03:04:03. Camping permit fees. The daily fee for the use of a campground site by one camper unit is as follows:

(1) Custer State Park modern campground fee, $26, including State Game Lodge; Sylvan Lake; Grace Coolidge; Legion Lake; Stockade North; Stockade South; and Blue Bell;

(2) Modern campground fee, $16, including Platte Creek; Swan Creek; West Whitlock; Indian Creek; Okobojo Point; Cow Creek; and West Pollock;

(3) Custer State Park semimodern campground fee, $19 for Center Lake;

(4) Basic campground fee, $11, including Burke Lake; Shadehill-Llewellyn Johns Memorial; Bear Butte Lake unit; Lake Hiddenwood; Sand Creek; East Whitlock; Tabor; North Wheeler; Spring Creek; Oakwood primitive area; Lake Carthage; South Shore; Whetstone Bay; South Scalp Creek; White Swan; Walth Bay; and Amsden Dam;

(5) Custer State Park French Creek natural area, seven dollars for each person;

(6) Use of a campground site at Fort Sisseton during the annual Fort Sisseton Festival, $25, provided that participants and festival campers are exempt from paying the camping fee;

(7) Equestrian campground fee, $18, including Bear Butte Horse Camp and Sica Hollow Horse Camp. For Lewis and Clark Horse Camp, Newton Hills Horse Camp, Oakwood Lakes Horse Camp, Pease Creek Horse Camp, Pelican Lake Horse Camp, Union Grove Horse Camp, and Sheps Canyon Horse Camp the camping fee is $22;

(8) Camping cabin fee, $55;

(9) Modern cabin and suite fees subject to size, amenities, and occupancy rates~~, $150~~ $85 to $205, these facilities range from single bedroom cabin with full bathroom to three-bedroom cabins, full kitchen and bathrooms including those campgrounds in all state parks and recreation areas where modern cabins or suites are located~~;~~. The Department shall provide the Commission an annual fee schedule for all modern cabins and suites. Discounts to these fees may not exceed 25% for the purposes of increasing occupancy during periods of lower demand;

(10) Nonprofit youth group camping fee, fifty cents for each person or six dollars, whichever is greater;

(11) Preferred campground fee, $19, including Fisher Grove; Buryanek; Oahe Downstream; Springfield; West Bend; and Randall Creek;

(12) Prime campsite fee, $22, including all campsites furnished with sewer, water, and electrical service; Lewis and Clark; Chief White Crane; Angostura including Sheps Canyon; Palisades; Big Sioux; Lake Vermillion; Rocky Point; Mina Lake; Lake Herman; North Point; Walker's Point; Lake Poinsett; Oakwood Lakes; South Pelican; Newton Hills; Shadehill Ketterlings Point; Pickerel Lake; Lake Cochrane; Sandy Shore; Pierson Ranch; Union Grove; Richmond Lake; Pease Creek; Lake

Thompson; Roy Lake; Farm Island; Snake Creek; Lake Louise; Hartford Beach; and Fort Sisseton, except during the Fort Sisseton Festival in accordance with subdivision (6) of this section;

(13) Custer State Park group camping area fee, seven dollars a person for overnight use with a minimum fee of $140;

(14) The group lodging fee at Lake Thompson State Recreation Area, Palisades State Park, Sheps Canyon State Recreation Area, Newton Hills State Park, and Shadehill State Recreation Area is $280 per night for the first 12 persons plus $10 for each additional person with a maximum occupancy of 15 persons;

(15) Custer State Park, French Creek Horse Camp fee, $31;

(16) Oahe Downstream Group Lodge use fee is $40 per night for nonprofit youth groups year-round and for nonprofit groups and government agencies from November 1 through March 31 and $125 per night for all other groups year-round. The use fee for all groups except nonprofit youth groups is $125 from April 1 through October 31;

(17) Campsites designated for tent camping only, regardless of campground designation, $15.

An additional charge of four dollars per unit is made for campground sites with electricity.

A resident of this state who may purchase a camping permit and campsite electrical service for one-half price pursuant to SDCL 41-17-13.4 shall submit written verification of that status from the United States Veterans Administration to the licensing office of the department in Pierre. The licensing office shall send the resident a billfold-size card to use as proof of eligibility for half-price camping fees.

Source: SL 1975, ch 16, § 1; 1 SDR 30, effective October 13, 1974; 2 SDR 90, effective July 11, 1976; 3 SDR 73, effective April 25, 1977; 6 SDR 96, effective April 1, 1980; 7 SDR 69, effective January 25, 1981; 8 SDR 170, effective June 20, 1982; 9 SDR 147, effective May 22, 1983; 10 SDR 73, effective January 17, 1984; 10 SDR 76, 10 SDR 102, effective July 1, 1984; 11 SDR 156, effective May 27, 1985; 13 SDR 128, effective March 22, 1987; 13 SDR 192, effective June 22, 1987; 14 SDR 14, effective August 6, 1987; 14 SDR 81, effective December 10, 1987; 14 SDR 114, effective March 9, 1988; 14 SDR 164, effective June 16, 1988; 15 SDR 139, effective March 20, 1989; 16 SDR 114, effective January 18, 1990; 16 SDR 135, effective February 18, 1990; 17 SDR 12, effective July 31, 1990; 17 SDR 139, effective March 21, 1991; 17 SDR 170, effective May 14, 1991; 17 SDR 188, effective June 13, 1991, and July 1, 1991; 18 SDR 98, effective December 12, 1991; 18 SDR 144, effective March 15, 1992; 19 SDR 82, effective December 7, 1992; 19 SDR 190, effective June 15, 1993; 20 SDR 150, effective March 23, 1994; 21 SDR 86, effective November 10, 1994; 21 SDR 148, effective March 6, 1995; 22 SDR 82, effective December 10, 1995; 22 SDR 89, effective December 26, 1995; 23 SDR 87, effective December 3, 1996; 23 SDR 197, effective May 27, 1997; 24 SDR 99, effective February 2, 1998; 24 SDR 107, effective February 26, 1998; 24 SDR 156, effective May 17, 1998; 25 SDR 108, effective February 28, 1999; 25 SDR 141, effective May 27, 1999; 26 SDR 41, effective September 28, 1999; 26 SDR 85, effective December 26, 1999; 26 SDR 117, effective March 16, 2000; 26 SDR 162, effective June 14, 2000; 27 SDR 49, effective November 16, 2000; 27 SDR 85, effective February 26, 2001; 28 SDR 103, effective January 30, 2002; 29 SDR 80, effective December 10, 2002; 30 SDR 99, effective December 22, 2003; 30 SDR 171, effective May 11, 2004; 31 SDR 62, effective November 4, 2004; 32 SDR 109, effective December 27, 2005; 32 SDR 128, effective January 31, 2006; 33 SDR 107, effective December 27, 2006; 33 SDR 180, effective May 7, 2007; 33 SDR 225, effective June 25, 2007; 34 SDR 179, effective December 24, 2007; 36 SDR 112, effective January 11, 2010; 37 SDR 112, effective December 8, 2010; 38 SDR 101, effective December 5, 2011; 39 SDR 32, effective September 5, 2012; 39 SDR 100, effective December 3, 2012; 39 SDR 204, effective June 11, 2013; 40 SDR 113, effective December 16, 2013; 41 SDR 93, effective December 3, 2014; 44 SDR 93, effective December 4, 2017; 45 SDR 89, effective December 31, 2018; 46 SDR 74, effective December 2, 2019.

General Authority: SDCL 41-17-1.1(7), 41-17-13.4.

Law Implemented: SDCL 41-2-24, 41-17-1.1(7), 41-17-13.4.

SUPPORTIVE INFORMATION

Parks currently has only two categories for assessing fees on overnight rental facilities; $55 for a camping cabin and $150 for a modern cabin. With the acquisition of facilities at Spring Creek and Roy Lake, there are now many different variations of cabins and suites that do not fit into either of these categories. Many of the units have full kitchens and include one bedroom, two-bedroom and three-bedroom options. Several comments have been received indicating the current rental fee of $150 may be too low for some facilities and too high for others, requiring a review of the current pricing structure to reflect what each facility offers.

Rather than identifying each of the 16 variations of facilities and an associated fee in rule, the Department is suggesting a range of pricing from $85-$205 to cover all types of facilities. A fee schedule would be provided to the commission each year identifying the fee for each type of facility. In addition, the Department is asking for the ability to reduce the price of modern cabins and suites by up to 25% to align rental facilities fees with the local market, occupancy rates and create marketing packages that will promote increased use.

GAME, FISH AND PARKS COMMISSION ACTION
PROPOSAL

☐ **APPROVE** ☐ **MODIFY** ☐ **REJECT** ☐ **NO ACTION**

	Current Fee	**Past Private Resort Fee**	**Suggested Maximum Fee**
Modern Cabins			
Roy Lake - 5 Units with 2-bedroom, bath, full kitchen	$150	$165-185	$150
Roy Lake - 3 units with 1-bedroom, bath, full kitchen	$150	$135-155	$120
Spring Creek - Modern Cabin with 3-bedrooms, bath, no kitchen	$150	$250	$150
Spring Creek - Modern Cabin with 2-bedroom, bath, no kitchen	$150	$200	$150
Mina Lake - 1 unit with 3-bedroom bath, full kitchen	$150	NA	$150
Newton Hills - Modern Cabin 2-bedroom, bath, full kitchen	NA	NA	$150
Oahe Downstream - 2 Units with 2-bedroom, bath, full kitchen	$150	$185	$150
Oahe Downstream - 2 Units with 2-bedroom, bath, full kitchen	$150	$155	$120
Pickerel Lake - Modern Cabin 2-bedroom, bath, full kitchen	NA	NA	$150
Suites			
Roy Lake - Suite - 4 units with 2-bedroom, bath and full kitchen	$150	$205	$175
Roy Lake - Suite -1 unit with 2-bedroom, bath and full kitchen	$150	$169	$150
Roy Lake - Suite - 1 unit with 3-bedroom, 2 bath, and full kitchen	$150	$215	$205
Roy Lake - Suite - 1 Unit with 2-bedroom, bath, full kitchen	$150	NA	$150
Roy Lake - Small suite with 1-bedroom, bath	NA	NA	$85
Spring Creek - Small suites - 4 units with 1 bedroom and bathroom	$55	$100	$85
Spring Creek - 4-Plex -2 units each with 4 large suite, single bedroom, bath, no kitchen, common area	$150ea. Or $600	$150 ea. or $600	$125 ea. or $400

GAME, FISH AND PARKS COMMISSION ACTION
PROPOSAL

Camping permits and rules
Chapters 41:03:04

Commission Meeting Dates:	**Proposal**	September 3, 2020	Teleconference
	Public Hearing	October 1, 2020	Fort Pierre
	Finalization	October 1-2, 2020	Fort Pierre

DEPARTMENT RECOMMENDATION

Recommended changes:

41:03:04:01. Definitions. As used in this chapter:

(1) "Basic campground" means a campground equipped with vault toilets if camping is allowed on camping pads, grassed areas, or parking lots;

(2) "Camper unit" means a powered vehicle, motor home, camping bus, pull-type camper, tent, or any other device designed for sleeping;

(3) "Campground site" or "campsite" means a specific camping pad or a temporary area that is specifically designated by the park manager;

(4) "Camping cabin" means a campsite with a wood structure provided by the department, furnished with beds and electricity;

(5) "Equestrian campground" means a campground designed to accommodate camper units with horses;

(6) "Family" means parents or grandparents and unmarried minor children;

(7) "Hard sided camper" means any type of device that is designed for sleeping and shelter that is attached to at least a single axle;

(8) "Large group camping reservation" means a reservation for a group camping loop at Lewis and Clark Recreation area or for 10 or more campsites at any other state park campground that accepts a group camping reservation;

(9) "Lodge" means a permanent structure provided by the department, furnished with beds, appliances, and home decor;

(10) "Modern cabin" means a campsite with a wood structure provided by the department, furnished with beds, electricity, sewer and water;

(11) "Suite" means a campsite with a wood structure that contains multiple rental units provided by the department, furnished with beds, electricity, sewer and water;

(12) "Modern campground" means a campground equipped with flush toilets, lavatories, hot showers, and individual camping pads;

(13) "Nonprofit youth group" means an organized group of persons under age 18, sponsored by a nonprofit organization, and accompanied by a smaller group of adult leaders that have been designated by the organization to provide supervision, guidance, and instruction to the group. Any

adult accompanying the youth group for the primary purpose of supervising the adult's own children is not considered an adult leader of the group;

(14) "Preferred campground" means a modern campground with weekend occupancy of 80 percent to 89 percent from the Friday before Memorial Day through Labor Day on nonequestrian and electrical campsites;

(15) "Prime campground" means a modern campground with weekend occupancy of and greater than 90 percent from the Friday before Memorial Day through Labor Day on non-equestrian and electrical campsites;

(16) "Recreational vehicle campsite" means a campsite where a self-contained, pull-type camping unit designed for recreational use is provided by the department;

(17) "Rent-a-camper" means a campsite with a hard sided camper provided by the department, furnished with beds, appliances, and electricity; and

(18) "Semi-modern campground" means a campground equipped with individual camping pads and either flush toilets and lavatories without showers or a shower house and vault toilets.

Source: SL 1975, ch 16, § 1; 3 SDR 73, effective April 25, 1977; 6 SDR 96, effective April 1, 1980; 10 SDR 73, effective January 17, 1984; 10 SDR 76, 10 SDR 102, effective July 1, 1984; 14 SDR 81, effective December 10, 1987; 15 SDR 139, effective March 20, 1989; 16 SDR 114, effective January 18, 1990; 17 SDR 170, effective May 14, 1991; 19 SDR 190, effective June 15, 1993; 20 SDR 150, effective March 23, 1994; 23 SDR 87, effective December 3, 1996; 23 SDR 142, effective March 17, 1997; 24 SDR 99, effective February 2, 1998; 24 SDR 156, effective May 17, 1998; 27 SDR 49, effective November 16, 2000; 28 SDR 150, effective May 7, 2002; 36 SDR 112, effective January 11, 2010; 44 SDR 93, effective December 4, 2017; 45 SDR 89, effective December 31, 2018; 46 SDR 74, effective December 2, 2019.
General Authority: SDCL 41-17-1.1(1).
Law Implemented: SDCL 41-2-24, 41-17-1.1(1).

SUPPORTIVE INFORMATION

In 2019 a definition for modern cabin lodging was created for lodging in parks such as Oahe Downstream, Mina Lake and a new proposed modern cabin at Newton Hills. The acquisition of facilities at Spring Creek and Roy Lake has further diversified the options to include one bedroom, two-bedroom, three-bedroom and four-bedroom units contained in one structure similar to a motel/hotel type of experience. By adding the suite definition our customers will have much clearer understanding of this new facility type.

☐ **APPROVE** ☐ **MODIFY** ☐ **REJECT** ☐ **NO ACTION**

GAME, FISH AND PARKS COMMISSION ACTION
FINALIZATION

Duck Hunting Season
Chapter 41:06:16; 41:06:02

Commission Meeting Dates:	Proposal	July 16-17, 2020	Virtual Meeting
	Public Hearing	September 2, 2020	Virtual Meeting
	Finalization	September 2-3, 2020	Virtual Meeting

COMMISSION PROPOSAL

Duration of Proposal: 2021-2024 hunting seasons

Proposed changes from last year:

1. Implementation of an experimental 2-tiered duck regulation in South Dakota with a 3-splash option.
2. Modify the special nonresident waterfowl hunting license by reducing the cost from $115 to $110 and by removing the inclusion of the migratory bird certification permit.

