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Space-use and habitat associations of Black-backed Woodpeckers (*Picoides arcticus*) occupying recently disturbed forests in the Black Hills, South Dakota

Christopher T. Rota [a,*], Mark A. Rumble [b], Joshua J. Millspaugh [a], Chadwick P. Lehman [c], Dylan C. Kesler [a]

[a] University of Missouri, Department of Fisheries and Wildlife Sciences, 302 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA
[b] Forest and Grassland Research Laboratory, U.S. Forest Service Rocky Mountain Research Station, 8221 South Highway 16, Rapid City, SD 57702, USA
[c] Custer State Park, 13329 US Highway 16A, Custer, SD 57730, USA

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ABSTRACT

Black-backed Woodpeckers (*Picoides arcticus*) are a disturbance-dependent species that occupy recently burned forest and mountain pine beetle (MPB) infestations. Forest management practices that reduce the amount of disturbed forest may lead to habitat loss for Black-backed Woodpeckers, which have recently been petitioned for listing under the Endangered Species Act. We studied home range size and resource selection of Black-backed Woodpeckers occupying habitat created by summer wildfire, fall prescribed fire, and MPB infestations in the Black Hills, South Dakota. We studied home range size and resource selection by attaching radio-transmitters to adult Black-backed Woodpeckers. We estimated home range size using fixed kernel density techniques ($n = 28$ in habitat created by summer wildfire, $n = 19$ in habitat created by fall prescribed fire, and $n = 27$ in MPB infestations). We evaluated resource selection with a random-effects discrete choice model in a Bayesian framework ($n = 5$ in habitat created by summer wildfire, $n = 16$ in habitat created by fall prescribed fire, and $n = 8$ in habitat created by MPB infestations). Home range size was smallest in 1–2 year post summer wildfire habitat (mean home range size = 79 ha) and 2-year post fall prescribed fire habitat (mean home range size = 143 ha). Home range size was intermediate in MPB infestations (mean home range size = 307 ha) and was greatest in 3–4 year post fire habitat (mean summer wildfire home range size = 430 hectares, mean fall prescribed fire home range size = 460 ha). The relative probability that a Black-backed Woodpecker used a tree increased with increasing diameter at breast height (DBH) and basal area and was greatest on disturbance-killed trees. These results suggest 1–2 year post summer wildfire habitat may have the greatest relative value to Black-backed Woodpeckers and that MPB infestations may be more important as post-fire habitats age. We recommend retaining patches of 1–2 year post summer wildfire habitat that are at least 200 ha by exempting portions of recently burned forest from salvage logging. This recommendation can be accomplished by exempting salvage logging in summer wildfires <200 ha and retaining at least 50% of summer wildfires >400 ha. Ideally, recently burned forest patches should be composed of $\geqslant 27$ m^2 basal area/ha of trees that burned at moderate or high severity, with at least 40% of the basal area composed of trees $\geqslant 27$ cm DBH.

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1. Introduction

Black-backed Woodpeckers (*Picoides arcticus*) are a disturbance dependent species that rely on recently killed forest habitat. Throughout their range, Black-backed Woodpeckers are associated with habitat created by wildfire (Bock and Lynch, 1970; Hobson and Schieck, 1999; Hoyt and Hannon, 2002; Hutto, 1995, 2008; Murphy and Lehnhausen, 1998; Nappi and Drapeau, 2009; Nappi et al., 2003). Additionally, Black-backed Woodpeckers are attracted to habitat created by prescribed fire (Russell et al., 2009). Despite this burn-centric association, mountain pine beetle (*Dendroctonus ponderosae*, MPB) infestations are thought to play an important role in creating habitat for Black-backed Woodpeckers, particularly in isolated populations occurring in the Black Hills (Bonnot et al., 2008, 2009) and the Cascade Mountains (Goggans et al., 1989). Finally, Black-backed Woodpeckers also occur in undisturbed forest (Mohren, 2002; Tremblay et al., 2009), though often only when recently burned forest is not available (Hoyt and Hannon, 2002). Even in undisturbed forest, Black-backed Woodpeckers are often associated with small patches of recently killed forest (Hutto, 1995; S. Mohren, *personal communication*).