DEPARTMENT RECOMMENDATION

Recommended changes from proposal: None

SUPPORTIVE INFORMATION

- **Duck hunter trends:** Duck hunter participation in South Dakota and the Central Flyway is declining (Figure 1). Historically, duck hunter numbers rose and fell with duck numbers. Unfortunately, since the mid 1990's this trend as not held with declining hunter numbers and abundant waterfowl (Figure 2).
- **Current duck regulations:** maximize harvest potential, complex system of species-specific regulations. Challenge for inexperienced hunters.
    - The ability to identify ducks on the wing has been identified as a potential barrier to duck hunter recruitment, retention and reactivation (R3).
- **Potential future regulations:** increase participation in duck hunting by providing two options for all hunters to choose from. Duck hunters would register themselves under one of two different regulatory options
    - **Tier 1:** The current regulatory package: would maximize harvest potential with current species-specific regulations (i.e., current daily bag limits with all species-specific daily bag restrictions).
    - **Tier 2:** A new "3-splash" regulatory package: available only to those who desire it. Simplified regulations (i.e., 3-splash daily bag limit).
- **Regulation development:** Working cooperatively with the all flyways and the USFWS, a study design and evaluation plan has been developed and approved by the Service Regulations Committee (SRC) for the states of Nebraska and South Dakota.
    - If approved by both commissions, beginning in the 2021-2022 duck hunting season both states will implement and evaluate a pilot two-tier system of duck hunting regulations for a minimum of 4 years.
- **GOAL:** To see if experimental regulations can flatten the decline, if not increase participation in waterfowl hunting.
- **License fee adjustment:** Currently the special nonresident waterfowl license includes the migratory bird certification permit. With the 2-tiered license option, applicants will select a migratory bird certification permit to reflect their choice of the traditional or 3-splash license option.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

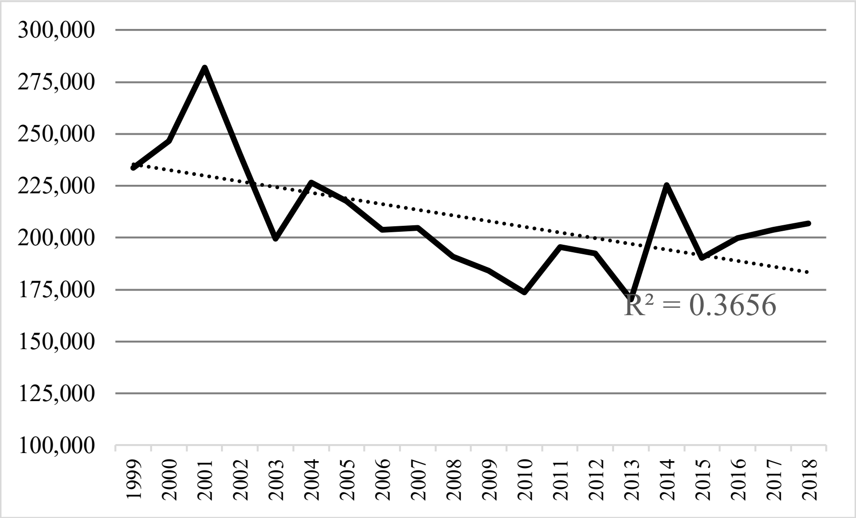


Figure 1. The number of active duck hunters in the Central Flyway, 1999-2018 (Dubovsky 2019).

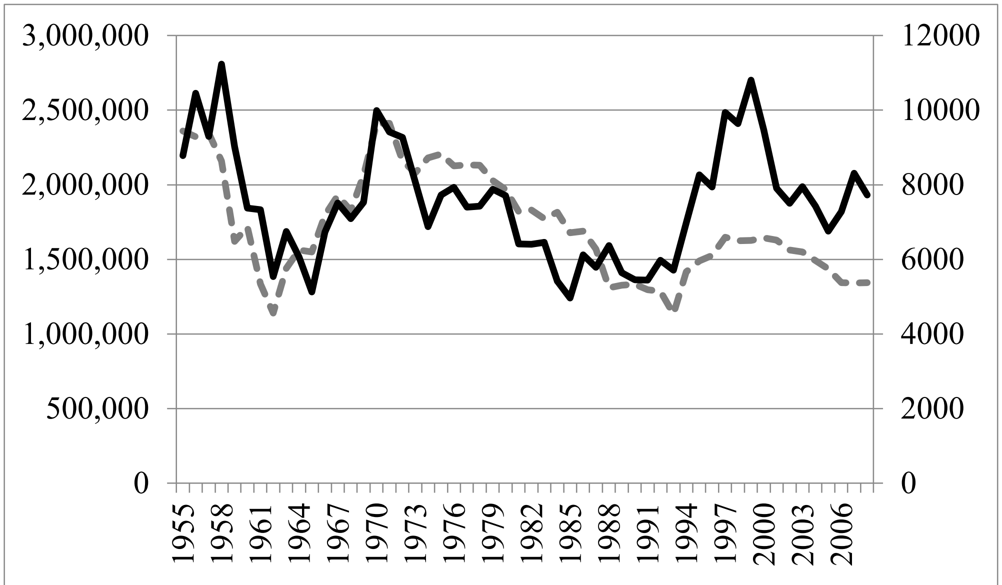


Figure 2. Federal Migratory Bird Hunting and Conservation Stamp (Federal Duck Stamp) and mallard breeding populations (Bpop), 1955-2008.

APPROVE _____	MODIFY _____	REJECT _____	NO ACTION _____

RESIDENT/NONRESIDENT CRITERIA

1. The Issue
    - Duck hunter numbers in SD have been falling 3% per year on average since the mid 1990's. This loss of waterfowl hunters means an erosion of waterfowl hunting traditions and less support for waterfowl conservation and management. Through purchases of licenses, stamps and gear, waterfowl hunters contribute to perpetuating waterfowl by conserving their habitats. The goal of this experiment is to see if removing the barrier of having to identify ducks in flight can assist R3 efforts. Direct engagement of stakeholder's groups is planned, and a standard public comment process is anticipated. A comprehensive evaluation plan has been developed in cooperation with the National Flyway Council, USFWS, and the Nebraska Game and Parks Commission.

2. Historical Considerations – Not Applicable

3. Biological Considerations
    - Because the experiment is limited to two states (SD/NE), and because the bag associated with the simplified license option is smaller than allowed under a regular limit, impact to species with reduced bags (e.g. pintail, scaup, canvasbacks) will be minimal. Cooperative monitoring efforts on harvest will continue throughout the experiment to assess whether negative impacts occur during the experiment.

4. Social Considerations
    - SDGFP and NGPC, and the University of Nebraska Lincoln recently completed a human dimensions survey of current and past duck hunters in each state. Highlights included 40% of respondents felt duck ID was difficult for them, 2/3 did not oppose the regulation experiment, and 25% would consider taking a mentee duck hunting if they could use the 3-splash option. Rigorous communications efforts are expected to garner support and promote the 3-splash opportunity. The main concerns from current hunters involved concern for species with reduced bags and the idea that in order to be a duck hunter you needed to know duck identification.

5. Financial considerations
    - If successful, increased revenue from both license sales and Federal Duck stamps would be realized. These funds could then be used to help sustain the North American Model for wildlife conservation.

RECRUITMENT, RETENTION, REACTIVATION (R3) CRITERIA

1. Does the regulation or fee inhibit a user's ability to participate? Not applicable.

2. Does the regulation increase the opportunity for new and existing users?
    - Yes

3. How does the regulation impact the next generation of hunters, anglers, trappers and outdoor recreationists?
    - The goal of these experimental hunting regulations is to support R3 efforts for duck hunting in South Dakota, the Central Flyway, and perhaps nationwide.

4. Does the regulation enhance the quality of life for current and future generations by getting families outdoors?
    - If successful, participation in duck hunting will increase and allow novice hunters a chance to participate without fear of violation. Sustaining waterfowl hunting traditions will contribute to an enhanced quality of life and encourage families to recreate outside.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

GAME, FISH AND PARKS COMMISSION ACTION
FINALIZATION

Spring Wild Turkey Hunting Season
Chapter 41:06:13; 41:03:01

Commission Meeting Dates:	**Proposal**	**July 16-17, 2020**	**Virtual Meeting**
	Public Hearing	**September 2, 2020**	**Virtual Meeting**
	Finalization	**September 2-3, 2020**	**Virtual Meeting**

COMMISSION PROPOSAL

Duration of Proposal: 2021 and 2022 seasons (only 2021 season dates listed below)

Season Dates:	April 3 – May 31, 2021	Archery
	April 10 – May 31, 2021	Black Hills regular and single-season Prairie units
	April 10 – April 30, 2021	Split-season early Prairie units
	May 1 – May 31, 2021	Split-season late Prairie units; Black Hills late season

Licenses:	Black Hills:	Unlimited resident and nonresident one-tag “male turkey” licenses
	Prairie:	5,797 resident and 246 nonresident one-tag “male turkey” licenses 600 resident and 48 nonresident two-tag “male turkey” licenses
	Archery:	Unlimited resident and nonresident one-tag “male turkey” licenses

Access Permits: Access permits valid April 3-30
Good Earth State Park: 5 archery turkey access permits
Adams Homestead and Nature Preserve: 30 archery turkey access permits
Adams Homestead and Nature Preserve: 20 mentored turkey access permits

Requirements and Restrictions:

1. Turkey hunters may apply for and receive one license in each of the Black Hills regular season, Black Hills late season, Prairie and Archery Units in the first and second lottery drawings.
2. Turkey hunters may purchase only one regular Black Hills and one archery turkey license.
3. Residents may purchase one late Black Hills late season license.
4. One-half of the licenses in each prairie unit are available for landowner/operator preference.
5. Prairie units adjoining the White River and Cheyenne River also include an adjacent area one mile wide on the opposite side of the river.
6. No person may shoot a turkey in a tree or roost.
7. A person may use only bow and arrow, a shotgun using shot shells or a muzzleloading shotgun to hunt turkeys during the spring turkey season.

Proposed changes from last year:

1. Offer residents 140 more one-tag “male turkey” licenses for the Prairie Units than 2020.
2. Add Clark County to Hamlin County unit.
3. Remove Douglas County from Charles Mix County unit.
4. Create Unit 10A that includes both Aurora and Douglas counties.
5. Add Buffalo County to Brule County unit.
6. Add Beadle and Hand counties to Jerauld County unit.
7. Increase the number of archer turkey access permits for Adams Homestead and Nature Preserve from 20 to 30.
8. Establish 20 mentored turkey access permits for Adams Homestead and Nature Preserve that would be limited to a bow or crossbow.
9. For Adams Homestead and Nature Preserve, allow for uncased bows and crossbows for a resident hunter who possesses a valid mentored spring turkey license and an access permit.

DEPARTMENT RECOMMENDATION

Recommended changes from proposal: None

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

SUPPORTIVE INFORMATION

Year	Licenses			Harvest			Success		
	BH	Prairie	Archery	BH	Prairie	Archery	BH	Prairie	Archery
2015	3,877	6,961	2,919	1,258	3,565	790	32%	42%	27%
2016	4,056	6,850	3,202	1,575	2,486	885	39%	31%	28%
2017	4,401	6,577	3,847	1,701	3,328	912	39%	45%	28%
2018	4,274	6,510	3,264	1,441	2,733	719	32%	38%	22%
2019	4,545	6,375	3,129	1,365	2,72	915	30%	39%	26%

*Includes both resident and nonresident harvest statistics.

RESIDENT/NONRESIDENT CRITERIA

1. The Issue
    - Why make the change, what are the change alternatives, how will public/stakeholder input be solicited, and how will the change be evaluated if implemented?
        i. Turkey hunting opportunities are available in marginal habitats for these added counties in eastern South Dakota.
        ii. Input will be solicited during the public comment period and GFP Commission public hearing.

2. Historical Considerations – Not Applicable

3. Biological Considerations
    - What is the current and projected status of the population and habitat conditions for these populations?
        i. While no population estimates exist for prairie turkeys, there are opportunities that can be made available to hunters.

4. Social Considerations
    - Enhanced hunting opportunities.

5. Financial considerations – Not Applicable

RECRUITMENT, RETENTION, REACTIVATION (R3) CRITERIA

1. Does the regulation or fee inhibit a user's ability to participate? No.

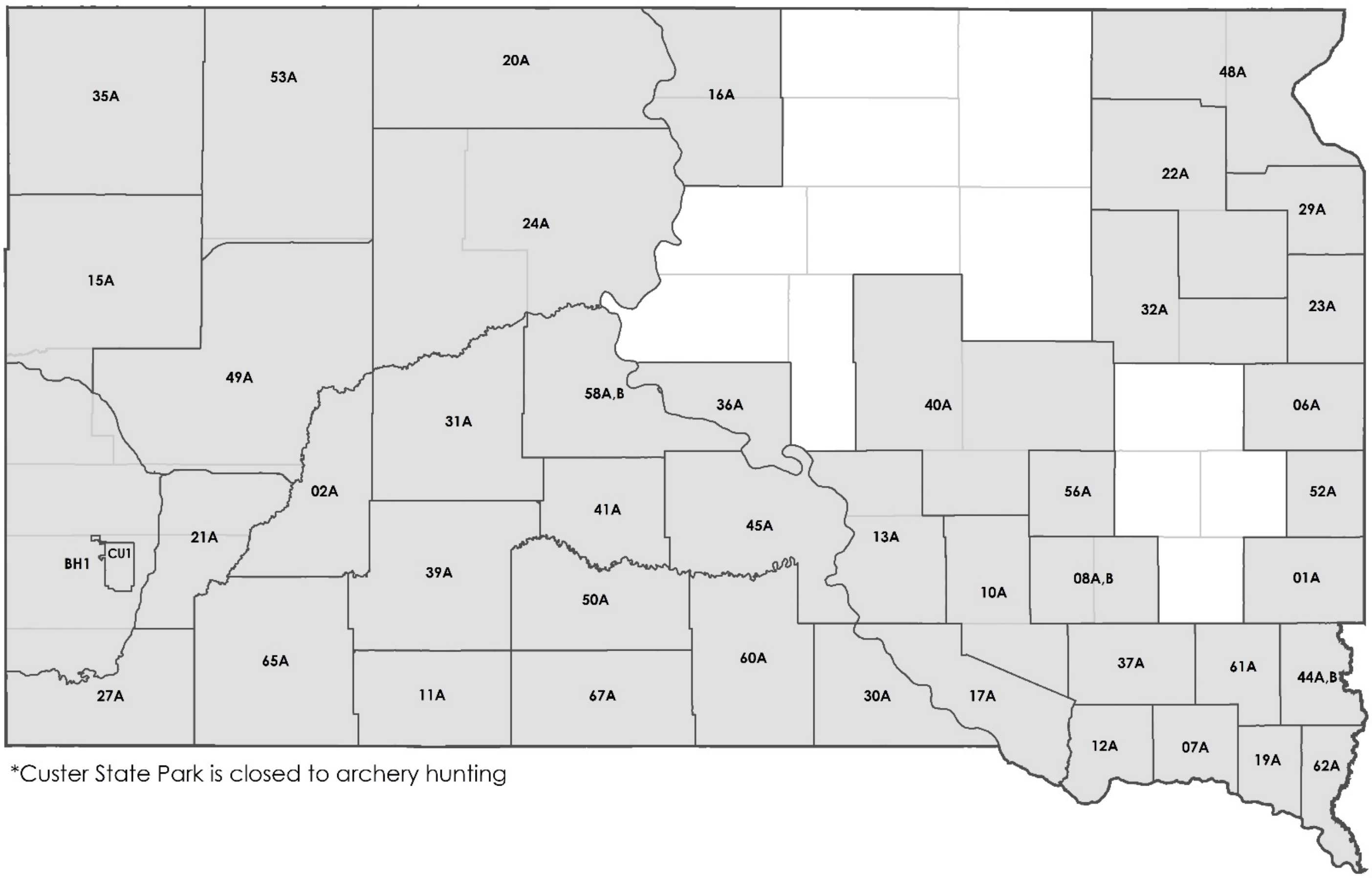
2. Does the regulation increase the opportunity for new and existing users?
    - Expanding open areas and increasing access to Adams Homestead and Nature Preserve increases hunting opportunity and will provide a unique experience for mentored turkey hunters.

3. How does the regulation impact the next generation of hunters, anglers, trappers and outdoor recreationists?
    - Enhanced hunting opportunities.

4. Does the regulation enhance the quality of life for current and future generations by getting families outdoors? Yes.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

SPRING TURKEY UNITS



*Custer State Park is closed to archery hunting

GAME, FISH AND PARKS COMMISSION ADMINISTRATIVE ACTION

Spring Turkey Hunting Seasons – Hunting Unit License Allocations

Commission Meeting Dates:	**Proposal**	**July 16-17, 2020**	**Virtual Meeting**
	Public Hearing	**September 2, 2020**	**Virtual Meeting**
	Finalization	**September 2-3, 2020**	**Virtual Meeting**

LICENSE ALLOCATION BY UNITS

See Attached Spreadsheets

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

SPRING TURKEY
2019-2020 and 2021-2022 Comparison

Unit #	Unit Name	2019-2020 Resident Licenses	2021-2022 Resident Licenses	# Change	% Change	2019-2020 Resident Tags	2021-2022 Resident Tags	# Change	% Change
01A	Minnehaha	80	80	0	0%	80	80	0	0%
02A	Pennington	200	200	0	0%	200	200	0	0%
06A	Brookings	20	20	0	0%	20	20	0	0%
07A	Yankton	260	260	0	0%	260	260	0	0%
08A	Davison/Hanson	80	80	0	0%	80	80	0	0%
08B	Davison/Hanson	80	80	0	0%	80	80	0	0%
10A	Aurora/Douglas	0	30	30	#DIV/0!	0	30	30	#DIV/0!
11A	Bennett	30	30	0	0%	30	30	0	0%
12A	Bon Homme	250	250	0	0%	250	250	0	0%
13A	Brule/Buffalo	150	150	0	0%	150	150	0	0%
15A	Butte/Lawrence	350	350	0	0%	350	350	0	0%
16A	Campbell/Walworth	10	10	0	0%	10	10	0	0%
17A	Charles Mix	350	350	0	0%	350	350	0	0%
19A	Clay	120	120	0	0%	120	120	0	0%
19B	Clay	0	0	0	0%	0	0	0	0%
20A	Corson	50	50	0	0%	50	50	0	0%
21A	Custer	150	150	0	0%	150	150	0	0%
22A	Day/Codington	80	90	10	13%	80	90	10	13%
23A	Deuel	100	110	10	10%	100	110	10	10%
24A	Dewey/Ziebach	150	150	0	0%	150	150	0	0%
27A	Fall River	75	75	0	0%	75	75	0	0%
29A	Grant	220	260	40	18%	220	260	40	18%
30A	Gregory	700	700	0	0%	700	700	0	0%
31A	Haakon	200	200	0	0%	400	400	0	0%
32A	Hamlin/Clark	10	20	10	100%	10	20	10	100%
35A	Harding	100	100	0	0%	100	100	0	0%
36A	Hughes	30	30	0	0%	30	30	0	0%
37A	Hutchinson	60	60	0	0%	60	60	0	0%
39A	Jackson	150	150	0	0%	150	150	0	0%
40A	Jerauld/Beadle/Hand	10	20	10	100%	10	20	10	100%
41A	Jones	75	75	0	0%	75	75	0	0%
44A	Lincoln	50	50	0	0%	50	50	0	0%
44B	Lincoln	50	50	0	0%	50	50	0	0%
45A	Lyman	100	100	0	0%	100	100	0	0%
48A	Marshall/Roberts	400	440	40	10%	400	440	40	10%
49A	Meade	300	300	0	0%	600	600	0	0%
50A	Mellette	350	350	0	0%	350	350	0	0%
52A	Moody	60	60	0	0%	60	60	0	0%
53A	Perkins	100	100	0	0%	200	200	0	0%
56A	Sanborn	10	10	0	0%	10	10	0	0%
58A	Stanley	40	40	0	0%	40	40	0	0%
58B	Stanley	2	2	0	0%	2	2	0	0%
60A	Tripp	400	400	0	0%	400	400	0	0%
61A	Turner	20	20	0	0%	20	20	0	0%
62A	Union	120	120	0	0%	120	120	0	0%
62B	Union	0	0	0	0%	0	0	0	0%
65A	Oglala Lakota	40	40	0	0%	40	40	0	0%
67A	Todd	75	75	0	0%	75	75	0	0%
TOTAL		**6,257**	**6,407**	**150**	**2.4%**	**6,857**	**7,007**	**150**	**2.2%**

Note: An additional 8% of the number of licenses will be available to nonresidents in West River units.

2021 - 2022 Spring Turkey

Unit #	Unit Name	Resident		Nonresident		License Totals							
		TomT 32	2 TomT 35	TomT 32	2 TomT 35	RES 1-tag	RES 2-tag	RES Licenses	RES Tags	NR 1-tag	NR 2-tag	NR Licenses	NR Tags
01A	Minnehaha	80	0	0	0	80	0	80	80	0	0	0	0
02A	Pennington	200	0	16	0	200	0	200	200	16	0	16	16
06A	Brookings	20	0	0	0	20	0	20	20	0	0	0	0
07A	Yankton	260	0	0	0	260	0	260	260	0	0	0	0
08A	Davison/Hanson	80	0	0	0	80	0	80	80	0	0	0	0
08B	Davison/Hanson	80	0	0	0	80	0	80	80	0	0	0	0
10A	Aurora/Douglas	30	0	0	0	30	0	30	30	0	0	0	0
11A	Bennett	30	0	3	0	30	0	30	30	3	0	3	3
12A	Bon Homme	250	0	0	0	250	0	250	250	0	0	0	0
13A	Brule/Buffalo	150	0	0	0	150	0	150	150	0	0	0	0
15A	Butte/Lawrence	350	0	28	0	350	0	350	350	28	0	28	28
16A	Campbell/Walworth	10	0	0	0	10	0	10	10	0	0	0	0
17A	Charles Mix	350	0	0	0	350	0	350	350	0	0	0	0
19A	Clay	120	0	0	0	120	0	120	120	0	0	0	0
19B	Clay	0	0	0	0	0	0	0	0	0	0	0	0
20A	Corson	50	0	4	0	50	0	50	50	4	0	4	4
21A	Custer	150	0	12	0	150	0	150	150	12	0	12	12
22A	Day/Codington	90	0	0	0	90	0	90	90	0	0	0	0
23A	Deuel	110	0	0	0	110	0	110	110	0	0	0	0
24A	Dewey/Ziebach	150	0	12	0	150	0	150	150	12	0	12	12
27A	Fall River	75	0	6	0	75	0	75	75	6	0	6	6
29A	Grant	260	0	0	0	260	0	260	260	0	0	0	0
30A	Gregory	700	0	56	0	700	0	700	700	56	0	56	56
31A	Haakon	0	200	0	16	0	200	200	400	0	16	16	32
32A	Hamlin/Clark	20	0	0	0	20	0	20	20	0	0	0	0
35A	Harding	100	0	8	0	100	0	100	100	8	0	8	8
36A	Hughes	30	0	0	0	30	0	30	30	0	0	0	0
37A	Hutchinson	60	0	0	0	60	0	60	60	0	0	0	0
39A	Jackson	150	0	12	0	150	0	150	150	12	0	12	12
40A	Jerauld/Beadle/Hand	20	0	0	0	20	0	20	20	0	0	0	0
41A	Jones	75	0	6	0	75	0	75	75	6	0	6	6
44A	Lincoln	50	0	0	0	50	0	50	50	0	0	0	0
44B	Lincoln	50	0	0	0	50	0	50	50	0	0	0	0
45A	Lyman	100	0	8	0	100	0	100	100	8	0	8	8
48A	Marshall/Roberts	440	0	0	0	440	0	440	440	0	0	0	0
49A	Meade	0	300	0	24	0	300	300	600	0	24	24	48
50A	Mellette	350	0	28	0	350	0	350	350	28	0	28	28
52A	Moody	60	0	0	0	60	0	60	60	0	0	0	0
53A	Perkins	0	100	0	8	0	100	100	200	0	8	8	16
56A	Sanborn	10	0	0	0	10	0	10	10	0	0	0	0
58A	Stanley	40	0	4	0	40	0	40	40	4	0	4	4
58B	Stanley	2	0	1	0	2	0	2	2	1	0	1	1
60A	Tripp	400	0	32	0	400	0	400	400	32	0	32	32
61A	Turner	20	0	0	0	20	0	20	20	0	0	0	0
62A	Union	120	0	0	0	120	0	120	120	0	0	0	0
62B	Union	0	0	0	0	0	0	0	0	0	0	0	0
65A	Oglala Lakota	40	0	4	0	40	0	40	40	4	0	4	4
67A	Todd	75	0	6	0	75	0	75	75	6	0	6	6
	TOTAL	5,807	600	246	48	5,807	600	6,407	7,007	246	48	294	342
	Unit	TomT 32	2 TomT 35	TomT 32	2 TomT 35	RES 1-tag	RES 2-tag	RES Licenses	RES Tags	NR 1-tag	NR 2-tag	NR Lic	NR Tags
				RES & NR:		**6,053**	**648**	**6,701**	**7,349**				

GAME, FISH AND PARKS COMMISSION ACTION
FINALIZATION

Pheasant Hunting Season
Chapter 41:06:08

Commission Meeting Dates:	**Proposal**	**July 16-17, 2020**	**Virtual Meeting**
	Public Hearing	**September 2, 2020**	**Virtual Meeting**
	Finalization	**September 2-3, 2020**	**Virtual Meeting**

COMMISSION PROPOSAL

Duration of Proposal: 2020 and 2021 hunting season

Season Dates: October 17, 2020 – January 31, 2021
October 16, 2021 – January 31, 2022

Open Area: Statewide

Daily Limit: 2020: 3 rooster pheasants

2021: Third Saturday of October to November 30: 3 rooster pheasants
December 1 to end of season: 4 rooster pheasants

Possession Limit: Five times the daily bag limit.

Requirements and Restrictions:
1. Renziehausen GPA and State Game Bird Refuge in Brown County and Gerken State Game Bird Refuge in Faulk County are open beginning on December 1 and are open for the remainder of the season.
2. Sand Lake National Wildlife Refuge in Brown County is open beginning on the second Monday of December and is open for the remainder of the season.

Recommended changes from last year:
1. Modify the shooting hours for the first week of the regular from Noon to 10:00 a.m. Central Time beginning with the 2020 hunting season.
2. Modify the season end date from the first Sunday in January to January 31 beginning with the 2020 hunting season.
3. Increase the daily bag limit from 3 to 4 and modify the possession limit accordingly for rooster pheasants beginning December 1st beginning with the 2021 hunting season.

DEPARTMENT RECOMMENDATION

Recommended changes from proposal: None

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

SUPPORTIVE INFORMATION

Proposed changes are topics discussed and supported by both the pheasant marketing workgroup and the Department.

Year	Resident Hunters	Nonresident Hunters	Pheasant Harvest
2015	65,135	84,901	1,255,878
2016	61,746	81,141	1,170,596
2017	52,538	67,232	828,709
2018	53,577	69,018	950,883
2019	47,401	60,211	829,501

RESIDENT/NONRESIDENT CRITERIA

1. The Issue
    - Why make the change, what are the change alternatives, how will public/stakeholder input be solicited, and how will the change be evaluated if implemented?
        i. Is related to topics discussed with the pheasant marketing workgroup and supported by the Department.
        ii. Input will be solicited during the public comment period and GFP Commission public hearing.

2. Historical Considerations
    - Over the years the season end dates for upland game birds has been extended with the desire to maximize hunting opportunities in balance with landowner tolerance.

3. Biological Considerations
    - What is the current and projected status of the population and habitat conditions for these populations?
        i. Over the past five years the pheasant population has remained steady and there are no biological concerns with this recommended regulatory change.

4. Social Considerations
    - Would provide additional pheasant hunting opportunities.

5. Financial considerations
    - Not applicable.

RECRUITMENT, RETENTION, REACTIVATION (R3) CRITERIA

1. Does the regulation or fee inhibit a user’s ability to participate? No.

2. Does the regulation increase the opportunity for new and existing users? Yes.

3. How does the regulation impact the next generation of hunters, anglers, trappers and outdoor recreationists? Provides additional hunting opportunity.

4. Does the regulation enhance the quality of life for current and future generations by getting families outdoors? Yes.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

GAME, FISH AND PARKS COMMISSION ACTION

FINALIZATION

Resident Pheasant Hunting Season

Chapter 41:06:58

Commission Meeting Dates:	**Proposal**	**July 16-17, 2020**	**Virtual Meeting**
	Public Hearing	**September 2, 2020**	**Virtual Meeting**
	Finalization	**September 2-3, 2020**	**Virtual Meeting**

COMMISSION PROPOSAL

Duration of Proposal: 2020 hunting season

Season Dates: October 10-12, 2020

Open area: Lands open to public hunting that include U.S. Fish and Wildlife Service Waterfowl Production Areas, U.S. Army Corps of Engineers property adjacent to the Missouri River, U.S. Forest Service National Grasslands property, U.S. Bureau of Reclamation property, State School and Public Land, Department owned, managed or leased property otherwise open to hunting, and Department managed or leased property designated as Walk-In Area. Also includes public road rights-of-way as defined in state law which are contiguous to and a part of those public lands as identified above. U. S. Fish and Wildlife Service National Wildlife Refuges are not open.

Daily limit: 3 cock pheasants

Possession limit: 9 cock pheasants

Requirements and Restrictions:

1. Shooting hours are 10:00 a.m. (central time) to sunset.
2. Only residents of the state are eligible to hunt during this season.

Proposed changes from last year:

1. Modify the shooting hours from Noon to 10:00 a.m. Central Time beginning with the 2020 hunting season.

DEPARTMENT RECOMMENDATION

Recommended changes from proposal: None

SUPPORTIVE INFORMATION

To provide additional hunting opportunity and take advantage of cooler temperatures.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

RESIDENT/NONRESIDENT CRITERIA

1. The Issue
    - Why make the change, what are the change alternatives, how will public/stakeholder input be solicited, and how will the change be evaluated if implemented?
        - i. Was a topic discussed with the pheasant marketing workgroup and supported by the Department.
        - ii. Input will be solicited during the public comment period and GFP Commission public hearing.

2. Historical Considerations
    - There is a traditional connection to the 10:00 a.m. start time. Over the years, however, this has been modified during the regular season to now only include the first seven days of the regular season.

3. Biological Considerations
    - What is the current and projected status of the population and habitat conditions for these populations?
        - i. Pheasant population has remained stable over the past five years and there are no biological concerns with this recommended regulatory change.

4. Social Considerations
    - Would make start time consistent for entire hunting season.

5. Financial considerations
    - Not applicable.

RECRUITMENT, RETENTION, REACTIVATION (R3) CRITERIA

1. Does the regulation or fee inhibit a user’s ability to participate? No.

2. Does the regulation increase the opportunity for new and existing users? Yes.

3. How does the regulation impact the next generation of hunters, anglers, trappers and outdoor recreationists? Provides additional hunting opportunity.

4. Does the regulation enhance the quality of life for current and future generations by getting families outdoors? Yes.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

GAME, FISH AND PARKS COMMISSION ACTION
FINALIZATION

Upland Game Bird Hunting Seasons
Chapter 41:06:09; 41:06:11; 41:06:12

Commission Meeting Dates:	Proposal	July 16-17, 2020	Virtual Meeting
	Public Hearing	September 2, 2020	Virtual Meeting
	Finalization	September 2-3, 2020	Virtual Meeting

COMMISSION PROPOSAL

Duration of Proposal: 2020 grouse, partridge and quail hunting seasons

Proposed changes from last year:

1. Modify the season end date from the first Sunday in January to January 31 beginning with the 2020 hunting season.

DEPARTMENT RECOMMENDATION

Recommended changes from proposal: None

SUPPORTIVE INFORMATION

To align the season end date for all upland game bird hunting seasons as proposed by the Commission for the pheasant hunting season.

RESIDENT/NONRESIDENT CRITERIA

1. The Issue
    - Why make the change, what are the change alternatives, how will public/stakeholder input be solicited, and how will the change be evaluated if implemented?
        i. Is related to a topic discussed with the pheasant marketing workgroup and supported by the Department.
        ii. Input will be solicited during the public comment period and GFP Commission public hearing.
2. Historical Considerations
    - Over the years the season end dates for upland game birds has been extended with the desire to maximize hunting opportunities in balance with landowner tolerance.
3. Biological Considerations
    - What is the current and projected status of the population and habitat conditions for these populations?
        i. There are no biological concerns with this recommended regulatory change.
4. Social Considerations
    - Would make season end dates consistent for all upland game bird hunting seasons.
5. Financial considerations
    - Not applicable.

RECRUITMENT, RETENTION, REACTIVATION (R3) CRITERIA

1. Does the regulation or fee inhibit a user's ability to participate? No.
2. Does the regulation increase the opportunity for new and existing users? Yes.
3. How does the regulation impact the next generation of hunters, anglers, trappers and outdoor recreationists? Provides additional hunting opportunity.
4. Does the regulation enhance the quality of life for current and future generations by getting families outdoors? Yes.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

GAME, FISH AND PARKS COMMISSION ACTION
FINALIZATION

Private Shooting Preserves
Chapters 41:06:02:03 and 41:09:01

Commission Meeting Dates:	**Proposal**	**July 16-17**	**Teleconference**
	Public Hearing	**Sept 2-3**	**Teleconference**
	Finalization	**Sept 2-3**	**Teleconference**

COMMISSION PROPOSAL

Recommended changes:

1. Create two new small game permit types and establish fee of $150.00:
   a. Resident small game unrestricted permit (Unrestricted – Valid on private shooting preserves only).
   b. Nonresident shooting preserve unrestricted permit (Unrestricted).
2. Amend bag limits on for individuals hunting private shooting preserves to reflect no bag limit when hunting with an unrestricted small game license or an unrestricted shooting preserve license.
3. Licenses would only be valid if used in conjunction with an already existing license that authorizes a hunter to hunt on PSP properties. For example: a nonresident would have to purchase either a nonresident small game license or 1 day, 5 day or annual PSP license first, and then could purchase an unrestricted nonresident shooting preserve license on top of their existing license and hunt unrestricted on PSPs that offer the option.
4. Amend language that would only allow an individual to exercise the unrestricted portion of their license in party hunting if all parties to the hunt have the same license.
5. Depending on method of sale, may have to amend reporting requirements by PSP operators to include tracking of unrestricted license sales.

DEPARTMENT RECOMMENDATION

Recommended changes from proposal: The Department has received a recommended change to the proposal submitted on behalf of the South Dakota Upland Outfitters Association. The Department supports their recommended changes.

SUPPORTIVE INFORMATION

The Department has been in contact with private shooting preserve operators and other stake holders to determine whether there is support for the opportunity for hunters to shoot an unrestricted bag limit on private shooting preserves. There was support among the groups so long as the additional cost was on the hunter and not the preserve operators and if preserve operators had the abilities to choose whether or not they offered unrestricted harvest limits to their clients.

RESIDENT/NONRESIDENT CRITERIA

1. The Issue
   - Why make the change, what are the change alternatives, how will public/stakeholder input be solicited, and how will the change be evaluated if implemented?
     i. Answer: The change was requested by several preserve operators. After group discussions with preserve operators across the state, there was support for an unlimited opportunity as long as the cost did not impact those preserves that did not wish to provide this opportunity.

2. Historical Considerations

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

- What are the current and projected trends in resident and nonresident license sales, documented and/or perceived hunter densities and the ramifications of these densities?
    - i. Answer: No significant changes in license sales or hunter densities.
- How do neighboring states address the identified issue?
    - i. Answer: Many states allow for an unrestricted take of birds on private shooting preserves. These modifications would

3. Biological Considerations
    - What is the current and projected status of the population and habitat conditions for these populations?
        - i. Answer: Shooting preserves harvest is primarily made up of released birds and therefore have little to no impact on the wild population of pheasants.

4. Social Considerations
    - How would the change affect resident and nonresident: current and future generations of families, opportunities to expand outdoor recreation participation and patterns of land ownership.
        - i. Answer: Offering an additional opportunity to purchase an unrestricted license could attract additional hunters who are looking for this opportunity. Furthermore, it does not restrict or change how people have traditionally hunted on private shooting preserves.

5. Financial considerations
    - What are the financial implications of the change for current and future: revenue for GFP; the proportional contributions of revenue from residents and nonresidents to support species and habitat management programs, and the ability of GFP to support species and habitat management programs, program income for landowners to manage habitat, sales tax collections in SD, and personal income of business owners and their employees.
        - i. Answer: Allocating license dollars from these new licenses specifically for habitat could create a new source of revenue helping build better and more habitat.

RECRUITMENT, RETENTION, REACTIVATION (R3) CRITERIA

1. Does the regulation or fee inhibit a user's ability to participate?
    - a. No
2. Does the regulation increase the opportunity for new and existing users?
    - a. Yes
3. How does the regulation impact the next generation of hunters, anglers, trappers and outdoor recreationists?
    - a. The new regulation would allow an opportunity that does not currently exist.
4. Does the regulation enhance the quality of life for current and future generations by getting families outdoors?
    - a. Yes – the additional opportunity could attract a unique subset of hunters

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

GAME, FISH, AND PARKS COMMISSION ACTION
FINALIZATION

Custer State Park Elk Hunting Season (Any Elk)
Chapter 41:06:27

Commission Meeting Dates:	**Proposal**	**July 16-17, 2020**	**Virtual Meeting**
	Public Hearing	**September 2, 2020**	**Virtual Meeting**
	Finalization	**September 2-3, 2020**	**Virtual Meeting**

COMMISSION PROPOSAL

Duration of Proposal: 2021 hunting season

Proposed changes from last year:

1. Modify the drawing time period for the elk license raffle from at least 120 days before the Custer State Park rifle elk season begins to no later than July 15.

DEPARTMENT RECOMMENDATION

Recommended changes from proposal: None

SUPPORTIVE INFORMATION

The intent of the change is to allow an opportunity for unsuccessful applicants from the regular elk hunting season drawings to purchase raffle tickets for this elk license.

Year	Licenses	Applicants	Success Rate
2006	41	11,709	95%
2007	41	12,768	93%
2008	36	12,572	97%
2009	36	13,063	86%
2010	21	13,065	80%
2011	11	12,060	91%
2012	4	11,133	100%
2013	4	12,888	100%
2014	4	11,762	100%
2015	8	9,136	100%
2016	9	8,951	89%
2017	9	8,828	89%
2018	9	8,670	89%

RESIDENT/NONRESIDENT CRITERIA

Not Applicable.

RECRUITMENT, RETENTION, REACTIVATION (R3) CRITERIA

Not Applicable.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

GAME, FISH, AND PARKS COMMISSION ACTION
FINALIZATION

Bobcat Trapping and Hunting Season
Chapter 41:08:01

Commission Meeting Dates:	**Proposal**	**July 16-17, 2020**	**Virtual Meeting**
	Public Hearing	**September 2, 2020**	**Virtual Meeting**
	Finalization	**September 2-3, 2020**	**Virtual Meeting**

COMMISSION PROPOSAL

Duration of Recommendation: 2020-21 and 2021-22 trapping and hunting seasons

Season Dates:	**Area:**
December 26, 2020 – February 15, 2021	Statewide

Nonresident Season Dates:	**Area:**
January 9, 2021 – February 15, 2021	Statewide

Requirements and Restrictions:

1. Trappers or hunters who participate in the bobcat season east river are limited to one bobcat per trapper or hunter.

2. A bobcat taken must be presented to a conservation officer or wildlife damage specialist for registration and tagging of the pelt within 5 days of harvest. Additionally, once the season has closed, an individual has 24 hours to notify a conservation officer or wildlife damage specialist of any untagged bobcats harvested during the season. The pelt must be removed from the carcass and the carcass must be surrendered to the conservation officer or wildlife damage specialist. After the pelt has been tagged, it shall be returned to the hunter or trapper. Upon request, the carcass may be returned to the hunter or trapper after the carcass has been inspected and the lower jaw has been removed. A person may only possess, purchase or sell raw bobcat pelts that are tagged through the eyeholes with the tag provided by the department.

Proposed changes from last year:

1.) Modify the season dates in eastern South Dakota to align with western South Dakota. Proposed season dates would be December 15 to February 15, statewide.

2.) Modify the open area in eastern South Dakota to include all counties. The proposed open area would be statewide.

DEPARTMENT RECOMMENDATION

Recommended changes from proposal: None

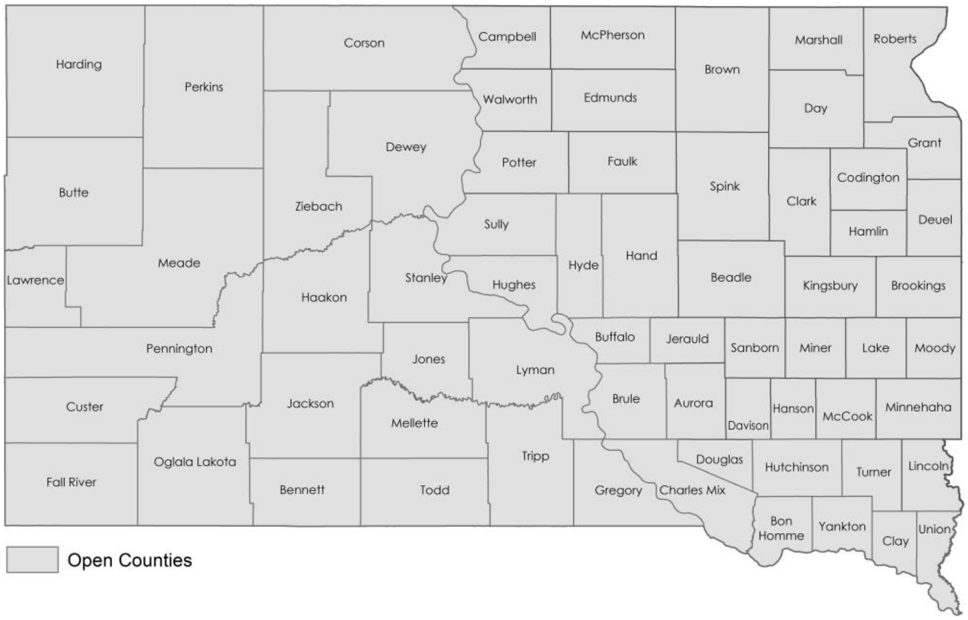
SUPPORTIVE INFORMATION

Bobcats occur in several areas of eastern South Dakota where the current bobcat season is not open. Minimal harvest in those areas would not be detrimental to bobcat populations and are protected by the limit of one bobcat per hunter or trapper. This expansion would create additional opportunity and aligning the two seasons' dates (eastern South Dakota and western South Dakota) brings consistency and simplifies regulations.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

Bobcat Season - Current Open Area

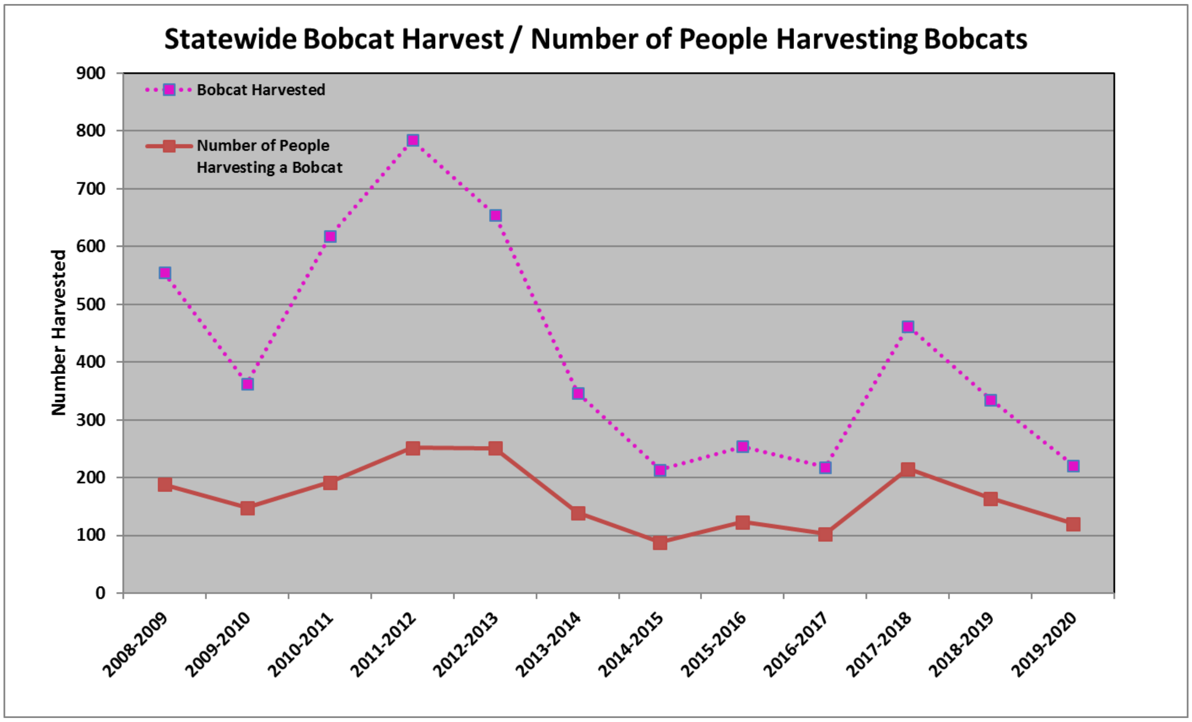
Bobcat Season - Proposed Open Area



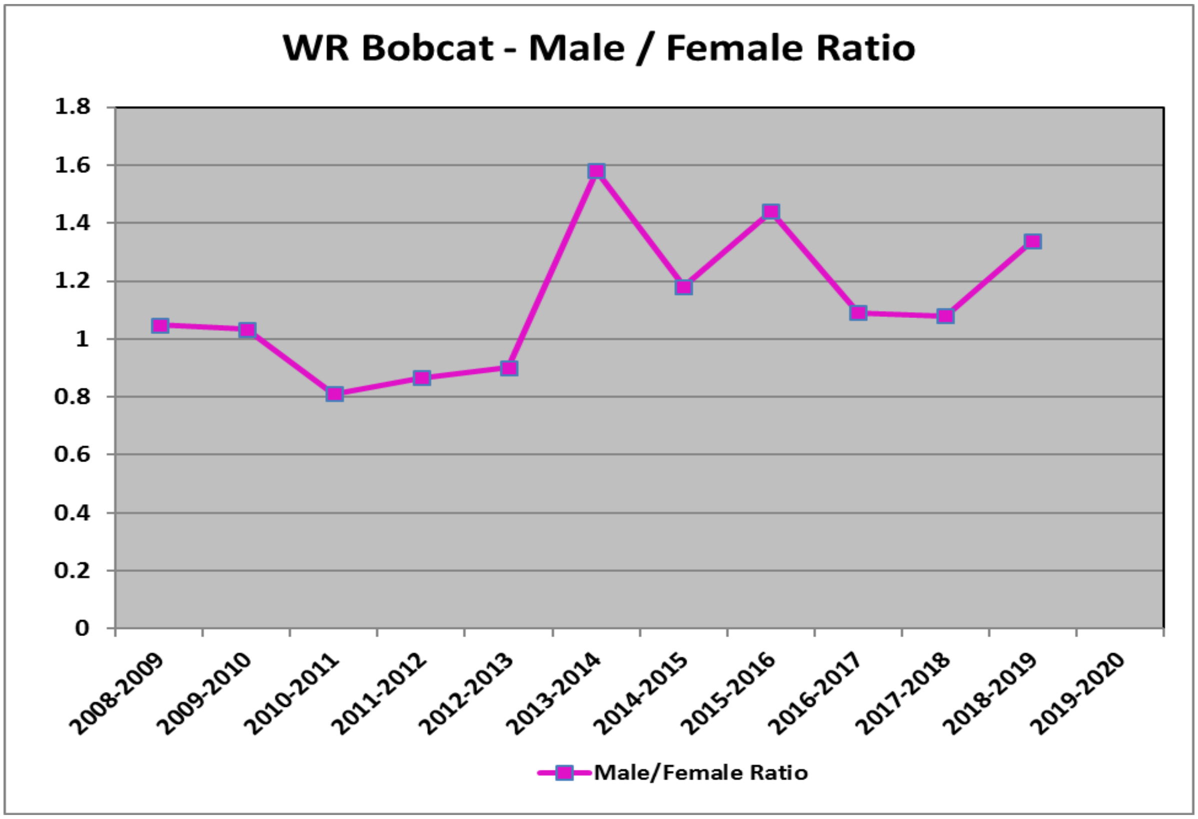
APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

Bobcat Harvest Statistics

	West River	East River
2009-2010	363	
2010-2011	618	
2011-2012	784	
2012-2013	615	40
2013-2014	323	24
2014-2015	206	8
2015-2016	242	12
2016-2017	206	12
2017-2018	428	34
2018-2019	312	23
2019-2020	190	31



APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____



RESIDENT/NONRESIDENT CRITERIA

1. The Issue
   - Why make the change, what are the change alternatives, how will public/stakeholder input be solicited, and how will the change be evaluated if implemented?
     1. The proposed change was brought forward to expand the open area and provide more opportunity and align season dates.
     2. Input will be sought through the commission process and be evaluated with GFP's annual bobcat harvest report.

2. Historical Considerations
   - In 2012, the east river bobcat season was established. At the same time, nonresident trappers were allowed to participate in the bobcat trapping and hunting season (in all open areas) with a shorter season, which remains today.

3. Biological Considerations
   - What is the current and projected status of the population and habitat conditions for these populations?
     1. The majority of bobcat habitat in eastern South Dakota occurs along brushy habitat along rivers and streams (i.e. riparian areas). The limit of one bobcat per hunter or trapper is enough of a restriction to limit overharvest where bobcats occur in eastern South Dakota. No biological effect is expected.

4. Social Considerations
   - The expansion would provide additional opportunities for hunters and trappers in eastern South Dakota, with a longer season and larger geographic area.

5. Financial considerations
   - Not applicable.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

RECRUITMENT, RETENTION, REACTIVATION (R3) CRITERIA

1. **Does the regulation or fee inhibit a user's ability to participate?** Not applicable.

2. **Does the regulation increase the opportunity for new and existing users?** Yes. Including the additional counties into the season would allow individuals in those areas to have a chance at harvesting a unique wildlife species and create additional opportunity for hunters and trappers.

3. **How does the regulation impact the next generation of hunters, anglers, trappers and outdoor recreationists?** The expanded open area creates a larger geographic area for people to participate and lengthening the season allows for more opportunity.

4. **Does the regulation enhance the quality of life for current and future generations by getting families outdoors?** The expanded open area creates a larger geographic area for people to participate and lengthening the season allows for more opportunity.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

GAME, FISH AND PARKS COMMISSION ACTION
FINALIZATION

SPEARING
Chapter 41:07:06

Commission Meeting Dates:			
	Proposal	July 17,2020	Pierre
	Public Hearing	September 2, 2020	Rapid City
	Finalization	September 2-3, 2020	Rapid City

COMMISSION PROPOSAL

1. Create a gamefish spearing season on the Missouri River from the Nebraska – South Dakota border up to Ft. Randall dam, May 1 – March 31, to match the season dates below other Missouri River dams.
2. Extend gamefish spearing hours for legal spear, legal speargun, legal crossbow and bow and arrow to one-half hour after sunset.

Department recommended changes to proposal:

None.

SUPPORTIVE INFORMATION

1. Currently there is no gamefish spearfishing season on the Missouri River from the Nebraska - South Dakota border up to Ft. Randall dam. To standardize spearfishing regulations in this area with other Missouri River dam tailrace areas, a May 1 – March 31 is recommended.

2. This was requested by a spearer. According to surveyed spearers, as with rod and reel angling, the last hour of light is one of the best times to spearfish. Currently gamefish can be taken with legal spear, legal speargun, legal crossbow and bow and arrow, one-half hour before sunrise to sunset. Extending the hours to one-half hour after sunset will allow for additional opportunity for those spearers who choose to utilize it. Rough fish spearing is currently allowed 24 hours a day.

RESIDENT/NONRESIDENT CRITERIA

Not Applicable.

RECRUITMENT, RETENTION, REACTIVATION (R3) CRITERIA

1. Does the regulation or fee inhibit a user’s ability to participate?

   No.

2. Does the regulation increase the opportunity for new and existing users?

   Opportunity to spear game fish is increased by opening a new area to game fish spearing and extending the hours it can occur.

3. How does the regulation impact the next generation of hunters, anglers, trappers and outdoor recreationists?

   There is no impact to the next generation.

4. Does the regulation enhance the quality of life for current and future generations by getting families outdoors?

   The recommended changes increase opportunity.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

GAME, FISH AND PARKS COMMISSION ACTION
FINALIZATION

PUBLIC WATERS
Chapters 41:04

Commission Meeting Dates:	**Proposal**	**July 17,2020**	**Pierre**
	Public Hearing	**September 2, 2020**	**Rapid City**
	Finalization	**September 2-3, 2020**	**Rapid City**

COMMISSION PROPOSAL

1. Require safety signage in association with operation of aeration systems during periods of ice cover on waters with open public access.

Department recommended changes to proposal:
None

SUPPORTIVE INFORMATION

1. Aeration is used to prevent fish kills during the summer and winter and to prevent ice from forming that may damage permanent docks or other structures anchored in the lakebed. Operation of aeration systems during the winter can cause significant public safety issues, as systems create open water and weakened ice conditions. Often, the public is unaware of system operation until it is accidentally discovered, while on the ice. Establishing a requirement that an aeration system in operation during periods of ice cover, on waters to which the public has open access, be signed and marked, would reduce safety issues associated with winter operation of aeration systems. Signage requirements would include:
   - Signs of highly visible size and design indicating "Danger Open Water", clearly showing the location of the open water created by the aeration system, posted at all boat ramps and public access points any time the aeration system is in operation.
   - Conspicuous markers, sufficient to notify the public of the location of the aeration system, shall be placed around the open water area during periods of ice cover.
   - Access area signs and on-lake markers must be removed by March 30 each year, or earlier, if weather conditions warrant.

RESIDENT/NONRESIDENT CRITERIA

Not Applicable.

RECRUITMENT, RETENTION, REACTIVATION (R3) CRITERIA

1. Does the regulation or fee inhibit a user’s ability to participate?

   No.

2. Does the regulation increase the opportunity for new and existing users?

   No.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

3. How does the regulation impact the next generation of hunters, anglers, trappers and outdoor recreationists?

   The regulation helps increase the safety of all these groups of outdoor recreationists.

4. Does the regulation enhance the quality of life for current and future generations by getting families outdoors?

   Yes, by increasing safety.

GAME, FISH AND PARKS COMMISSION ACTION
FINALIZATION

AQUATIC INVASIVE SPECIES
Chapters 41:10:04

Commission Meeting Dates:			
	Proposal	**July 17,2020**	**Pierre**
	Public Hearing	**September 2, 2020**	**Rapid City**
	Finalization	**September 2-3, 2020**	**Rapid City**

COMMISSION PROPOSAL

With the creation of **41-13A** during the 2020 Legislative Session and the discovery of zebra mussels in Pickerel Lake, the following changes to Aquatic Invasive Species (AIS) administrative rules are recommended:

1. Remove the prohibition on possessing, transporting, selling, purchasing, or propagating AIS from administrative rule.

2. Create an additional exemption for possession of AIS to allow an owner or agent of the owner of a conveyance to transport the conveyance for decontamination using a department approved process.

3. Remove prohibitions in administrative rule on launching a boat or boat trailer into the waters of the state with AIS attached.

4. Repeal the rule allowing for the creation of local boat registries.

5. Remove the exemption to the decontamination requirement for boats in a local boat registry in association with repealing the rule allowing the creation of registries.

6. Create a new rule to define the department-approved decontamination protocol.

7. Update the list of containment waters to include Lakes Pickerel, Waubay, North Rush, South Rush, and Minnewasta.

Department recommended changes to proposal:

7. Modify the Containment Waters rule by:

    a. Changing the title of the “Containment Waters” rule to “Infested Waters”.

    b. Define infested waters as waterbodies that have an established zebra or quagga mussel population, waterbodies downstream of infested waters with a high likelihood of becoming infested, and waters outside the state that are designated by a legal jurisdiction as infested for zebra or quagga mussels, for aquatic invasive species management purposes.

    c. Replace the term “Containment Waters” with “Infested Waters” in other administrative rules that reference containment waters.

SUPPORTIVE INFORMATION

1. Codified law 41-13A-2 contains prohibitions on possessing, importing, shipping, and transporting AIS, so prohibitions no longer need to be listed in administrative rule.

2. The addition of an exemption to allow for possession of AIS while transferring a conveyance for decontamination will facilitate decontaminations.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

3. Codified law 41-13A-3 contains prohibitions on launching a boat or boat trailer into the waters of the state with AIS attached or onboard, so prohibitions no longer need to be listed in administrative rule. Language remaining in the rule describes specifically when boat plugs and valves that control the drainage of water must be removed or open. This information is not included in statute

4. Two local boat registries currently exist on the Missouri River system. The expansion in the distribution of zebra mussels makes utilization of local boat registries impractical, resulting in the recommended repeal of this rule. The suggested addition to 41:10:04:02 that allows transport of infested boats for decontamination provides boatowners with a mechanism to transport boats for decontamination, in the absence of a local boat registry.

5. Removing exemptions to decontamination requirements for boats is a local boat registry coincides with repeal of the rule allowing for the creation of the registries.

6. The Pacific States Marine Fisheries Commission publishes a document titled "Uniform Minimum Protocols and Standards for Watercraft Inspection and Decontamination Programs for Dreissenid Mussels in the Western United States" (UMPS). The document is currently in its third edition and is the basis for inspection and decontamination protocols used by the department. Department-approved protocols for decontamination of conveyances are those contained in UMPS, 3rd edition, or subsequent versions of the document. Current protocols for conveyance decontamination involve hot water (140ºF or 120ºF at the point of contact) pressure washing and flushing of equipment, or a specified drying time, based on air temperature.

7. The department recommends a change from proposal. Replacing a specific list of containment waters for which certain decontamination requirements apply with a definition of infested waters, allows new waters to be considered infested, for application of decontamination or other regulatory requirements, without the GFP Commission needing to promulgate rules to do so. Currently, some waters not known to have established zebra mussel populations are included in the list of containment waters because they are immediately downstream from infested waters. These waters could be designated as infested waters, as a precautionary listing. An increase in monitoring for adult mussels for waters added as precautionary listings would occur. The initial list of infested waters would include all current containment waters, those waters added to the list by emergency rule in July 2020 (Pickerel, Waubay, North and South Rush, Minnewasta), and Lakes Cochrane and Kampeska.

RESIDENT/NONRESIDENT CRITERIA

Not Applicable.

RECRUITMENT, RETENTION, REACTIVATION (R3) CRITERIA

1. Does the regulation or fee inhibit a user's ability to participate?

   No.

2. Does the regulation increase the opportunity for new and existing users?

   No. There is no change in opportunity.

3. How does the regulation impact the next generation of hunters, anglers, trappers and outdoor recreationists?

   There is no impact other than the likelihood of fewer waters being infested with AIS in the future.

4. Does the regulation enhance the quality of life for current and future generations by getting families outdoors?

   Yes. Reducing the spread of AIS will positively contribute to the quality of water-based recreation in the future.

GAME, FISH AND PARKS COMMISSION ACTION
FINALIZATION

PUBLIC WATER ZONING 41:04:02
FISH LIMITS 41:07:03

Commission Meeting Dates:	**Proposal**	**July 17,2020**	**Pierre**
	Public Hearing	**September 2, 2020**	**Rapid City**
	Finalization	**September 2-3, 2020**	**Rapid City**

COMMISSION PROPOSAL

1. Establish an electric-motors-only zone on Canyon Lake in Pennington County and Bismarck Lake in Custer County.
2. Change Nebraska – South Dakota border trout limit from 7 daily to 5 daily to match South Dakota inland waters.

Department recommended changes to proposal:
None.

SUPPORTIVE INFORMATION

1. Canyon Lake and Bismarck Lake are utilized by canoers and kayakers. The City of Rapid City would like an electric motor only regulation on Canyon Lake. The United States Forest Service would like an electric motor only regulation on Bismarck Lake.

2. Currently the trout daily limit of 7 on Nebraska – South Dakota border waters does not match the South Dakota inland waters daily limit (5) or the Nebraska border water daily limit (5) for trout. Changing the daily limit for trout on Nebraska – South Dakota border waters to 5 would align the daily limit with those for South Dakota inland waters and Nebraska border waters.

RESIDENT/NONRESIDENT CRITERIA

Not Applicable.

RECRUITMENT, RETENTION, REACTIVATION (R3) CRITERIA

1. Does the regulation or fee inhibit a user’s ability to participate?

   No.

2. Does the regulation increase the opportunity for new and existing users?

   No.

3. How does the regulation impact the next generation of hunters, anglers, trappers and outdoor recreationists?

   There is no impact to the next generation of users

4. Does the regulation enhance the quality of life for current and future generations by getting families outdoors?

   The recommended changes will not change the quality of life.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

Division of Parks and Recreation

August 2020 Revenue by Item

	2019		2020		%
	Number	Dollar	Number	Dollar	Change
Annual	4,551	$ 136,524	5,368	$ 193,264	42%
2nd Annual	1,399	$ 20,987	1,439	$ 25,908	23%
Combo	974	$ 43,824	982	$ 53,010	21%
Transferable	40	$ 2,574	41	$ 3,304	28%
Daily License	22,298	$ 133,789	26,697	$ 213,579	60%
Unattended Vehicle Daily	523	$ 5,228	498	$ 7,470	43%
GSM Annual Trail Pass	245	$ 3,675	388	$ 5,820	58%
GSM Daily Trail Pass	1,234	$ 4,936	2,657	$ 10,628	115%
Motorcoach Permit	3,639	$ 10,917	1,936	$ 5,808	-47%
CSP 7 Day Pass	34,635	$ 692,704	40,099	$ 801,982	16%
CSP 7 Day Bike Pass	3,956	$ 39,556	8,676	$ 173,520	339%
Rally Bike Band	29,364	$ 293,640	29,638	$ 592,752	102%
One-Day Special Event		$ 3,550		$ 1,050	-70%
PERMITS	***102,857***	***$ 1,391,904***	***118,420***	***$ 2,088,095***	***50%***
Camping Services		$ 726,374		$ 1,181,632	63%
Picnic Reservations		$ 1,378		$ 1,660	20%
Firewood	10,014	$ 50,072	10,117	$ 60,700	21%
Gift Card		$ 70		$ 468	568%
Boat Slips		$ -		$ (3,160)	
LODGING	***10,014***	***$ 777,894***	***10,117***	***$ 1,241,300***	***60%***
TOTAL	***112,872***	***$ 2,169,798***	***128,536***	***$ 3,329,395***	***53%***

Division of Parks and Recreation

August YTD 2020 Revenue by Item

	2019		2020		%
	Number	Dollar	Number	Dollar	Change
Annual	43,352	$ 1,300,569	56,436	$ 2,031,711	56%
2nd Annual	10,497	$ 157,452	11,306	$ 203,500	29%
Combo	25,801	$ 1,161,043	28,618	$ 1,545,346	33%
Transferable	1,978	$ 128,583	1,849	$ 147,899	15%
Daily License	85,559	$ 513,354	108,573	$ 868,588	69%
Unattended Vehicle Daily	1,570	$ 15,697	1,928	$ 28,919	84%
GSM Annual Trail Pass	2,644	$ 39,660	4,744	$ 71,160	79%
GSM Daily Trail Pass	5,936	$ 23,744	9,439	$ 37,756	59%
Motorcoach Permit	11,751	$ 35,253	3,899	$ 11,697	-67%
CSP 7 Day Pass	132,082	$ 2,641,645	128,565	$ 2,571,298	-3%
CSP 7 Day Bike Band	16,606	$ 166,058	16,379	$ 327,585	97%
Rally Bike Band	29,364	$ 293,640	29,638	$ 592,752	102%
One-Day Special Event		$ 8,300		$ 2,400	-71%
PERMITS	***367,140***	***$ 6,484,998***	***401,373***	***$ 8,440,610***	***30%***
Camping Services		$ 7,789,365		$ 11,167,861	43%
Picnic Reservations		$ 11,676		$ 9,030	-23%
Firewood	36,780	$ 183,902	42,880	$ 257,283	40%
Gift Card		$ 7,078		$ 6,818	-4%
Boat Slips		$ -		$ 144,735	
LODGING	***36,780***	***$ 7,992,021***	***42,880***	***$ 11,585,727***	***45%***
TOTAL	***403,920***	***$ 14,477,019***	***444,254***	***$ 20,026,337***	***38%***

Division of Parks and Recreation

August YTD 2020 Camping by District

LOCATION	2019	2020	%
Pickerel Lake	5,020	5,049	1%
Fort Sisseton	1,013	1,038	2%
Roy Lake	5,269	6,618	26%
Sica Hollow	83	311	275%
DISTRICT 1	***11,385***	***13,016***	***14%***
Richmond Lake	1,383	1,467	6%
Mina Lake	2,405	2,516	5%
Fisher Grove	951	1,057	11%
Amsden	123	208	69%
Lake Louise	1,633	1,982	21%
DISTRICT 2	***6,495***	***7,230***	***11%***
Pelican Lake	4,659	5,193	11%
Sandy Shore	1,240	1,507	22%
Lake Cochrane	1,737	2,078	20%
Hartford Beach	4,836	6,043	25%
DISTRICT 3	***12,472***	***14,821***	***19%***
Oakwood Lakes	7,201	8,431	17%
Lake Poinsett	6,300	7,281	16%
Lake Thompson	5,634	6,098	8%
DISTRICT 4	***19,135***	***21,810***	***14%***
Lake Herman	4,291	4,603	7%
Walker's Point	2,371	2,629	11%
Lake Carthage	620	807	30%
DISTRICT 5	***7,282***	***8,039***	**10%**
Snake Creek	7,536	8,020	6%
Platte Creek	998	1,806	81%
Buryanek	1,707	2,452	44%
Burke Lake	5	55	1000%
DISTRICT 6	***10,246***	***12,333***	***20%***
Palisades	3,681	4,767	30%
Big Sioux	4,452	5,081	14%
Lake Vermillion	7,349	8,288	13%
DISTRICT 7	***15,482***	***18,136***	***17%***
Newton Hills	8,168	8,990	10%
Good Earth	1	-	
Union Grove	1,219	1,315	8%
DISTRICT 8	***9,388***	***10,305***	***10%***

LOCATION	2019	2020	%
Lewis & Clark	35,276	39,384	12%
Chief White Crane	9,862	11,070	12%
Pierson Ranch	3,851	4,536	18%
Springfield	1,016	1,202	18%
Sand Creek	104	70	-33%
Tabor	-	29	
DISTRICT 9	***50,109***	***56,291***	**12%**
North Point	4,113	9,314	126%
North Wheeler	567	782	38%
Pease Creek	1,267	1,472	16%
Randall Creek	11	4,100	37173%
South Shore	329	586	78%
South Scalp	21	50	138%
Whetstone	235	580	147%
White Swan	132	262	98%
DISTRICT 10	***6,675***	***17,146***	**157%**
Farm Island	6,048	6,429	6%
West Bend	7,902	7,838	-1%
DISTRICT 11	***13,950***	***14,267***	***2%***
Oahe Downstream	10,848	12,050	11%
Cow Creek	2,510	3,084	23%
Okobojo	1,257	2,175	73%
Spring Creek	-	696	
DISTRICT 12	***14,615***	***18,005***	***23%***
West Whitlock	4,035	4,531	12%
East Whitlock	42	92	119%
Swan Creek	673	896	33%
Indian Creek	6,489	6,757	4%
Lake Hiddenwood	-	-	
Walth Bay	7	39	457%
West Pollock	1,088	1,347	24%
DISTRICT 13	***12,334***	***13,662***	***11%***
Bear Butte	944	1,044	11%
DISTRICT 14	***944***	***1,044***	**11%**
Shadehill	4,579	5,423	18%
Llewellyn Johns	349	388	11%
Rocky Point	5,160	5,956	15%
DISTRICT 15	***10,088***	***11,767***	***17%***
Custer	38,496	42,422	10%
DISTRICT 16	***38,496***	***42,422***	***10%***
Angostura	16,500	17,507	6%
Sheps Canyon	1,606	1,987	24%
DISTRICT 17	***18,106***	***19,494***	***8%***
TOTAL YTD	***257,202***	***299,788***	***17%***
TOTAL for Month	***67,388***	***69,946***	***4%***

Division of Parks and Recreation

August YTD 2020 Visitation by District

LOCATION	**2019**	**2020**	**%**
Pickerel Lake	38,215	45,189	18%
Fort Sisseton	35,203	34,095	-3%
Roy Lake	120,125	151,415	26%
Sica Hollow	9,073	18,392	103%
DISTRICT 1	***202,616***	***249,091***	***23%***
Richmond Lake	26,944	41,285	53%
Mina Lake	31,549	45,366	44%
Fisher Grove	14,726	16,324	11%
Lake Louise	23,239	30,374	31%
DISTRICT 2	***96,458***	***133,349***	***38%***
Pelican Lake	42,680	59,577	40%
Sandy Shore	18,475	31,836	72%
Lake Cochrane	16,039	27,912	74%
Hartford Beach	86,857	113,906	31%
DISTRICT 3	***164,051***	***233,231***	***42%***
Oakwood Lakes	52,163	86,944	67%
Lake Poinsett	49,261	59,803	21%
Lake Thompson	32,510	44,046	35%
DISTRICT 4	***133,934***	***190,793***	***42%***
Lake Herman	67,132	103,050	54%
Walker's Point	31,217	45,453	46%
DISTRICT 5	***98,349***	***148,503***	***51%***
Snake Creek	101,727	134,999	33%
Platte Creek	98,014	144,889	48%
Buryanek	17,280	31,192	81%
Burke Lake	12,588	13,685	9%
DISTRICT 6	***229,609***	***324,765***	***41%***
Palisades	65,301	111,856	71%
Big Sioux	35,252	49,559	41%
Beaver Creek	12,169	18,062	48%
Lake Vermillion	80,184	119,392	49%
DISTRICT 7	***192,906***	***298,869***	***55%***
Newton Hills	90,821	157,871	74%
Good Earth	40,845	57,047	40%
Union Grove	11,687	18,497	58%
Lake Alvin	23,766	65,678	176%
Spirit Mound	14,891	19,511	31%
Adams	15,394	20,791	35%
DISTRICT 8	***197,404***	***339,395***	***72%***

LOCATION	**2019**	**2020**	**%**
Lewis & Clark	556,326	883,144	59%
Chief White Crane	39,902	46,310	16%
Pierson Ranch	50,732	70,075	38%
Springfield	87,095	127,696	47%
DISTRICT 9	***734,055***	***1,127,225***	***54%***
North Point	60,789	87,493	44%
North Wheeler	10,210	12,274	20%
Pease Creek	30,699	36,797	20%
Randall Creek	21,140	44,065	108%
Fort Randall Marina	13,478	16,311	21%
DISTRICT 10	***136,316***	***196,940***	***44%***
Farm Island	109,298	129,341	18%
West Bend	36,513	40,874	12%
LaFramboise Island	50,462	62,560	24%
DISTRICT 11	***196,273***	***232,775***	***19%***
Oahe Downstream	228,088	293,923	29%
Cow Creek	156,696	177,454	13%
Okobojo	34,773	49,557	43%
Spring Creek	157,216	225,027	43%
DISTRICT 12	***576,773***	***745,961***	***29%***
West Whitlock	37,531	40,016	7%
Swan Creek	23,714	18,314	-23%
Indian Creek	53,913	61,866	15%
Lake Hiddenwood	-	-	
Revheim Bay	33,144	43,878	32%
West Pollock	55,402	61,037	10%
DISTRICT 13	***203,704***	***225,111***	***11%***
Bear Butte	13,985	14,292	2%
DISTRICT 14	***13,985***	***14,292***	***2%***
Shadehill	31,594	34,451	9%
Llewellyn Johns	3,192	3,865	21%
Little Moreau	13,573	9,311	-31%
Rocky Point	63,036	86,318	37%
DISTRICT 15	***111,395***	***133,945***	***20%***
Custer	1,422,356	1,484,002	4%
DISTRICT 16	***1,422,356***	***1,484,002***	***4%***
Angostura	145,977	183,890	26%
Sheps Canyon	31,144	39,905	28%
DISTRICT 17	***177,121***	***223,795***	***26%***
TOTAL YTD	***4,887,305***	***6,302,042***	***29%***
TOTAL for Month	***937,735***	***1,238,344***	***32%***

GAME, FISH AND PARKS COMMISSION ADMINISTRATIVE ACTION

River Otter Management Plan

Commission Meeting Dates:	**Draft Shared**	**June 4-5, 2020**	**Virtual Meeting**
	Public Hearing	**September 2, 2020**	**Virtual Meeting**
	Adoption	**September 2-3, 2020**	**Virtual Meeting**

ADOPTION OF MANAGEMENT PLAN

Executive Summary

Over the last 41 years the number of incidental river otter reports continues to increase and their geographic distribution continues to expand. Age structure indicates a young and growing population. Delisting criteria developed as part of a status review have been met and the species has been delisted. South Dakota will manage river otter populations with scientifically sound data and techniques to encourage occupation of suitable available habitats and to provide sustainable use and enjoyment within the social tolerance level for this species. Although the river otter is secretive and difficult to survey, the need to develop a long-term monitoring program is a priority. Feasible and flexible survey methods will be used to meet monitoring program objectives, be suited to the state's climate and landscape, and implemented with available resources. Information, education and outreach will continue to enhance river otter management in South Dakota.

Introduction

In December of 2010, a group of South Dakota Department of Game, Fish and Parks (SDGFP) staff began developing a plan for the conservation and management of river otters. This team produced the South Dakota River Otter Management Plan. That 5-year plan provided general, strategic guidance to SDGFP and potential partners for the recovery and sustained management of river otter in South Dakota. It also included background information on the biology, ecology and management of river otter.

The current plan identifies what we strive to accomplish related to the management of river otter in South Dakota over the next 10 years; including development of a feasible long-term monitoring program and continued outreach about this species. It also includes updates to the relevant supporting information included in the first river otter management plan. These two documents should be used in concert with one another.

The current plan update will be used by SDGFP staff and Commission on an annual basis and will be formally evaluated at least every 10 years. Supporting information will be formally updated at least every 5 years. All text and data contained within this document are subject to revision for corrections, updates, and data analyses.

Management Goal

South Dakota will manage river otter populations with scientifically sound data and techniques to encourage occupation of suitable available habitats and to provide sustainable use and enjoyment within the social tolerance level for this species.

Public Involvement

An initial public comment period on the revised plan was announced following the May Commission with a deadline of June 19, 2020. Another public comment period was made available following the July 2020 Commission meeting with a deadline of August 16, 2020. A draft of the revised river otter management plan was made available at https://gfp.sd.gov/management-plans/ under "Plans Up for Revision." Written comments were sent to 523 E. Capitol Ave., Pierre, SD 57501 or emailed to OtterPlan@state.sd.us.

APPROVE _____ MODIFY _____ REJECT _____ NO ACTION _____

SOUTH DAKOTA RIVER OTTER MANAGEMENT PLAN, 2020-2029

SOUTH DAKOTA DEPARTMENT OF GAME, FISH AND PARKS
PIERRE, SOUTH DAKOTA

WILDLIFE DIVISION REPORT 2020-02

September 2020

Acknowledgements

Management Plan Team - Jacquie Ermer, Randy Johnson, Silka Kempema (coordinator), Eileen Dowd Stukel, and Chad Switzer. Cover photo by Wayne Melquist.

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Executive Summary

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Management goal

South Dakota Department of Game, Fish and Parks (SDGFP) will manage river otter populations with scientifically sound data and techniques to encourage occupation of suitable available habitats and to provide sustainable use and enjoyment within the social tolerance level for this species.

Introduction

In December of 2010, a group of SDGFP staff began developing a plan for the conservation and management of the North American River Otter (*Lontra canadensis*; hereafter river otter). This team produced the South Dakota River Otter Management Plan (SDGFP 2012). That 5-year plan provided general, strategic guidance to SDGFP and potential partners for the recovery and sustained management of river otter in South Dakota. It also included background information on the biology, ecology and management of river otter.

The current document identifies what we strive to accomplish related to the management of river otter in South Dakota over the next 10 years; including development of a feasible long-term monitoring program and continued outreach about this species. It also includes updates to the relevant supporting information included in the first management plan (SDGFP 2012). These two documents should be used in concert with one another. For more background on the biology, ecology and threats to river otters, please refer to SDGFP (2012).

The current plan update will be used by SDGFP staff and Commission on an annual basis and will be formally evaluated at least every 10 years. Supporting information will be formally updated at least every 5 years. All text and data contained within this document are subject to revision for corrections, updates, and data analyses.

Ecological and legal status

As directed in the 2012 plan (SDGFP 2012), recovery criteria were developed to recommend removing the species from the state threatened species list when appropriate. This was done as part of the biennial status reviews conducted for all state threatened or endangered species, which included the river otter (Appendix A). Status reviews summarize what is known about the species in the state, identify delisting or downlisting criteria, and list monitoring and research needs. As per the river otter status review, delisting criteria for the river otter included: 1) verified reports of reproduction are documented in three of the five basins (60%) within the recovery area and 2) within each basin, the presence of river otter has been documented by verified reports in at least 40% of their subbasins. Both criteria were required for at least two of the five years prior to recommended delisting. These criteria were met in 2019. On 5 March 2020, SDGFP staff recommended to the SDGFP Commission (Commission) that the river otter be removed from the list of state threatened mammals (Appendix B). The Commission approved delisting of this species on 7 May 2020.

Recent research

The need to collect updated information on the distribution and population of river otter in South Dakota was identified in the first plan (SDGFP 2012). As such, a State Wildlife Grant-funded project was initiated with Dr. Wayne Melquist to determine current river otter distribution and evaluate habitat, including identifying suitable habitat of unoccupied sites with the potential for population expansion. Refer to Appendix A for a summary of findings from Melquist (2015).

Information on distribution and mortality

Reports of river otter

The South Dakota Natural Heritage Program (SDNHP), a part of SDGFP, maintains information on rare animal and plant species and plant communities in the state. The SDNHP monitors river otter by soliciting and collecting incidental reports from a variety of sources including universities, government wildlife agencies, private contractors, and the general public.

Reports of river otter are categorized based on the primary method used to identify the animal as a river otter: sighting, sign, incidental trap, and vehicle kill. Sightings are based upon the actual observation of a river otter. Reports of sign are based on tracks, slides, runs, scat, latrines, and/or natal dens. Incidental trap reports are of river otter that were incidentally caught while targeting other species. Vehicle kills are reports of river otter found dead on the road or hit by a vehicle. A report can be of an individual animal or a group of animals.

Certain criteria are used to determine the reliability of each report. A verified report is one of a carcass or live-captured individual(s) or where evidence exists that proves the report was a river otter. Photos where the animal can clearly be identified as a river otter may also be considered verified. Tracks associated with sliding marks in the snow, if confirmed by knowledgeable reviewers can also be considered a verified sighting. Knowledgeable reviewers may include agency staff familiar with river otter or other river otter experts. A probable report is a sighting not accompanied by a photo but is observed by someone with river otter experience and knowledge. In addition, tracks and scats not in snow are considered probable reports in part because of the difficulty of correctly identifying them. Photos are evaluated by knowledgeable reviewers. Unverified reports are those with no evidence to support or reject the report.

The SDNHP database contains 575 reports of river otter from 1979 through 2019. The number of reports received has steadily increased since 1998 (Figure 1). Since 1979, we received an average of 14.0 (SD = 19.3) river otter reports per year. From 1979 through 1999, an average of less than 1 report (SD = 1.5) was received annually. During the last 20 years (2000-2019), we received a annual average of 27.9 (SD = 19.6) reports. During the last 5 years (2015-2019), we received an average of 50.6 (SD = 11.7) river otter reports each year. The highest number of river otter reports occurred in 2016 (n = 65).

Although river otter have been reported to be in 9 of the 10 watersheds in South Dakota, 80.2% of all reports came from three watersheds: Big Sioux (n = 302, 52.5%), Minnesota (n = 112, 19.5%), and James (n = 76, 13.2%; Table 1 and Figure 2). We define watersheds as hydrological unit level two subregions delineated by the U.S. Geological Survey National Watershed Boundary Dataset. River otter have been observed in 47 of the 66 South Dakota counties (Table 2 and Figure 3). Approximately half (51.5%) of all reports came from four counties: Moody (n = 97, 16.9%), Roberts (n = 71; 12.4%), Grant (n = 65; 11.3%) and Minnehaha (n = 63; 11.0%) counties.

We received a similar number of sightings (n = 220) and incidental trap reports (n = 216) over the last 41 years (Figure 4). Together they account for 76% of all report types. The remainder of reports were based on sign left by a river otter (n = 84, 14.6%), river otter struck by a vehicle (n = 48, 8.3%) and seven locations where river otter were detected by field cameras as part of a SDGFP project evaluating the use of cameras for monitoring river otter.

River otter reports from 1979 through 2019 revealed some monthly patterns based on observation type (Figure 5). Over half (53.2%) of all reports are received in March (n = 92; 16%), April (n = 95; 16.5%), and November (n = 119; 20.7%). Sightings of live animals were reported throughout the year, but most frequently in March (n = 34) and April (n = 34). Incidentally caught river otter were reported in all months of the year but were most frequent in March (n = 27), April (n = 43), and November (n = 86). Observations of sign were common in March (n = 24). Reports of vehicle killed otter occurred throughout the year with the most reported in April (n = 12).

Reports are comprised of 379 (65.9%) verified, 120 (20.9%) probable, and 76 (13.2%) unverified reports. The first verified observation of a river otter was made in Hughes County in 1983. Since that time, we have received an average of 10.2 (SD = 13.9) verified reports per year. Verified reports have increased from an average of less than one report per year (SD = 1.0) in the first 21 years (1979-1999) to 18.6 (SD = 14.3) reports per year during the most recent 20 years (Figure 6). During the last five years (2015-2019), an average of 35.2 (SD = 7.6) verified river otter reports were made per year. We received the most verified reports (n = 42) in 2016.

Incidental Trapping

Although incidentally trapped river otter were reported from five of the 10 watersheds (Table 3), 85.7% came from the Big Sioux (n = 127; 58.8%) and Minnesota (n = 58; 26.9%) watersheds. Most (71.8%) of the 216 incidentally trapped otter from 1979 through 2019 occurred in five counties: Moody (n = 54; 25.0%), Roberts (n = 32; 14.8%), Grant (n = 31; 14.4%), Brookings (n = 19; 8.8%), Minnehaha (n = 19; 8.8%; Table 4). Three incidentally trapped otter were reported from west of the Missouri River. Two were incidentally trapped in Lyman County (2000 and 2017) and one was released alive after being incidentally trapped in Haakon County (1998).

Target species was known for 146 of the 216 (67.5%) incidentally trapped river otter (Table 5). Of these, 116 (53.7%) were caught in traps targeting beaver, 19 while targeting raccoon (8.8%), 5 in fish nets or traps (2.3%), and 3 in sets targeting mink (1.4%). Trap types reported included body-grip, foot-hold, snare, and live traps (Table 6). Five sizes of body-gripping conibear traps were reported but the 330 conibear was the most commonly reported. Live-trap types included Hancock and havahart traps. Other trap types included fyke and hoop nets for fish sampling.

Information on techniques to avoid incidental trapping of river otter while targeting other species is shared with the public and specific audiences. “River Otters in South Dakota” is a brochure that provides information on river otter identification and distribution, avoidance techniques to use when trapping, and requests reports of river otter. This brochure is distributed by staff and through targeted mailings to trapping organizations. It has also been mailed directly to furbearer license holders. It is available at SDGFP regional offices and on the SDGFP website (https://gfp.sd.gov/userdocs/docs/RiverOtter-online.pdf).

SDGFP surveyed resident and nonresident furbearer license holders who had a 2012 license or a 2013 license that was purchased prior to May 1, 2013 to learn more about the distribution of river otters in the state (Huxoll 2013). License holders were asked if they had incidentally trapped a river otter in the previous year and if so, in what county. Huxoll (2013) reported that river otter were incidentally caught in Grant (n = 4), Moody (n = 3), Minnehaha (n = 3), Lincoln (n =2), Clark, Deuel, and Robert counties (one from each county).

Causes of death

Of the 575 reports provided to SDGFP from 1979 through 2019, 229 (29.8%) were of river otter found dead or killed (euthanized) due to injuries determined likely to be fatal. Causes of death included: incidental trapping (n = 159; 69.4%), vehicle strike (n = 46; 20.1%), other (n = 14; 6.1%), and euthanized (n = 10; 4.4%; Table 7). Note that not all incidentally trapped river otter are killed. Forty-four of the 216 (20.4%) incidentally trapped otter were released alive. Other causes of death included nine unknown causes, four drownings in fish sampling gear, and one radio-marked otter that died of cardio myopathy. Of those euthanized, seven sustained trap-related injuries, two sustained injuries from being hit by a vehicle and one was incidentally trapped. The incidentally trapped animal bit the observer when being released. The river otter was tested for rabies; test results were negative.

Information gained from necropsies

Since 2003, SDGFP conducted necropsies on 200 opportunistically obtained carcasses from 5 watersheds and 22 counties (Tables 8 and 9). Eighty-four percent of all carcasses were collected from two watersheds: Big Sioux (n = 116, 58.0%) and Minnesota (n = 51, 25.5%). Half (51.5%) of necropsied carcasses were obtained from Moody (n = 43, 21.5%), Roberts (n = 31, 15.5%) and Grant (n = 29, 14.5%) counties. Half (n = 102, 51.8%) of the carcasses necropsied were collected between 2015 and 2019 during the months of April and November. Incidental trapping was the cause of death for 71.1% (n = 140) of necropsied river otter.

Sex ratio and age structure

Of the 200 river otters examined, 60.5% were male (n = 121) and 39% were female (n = 78) resulting in a male:female ratio of 1.7:1. The sex of one otter was unknown. We determined the age of 179 river otter (111 males, 67 females and 1 unknown sex) by analysis of cementum annuli in a lower canine (Table 10). Ages ranged from 0 to 12 years old. The oldest known river otter in South Dakota was a 12-year old male collected from Grant County in 2019. The oldest known female otter was an 8-year old collected from Brookings County in 2006. Over half of known-aged river otter were either juvenile (< 1-year old; n = 34; 19%) or yearlings (1-year old; n = 68, 38%). The age structure of both sexes reflected that of the entire sample. Juveniles and yearlings combined (subadults) comprised approximately half all known-age males (56%) and females (60%).

Reproduction

Reproduction has been documented in 21 counties and six of the 10 watersheds in South Dakota (Figure 7). Evidence of reproduction is based on verified reports of family groups (>2 individuals), observation of corpora lutea, evidence of lactation, or presence of a 0- or 1-year old river otter.

We observed corpora lutea in 39 of 51 (76.4%) females examined. Corpora lutea are thickened, glandular tissues that form where an egg was released from the ovary. Age was known for 32 of the 39 reproductive females. Of these 32 known-age females, two (6.3%) were juveniles, 13 (40.6%) were yearlings, and 17 were adult (53.1%; Table 11). Subadult (juvenile and yearlings combined) and adult females averaged 1.5 (SD = 1.3) and 2.2 (SD = 1.3) corpora lutea, respectively. The most corpora lutea observed in a subadult female was three. Five corpora lutea were observed in the ovaries of a 5-year old female. The proportion of ovulating females increased with age from 40% of juvenile, 68% of yearling to 80-100% of adult females examined (Table 11).

Morphology

In a sample of 109 male and 66 female river otter, males averaged larger than females (21.0 lbs; SD = 4.1 vs 17.6 lbs; SD = 2.7 [9.5 kg; SD = 1.9 vs 8.0 kg; SD = 1.2]; Figure 8).

Diet

We conducted a gross examination of 192 river otter stomachs to determine diet composition. Fish were found in 44% of stomach examined (Table 12) including pieces of minnow, carp, sucker, northern pike *(Esox lucius*), bullhead, catfish, green sunfish (*Lepomis cyanellus*), Johnny darter (*Etheostoma nigrum*), and sand shiner (*Notropis stramineus*). Frogs, crayfish, vegetation, black liquid, and birds were also observed. Not all items were identified to genus or species. Many stomachs were empty (56 of 192 stomachs). Eleven stomachs were too damaged to determine contents.

Fish were found in stomach contents year-round but increased in frequency during March, April and November (Figure 9). Frogs were present in stomach contents all year except in June and December. Crayfish remains were observed from March through September. Bird remains were found in June, September, and November. Empty stomachs were most frequent in April and November.

Parasites

During necropsies of opportunistically obtained otters in South Dakota, 30 of the 200 (15%) carcasses had visible wrist worms. These worms are not detrimental to river otter and do not pose a human health risk.

Harvest

Philosophy

The recovery of river otter populations in South Dakota, facilitated in part through protection as a state threatened species, is a conservation success story. Data collected and research conducted since the turn of the century indicate river otter have re-colonized many areas of their former range in eastern South Dakota, with a growing population expected to continue to expand into remaining suitable habitat across the state. Delisting criteria developed as part of a species status review have been met and the species delisted. Management and monitoring of river otter remain important to future sustainable use and enjoyment. A conservative harvest is considered sustainable at this time. A limited harvest would allow managers to create the opportunity for recreational trapping of river otter through a regulated harvest season while ensuring a growing population. SDGFP recognizes that river otter are incidentally trapped by licensed trappers in pursuit of other species, particularly beaver. Allowing a conservative and limited harvest during a short season will allow better utilization of those river otter otherwise caught incidentally. Efforts are ongoing to provide information and outreach to improve awareness and minimize incidental captures. Further, a regulated river otter harvest season can be informed by continued monitoring of the population, and any harvest closely monitored to ensure a stable or increasing population. Data collected from harvested river otter will add information toward a monitoring effort that would be difficult to obtain otherwise.

Recommendation for 2020

During the May 2020 Commission meeting, SDGFP staff recommended a river otter harvest season from 1 November through 31 December 2020 or until a harvest limit of 15 river otter is reached, whichever comes first. Resident trappers would be limited to a harvest of 1 river otter/trapper/season. Refer to Appendix C for more details.

CITES

The Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) regulates international trade of certain animal and plant species. Species are assigned to Appendix I, II, or III. River otter are included in the Appendix II category because this species is similar in appearance to others that may be threatened; thus the U.S. Fish and Wildlife Service (USFWS) regulates and monitors river otter export.

If international trade of pelts is desired, states recommending or considering a river otter harvest season need to request approval for export of river otter pelts under the CITES Export Program. CITES authorization follows standard federal rule-making procedures (50 CFR 23.69

(b)(2)). The CITES Scientific Authority has concluded that the exportation of river otter taken in states with open harvest seasons between 2018-2019 and 2023-2024, will not be detrimental to the survival of the species. This General Advice also applies to states opening river otter harvest seasons for the first time (USFWS 2018). Because the U.S. Scientific Authority has made this range-wide nondetrimental finding for North American river otter, states requesting export approval need to submit only the information in (b)(1)(ii) and (vi) to the Division of Management Authority: (ii) current harvest control measures, including laws regulating harvest seasons and methods and (iv) tagging or marking requirements for fur skins.

Once a state's request for an export program has been approved, the USFWS requires that the state provide annual updates on the status of their river otter population and any regulatory changes that may be needed.

Surveys and Monitoring

Use of cameras

The use of trail cameras to monitor river otter is a new survey technique and few published studies are available. Wagnon and Serfass (2016) had success capturing river otter via trail cameras placed at latrine sites but failed to detect river otter at non-latrine sites. Bieber (2016) deployed 14 cameras on three different rivers in Nebraska, but experienced 'technical and configuration problems' and therefore discontinued their use. Findlay et al. (2020) provided technical recommendations on improving camera trapping based on their experiences from a six-year study of a Eurasian otter (*Lutra lutra*) den site. Stevens and Serfass (2008) stated their study was the first use of trail cameras in a river otter study, and they reported success with detecting river otter at latrine sites. Despite the lack of published studies on trail camera surveys for river otter, the technique offers the advantages of being a noninvasive approach with continual improvements in trail camera technology and the possibility for improved efficiency over more traditional methods.

SDGFP staff conducted a small-scale trail camera survey in 2019-2020 to evaluate the effectiveness of the technique and to provide recommendations on its use for future management surveys in South Dakota. Factors evaluated included trail camera brand and model performance, data storage, battery life, and warranties; number and location of camera traps needed; use of attractants; camera trap maintenance and security; time of year, and river otter biology and behavior.

Although the trail camera study is ongoing, as of Spring 2020, we have the following recommendations.

- We were successful in detecting river otter with trail cameras set along stream banks. However, detection probabilities were less than 100%. Therefore, caution is advised when interpreting survey results.
- Camera traps should be operated during late summer through fall to take advantage of seasonal water lows and reduced chance of major flooding.

- Each camera trap site should be actively surveyed for at least two consecutive months; if no river otter are detected within the first month, consider small-scale movement of camera site.
- Focus survey efforts on streams of Order 3, 4, or 5.
- Camera traps should target stream sites with a ~90° bend revealing a mud flat, or alternatively streams with exposed sections of mud/sandbars that would be naturally attractive to moving river otter. Also consider junctions of multiple streams.
- Visual and olfactory attractants can be used, but priority should be placed on targeting sites that naturally funnel river otter movement.
- We configured trail cameras to take two photos followed by a 15 second video; this resulted in enhanced ability to determine species and did not result in battery or storage problems.
- Plan for flooding; try to keep cameras above any observable high-water marks.
- Install trail cameras using fence posts to achieve maximum placement opportunity and avoid raccoon (*Procyon lotor*) issues from trail cameras set on trees.

Methods used in nearby states and provinces

States and provinces employ various methods that help meet their needs in a feasible way that matches survey and monitoring needs with available resources. When river otter populations recover to harvestable levels, many entities shift from population surveys to harvest analyses and other, less intensive methods.

SDGFP learned the following based on contacts with appropriate staff in nearby states and provinces in 2020.

Colorado surveys for river otter sign within identified focal recovery river systems to evaluate reintroduction success and assess progress in meeting state recovery goals. Agency staff and volunteers survey for sign during early spring prior to bank green-up or peak run-off flows at most selected areas, with limited use of winter surveys. Specific monitoring protocols are described in the state recovery plan, with a handbook provided as a resource for new surveyors (Colorado Parks and Wildlife 2003, Flohrs, no date). State contact: Eric Odell, Colorado Parks and Wildlife.

Iowa does not conduct specific population surveys. Iowa Dept. of Natural Resources (IADNR) collects river otter information from a variety of sources, including annual bowhunters observation survey, data from harvested animals (date and method of kill, county, and gender), tooth aging for 20% of total annual harvest, attempts to document the annual numbers of vehicle-kills and nuisance reports, Fur Harvester Diary Survey (started in 2018 primarily to collect effort data for all furbearers), and feedback from staff, trappers and landowners. A PhD student is currently analyzing harvest/age information to construct a population estimation model. State contact: Vince Evelsizer, IADNR.

Kansas is in transition with river otter monitoring. Kansas Wildlife, Parks and Tourism (KWPT) collected teeth until recently. This extensive data set has demonstrated the state’s river otter population has a young age structure that has not been impacted by harvest. The agency previously tracked river otter damage complaints, a practice that was discontinued when harvesting began. At present, KWPT uses harvest-generated data to monitor frequency distribution and catch-per-unit-effort (CPUE) and monitors river otter distribution using all information sources. The agency also listens to input from agency staff and the public in managing this species. State contact: Matt Peek, KWPT.

Minnesota does not currently monitor river otter populations. Minnesota Dept. of Natural Resources (MNDNR) collects harvest statistics from mandatory furbearer registration and CPUE through voluntary trapper postcards. The agency previously evaluated the use of aerial snow-track surveys, with promising results, but the fact that this species is doing well in the state has made specific monitoring a low priority. State contact: John Erb, MNDNR.

Montana does not currently monitor river otter populations. Montana Fish, Wildlife and Parks (MTFWP) monitors age, sex and locations for harvested animals. State contact: Bob Inman, MTFWP.

Nebraska monitors changes in river otter distribution with winter bridge surveys. Nebraska Game and Parks Commission (NGPC) collects information from observations, vehicle-kills and incidentally trapped animals and recently began conducting sign surveys. State contact: Sam Wilson, NGPC.

New Mexico does not currently conduct river otter population surveys. New Mexico Game and Fish Department (NMGFD) collects photos and observations submitted on standardized data sheets from the public and agency staff to track distribution and persistence in two river systems, the Rio Grande and San Juan. Volunteers conduct sign surveys and camera trapping at various sites. State contact: Jim Stuart, NMGFD.

North Dakota collects and classifies furbearer reports from staff, the general public, hunters and trappers, and USDA-Wildlife Services staff. North Dakota Game and Fish Department (NDGFD) staff necropsy rare furbearers. Necropsy products include measurements, reproductive tracts, stomachs, and DNA samples (NDGFD 2019). State contact: Stephanie Tucker, NDGFD.

Oklahoma Department of Wildlife Conservation (ODWC) does not presently actively survey river otters. Activities include an annual (March) roadside survey that may reveal a limited number of animals and completion of CITES tagging requirements during the fur harvesting season. More detailed studies are desired but have not yet materialized. State contact: Jerrod Davis, ODWC.

Saskatchewan does not currently monitor river otter populations. The Saskatchewan Ministry of Environment (SKME) maintains records of trapped animals as an information source, although these numbers vary with the pelt price and related trapper efforts. Provincial contact: Rick Espie, SKME.

Texas does not currently monitor river otter populations. State contact: Jonah Evans, Texas Parks and Wildlife Department.

Wyoming recently developed a river otter survey protocol document (WGFD 2019). The Wyoming Game and Fish Department (WGFD) has funded a graduate project that will begin in

2020 or 2021 to address questions about populations and their connectivity. The project will also generate a robust river otter monitoring plan. In the meantime, agency regional staff are conducting preliminary surveys to locate latrine sites and collect genetic samples. State contact: Nichole Bjornlie, WGFD.

Additional information from neighboring states

To help address specific concerns raised during public comment opportunities, SDGFP staff asked state wildlife agency furbearer contacts in neighboring states two additional questions:

1. Do you have a river otter trapping season?
2. Do you have a river otter population estimate?

Iowa, Minnesota, Montana, and North Dakota have river otter trapping seasons. The river otter is a protected species in Wyoming. This species is currently a state threatened species in Nebraska. A delisting proposal is planned for an upcoming Nebraska Game and Parks Commission meeting.

Nebraska, North Dakota, Montana and Wyoming do not have a population estimate. Minnesota has a population estimate that is based on population modeling, rather than a field-based population estimator. A doctoral student is currently working on a population estimate for Iowa. That process has not yet been completed.

Future surveys and monitoring in South Dakota

The river otter is a difficult species to monitor, making the development of a meaningful and feasible monitoring program a continuing challenge. As with any species, clear objectives must be paired with suitable survey and monitoring tools. A monitoring program must help ensure the species status remains at least stable to demonstrate that delisting remains justified or until harvest or other data provide needed information. Survey and monitoring tools must also be adapted to South Dakota’s climate and landscape. A combination of methods may be needed that is best suited to South Dakota, with consideration given to limited funding and staff availability and dynamic weather and habitat conditions.

The following have been identified as guiding principles and needs in the development of a meaningful, long-term river otter monitoring program:

- Learn from the experience of other wildlife management entities.
- Ensure that delisting distribution and reproduction criteria continue to be met.
- Monitor changes in distribution and presence/absence.
- Obtain and interpret information on harvested populations including sex ratio, age distribution, reproductive rates and areas where harvest occurred.
- Monitor distribution for at least 5 years following delisting.
- Review existing data collected in the state regarding habitat suitability and incorporate this information into evaluations of areas that may support river otter expansion.
- Continue to refine specific state needs to understand river otter distribution and occupancy, abundance, and population trends.

- Consider different monitoring efforts within the primary recovery area vs the remainder of the state.

Goals, Objectives and Strategies, 2020-2029

South Dakota will manage river otter populations with scientifically sound data and techniques to encourage occupation of suitable available habitats and to provide sustainable use and enjoyment within the social tolerance level for this species.

1. Monitor river otter
    a. Collect population information
        i. Collect and summarize river otter reports to improve knowledge of distribution and document expansion; refine reporting process as needed
        ii. Collect information on age structure, sex ratio, reproduction, morphology, diet, and body condition by conducting necropsies on all carcasses; analyze information and report findings
        iii. Determine need for use of stored tissue samples in contaminant and genetics analyses; implement analyses and report findings
    b. Develop and implement a long-term monitoring program that is feasible and scientifically sound
        i. Evaluate feasibility of field cameras as a survey technique
        ii. Determine need to develop species occupancy model and population estimate
        iii. Incorporate habitat features important to river otter occupancy into occupancy modeling
2. Allow for sustainable harvest
    a. Annually review and analyze existing data to inform harvest season structure recommendations
    b. Comply with necessary state and federal requirement for harvest implementation and reporting
    c. Coordinate with conservation partners, such as Native tribes and federal land management agencies
3. Provide information, assistance and outreach
    a. Promote public awareness of river otter, including management needs and challenges
    b. Provide information on ways to reduce incidental river otter catches
    c. Explore opportunities to evaluate public attitudes towards river otter
    d. Continue to promote and coordinate with conservation partners to improve wetlands and riparian habitat management
    e. Respond to requests for service where river otter presence may conflict with other uses of aquatic habitats
        i. Implement river otter capture and translocation protocol outlined in the 2012 river otter management plan
        ii. Review translocation protocol and update as needed
        iii. Evaluate frequency and extent of requests for service
4. Evaluate plan
    a. Lead biologist shall be responsible for a mid-term plan evaluation by 31 December 2025

        i. Identify objectives, strategies and actions that have not been completed, are not needed or are ineffective by meeting with key management planning staff, including regional terrestrial resource supervisors
        ii. Summarize evaluation and provide to Wildlife Program Administrator
    b. Lead biologist shall be responsible for a final plan evaluation by 31 December 2029
        i. Identify objectives, strategies and actions that have not been completed, are not needed or are ineffective by meeting with key management planning staff
        ii. Coordinate with Wildlife Program Administrator to determine the need for a new or updated plan.
    c. Provide updates to SDGFP Commission on plan implementation progress as required and requested

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Tables

Table 1. Frequency of river otter reports in South Dakota watersheds, 1979-2019.

Watershed	Frequency	%
Big Sioux	302	52.5%
Minnesota	112	19.5%
James	76	13.2%
Red	39	6.8%
White	25	4.3%
Cheyenne	14	2.4%
Oahe	4	0.7%
Little	1	0.2%
Niobrara	1	0.2%
unknown	1	0.2%
	575	100%

Table 2. Frequency of river otter reports in South Dakota counties, 1979-2019.

County	Frequency	%	County	Frequency	%
Moody	97	16.9%	Hutchinson	4	0.7%
Roberts	71	12.4%	Sanborn	4	0.7%
Grant	65	11.3%	Clark	3	0.5%
Minnehaha	63	11.0%	Custer	2	0.3%
Brookings	35	6.1%	Kingsbury	2	0.3%
Brown	27	4.7%	Spink	2	0.3%
Lake	24	4.2%	Yankton	2	0.3%
Lincoln	24	4.2%	Aurora	1	0.2%
Marshall	24	4.2%	Brule	1	0.2%
Union	15	2.6%	Buffalo	1	0.2%
Codington	10	1.7%	Fall River	1	0.2%
Deuel	10	1.7%	Haakon	1	0.2%
Day	9	1.6%	Hanson	1	0.2%
Hamlin	9	1.6%	Harding	1	0.2%
Beadle	8	1.4%	Jerauld	1	0.2%
Hughes	7	1.2%	Jones	1	0.2%
Bon Homme	6	1.0%	Lawrence	1	0.2%
Lyman	6	1.0%	Meade	1	0.2%
McCook	6	1.0%	Miner	1	0.2%
Bennett	5	0.9%	Sully	1	0.2%
Pennington	5	0.9%	Todd	1	0.2%
Stanley	5	0.9%	Tripp	1	0.2%
Butte	4	0.7%	Turner	1	0.2%
Clay	4	0.7%	unknown	1	0.2%
				575	100.0%

Table 3. Frequency of reported incidentally trapped river otter in South Dakota watersheds, 1979-2019.

Watershed	Frequency	%
Big Sioux	127	58.8%
Minnesota	58	26.9%
Red	15	6.9%
James	12	5.6%
White	3	1.4%
unknown	1	0.5%
	216	

Table 4. Frequency of reported incidentally trapped river otter in South Dakota counties, 1979-2019.

County	Frequency	%
Moody	54	25.0%
Roberts	32	14.8%
Grant	31	14.4%
Brookings	19	8.8%
Minnehaha	19	8.8%
Lincoln	7	3.2%
Codington	7	3.2%
Deuel	7	3.2%
Marshall	6	2.8%
Union	6	2.8%
Lake	5	2.3%
Day	3	1.4%
Brown	3	1.4%
Hamlin	3	1.4%
Clay	2	0.9%
Lyman	2	0.9%
Clark	2	0.9%
Bon Homme	2	0.9%
Hutchinson	2	0.9%
unknown	1	0.5%
Haakon	1	0.5%
McCook	1	0.5%
Miner	1	0.5%
	216	100%

Table 5. Species targeted when river otter were incidentally captured in South Dakota, 1979-2019.

Species	Frequency	%
beaver	116	53.7%
unknown	70	32.4%
raccoon	19	8.8%
fish	5	2.3%
mink	3	1.4%
other	3	1.4%
	216	100%

Table 6. Trap types used when river otter were incidentally captured in South Dakota, 1979-2019.

Trap Type	Frequency	%
kill trap	106	49.1%
unknown	39	18.1%
foot-hold	35	16.2%
snare	22	10.2%
live trap	9	4.2%
other	5	2.3%
	216	

Table 7. Sources of mortality for 229 river otters in South Dakota, 1979-2019.

Cause of Death	Frequency	%
Incidentally trapped	159	69.4%
Vehicle strike	46	20.1%
other	14	6.1%
euthanized	10	4.4%
	229	100%

Table 8. Frequency of necropsied river otter in South Dakota watersheds, 1979-2019.

Watershed	Frequency	%
Big Sioux	116	58.0%
Minnesota	51	25.5%
Red	16	8.0%
James	11	5.5%
unknown	4	2.0%
White	2	1.0%
	200	

Table 9. Frequency of necropsied river otter in South Dakota counties, 1979-2019.

County	Frequency	%
Moody	43	21.5%
Roberts	31	15.5%
Grant	29	14.5%
Minnehaha	20	10.0%
Brookings	15	7.5%
Lincoln	10	5.0%
Lake	9	4.5%
Deuel	6	3.0%
Codington	5	2.5%
Union	5	2.5%
Marshall	4	2.0%
unknown	4	2.0%
Brown	3	1.5%
Day	3	1.5%
Hutchinson	3	1.5%
Clark	2	1.0%
Clay	2	1.0%
Hamlin	2	1.0%
Bennett	1	0.5%
Bon Homme	1	0.5%
Lyman	1	0.5%
Miner	1	0.5%
	200	

Table 10. Age structure of 179 necropsied river otter from South Dakota, 2003-2019.*

	Male		**Female**		**Total**	
Age	Freq	%	Freq	%	Freq	%
0	24	21.6%	10	14.9%	34	19%
1	39	35.1%	29	43.3%	68	38%
2	22	19.8%	12	17.9%	34	19%
3	5	4.5%	7	10.4%	12	7%
4	5	4.5%	3	4.5%	8	5%
5	5	4.5%	2	3.0%	8	4%
6	2	1.8%	2	3.0%	4	2%
7	4	3.6%	1	1.5%	5	3%
8	1	0.9%	1	1.5%	2	1%
9	1	0.9%	0	0.0%	1	1%
10	1	0.9%	0	0.0%	1	1%
11	1	0.9%	0	0.0%	1	1%
12	1	0.9%	0	0.0%	1	1%
	111		67		179	

*Sex is unknown for one 5-year old otter.

Table 11. Female river otter with corpora lutea (CL) from South Dakota, 2003-2019.

	Female Otter	
Age	# w/ CL	# examined
0	2	5
1	13	19
2	6	7
3	4	5
4	2	2
5	2	2
6	1	1
7	1	1
8	1	1
unkn	7	8
	39	51

Table 12. Contents of 192 river otter stomachs from South Dakota, 2003-2019.

Contents	**Frequency**	**%**
Fish	92	44%
Empty	56	27%
Frog	20	10%
Other*	15	7%
Crayfish	9	4%
Vegetation	8	4%
Black Liquid	5	2%
Bird	3	1%
	208	

*Stomach damaged or contents unidentifiable.

Figures

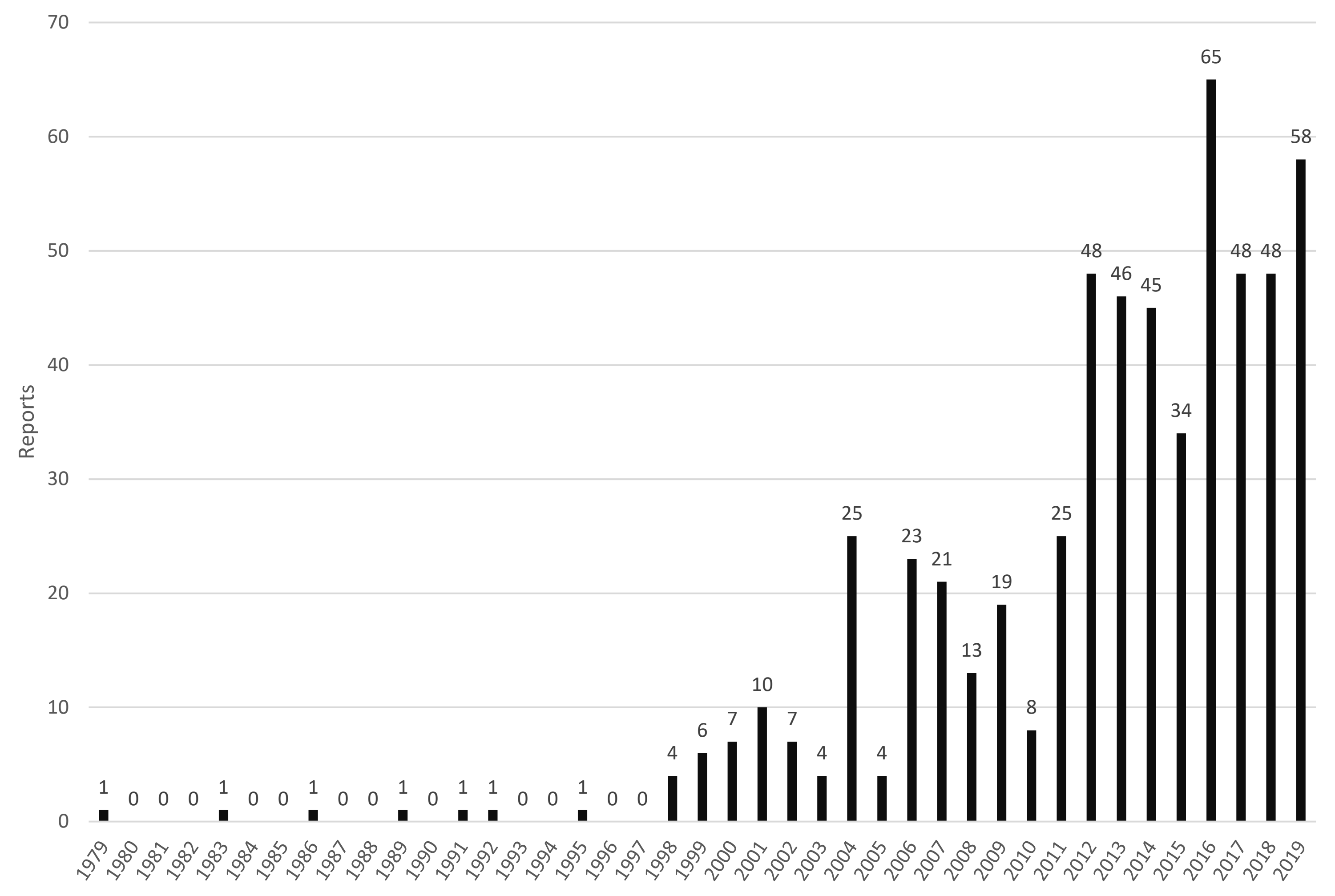

Figure 1. Annual frequency of 575 river otter reports in South Dakota, 1979 - 2019.