* Corresponding author. Tel.: +1 (573) 239 6975.
E-mail address: rotact@missouri.edu (C.T. Rota).

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Disturbances such as wildfire and MPB infestations occur naturally in most western North American forests, though the frequency and severity of such disturbances may be increasing (Raffa et al., 2008). However, these naturally occurring disturbances reduce the quality and quantity of timber and have historically been considered undesirable. As a result, much effort has been put into preventing or mitigating the effects of these disturbances through fire suppression, post-fire salvage logging, or sanitation logging in insect infestations (Nappi et al., 2004). Such efforts may result in habitat loss for Black-backed Woodpeckers, which is now considered a species of management concern throughout its range. In particular, Black-backed Woodpeckers are considered a sensitive species by Region 2 of the U.S. Forest Service, a Species of Greatest Conservation Concern by the State of South Dakota (SDGFP, 2006), and the Black Hills population has recently been petitioned for listing as Threatened or Endangered under the Endangered Species Act (Hanson et al., 2012).

Effective conservation strategies require detailed knowledge of resource selection patterns of this sensitive species. Many studies have evaluated resource selection in Black-backed Woodpeckers, particularly in response to burn severity, pre-burn forest conditions, and snag density. Black-backed Woodpeckers select foraging habitat (Hanson and North, 2008; Murphy and Lehnhausen, 1998) and occur with greater probability (Hutto, 2008) and abundance (Koivula and Schmiegelow, 2007) in forests that burned at high severity. Black-backed Woodpeckers also respond to pre-disturbance forest conditions and disproportionally forage on the largest diameter trees available (Dudley et al., 2012; Nappi and Drapeau, 2011; Nappi et al., 2003). Finally, in unburned forest, Black-backed Woodpeckers are most likely to occur (Goggans et al., 1989) and are more abundant (Mohren, 2002; Setterington et al., 2000) in areas with relatively high snag densities.

Most of this research has focused on understanding patterns of Black-backed Woodpecker resource selection in recently burned forest. Consequently, little is known about resource selection patterns in MPB infestations or in habitat created by prescribed fire. For example, although Bonnot et al. (2009) determined that nest site selection was correlated with food resources in MPB infestations, the extent to which foraging woodpeckers select recently infested trees relative to older beetle-killed trees remains unknown. Such knowledge may guide development of silvicultural treatments that both limit the economic impact of natural disturbances while simultaneously conserving Black-backed Woodpecker habitat.

An understanding of which resources are selected by Black-backed Woodpeckers is complemented by an understanding of the spatial requirements of these woodpeckers. Black-backed Woodpeckers are a highly mobile species with potentially large home ranges, making estimation of home range size challenging. Despite these challenges, Dudley and Saab (2007) report home range size for 4 woodpeckers in 6–8 year post-fire habitat and Goggans et al. (1989) report home range size for 3 woodpeckers in habitat created by MPB infestations. However, home range size is likely to vary across habitats and through time, particularly as the time since fire increases. Knowledge of such variation will enable managers to include spatial components into silvicultural prescriptions.

For this study we evaluated resource selection and home range size of Black-backed Woodpeckers occupying habitat created by wildfire, prescribed fire, and MPB infestations in the Black Hills, South Dakota. We evaluated resource selection with a random-effects discrete choice model that accounted for repeated observations collected from individual woodpeckers, allowing us to evaluate patterns of resource selection at the population level. We also estimated home range size of Black-backed Woodpeckers and evaluated how home range size varied among habitats and as burned forests age.

2. Materials and methods

2.1. Study sites

This study was divided among numerous study sites in the Black Hills, South Dakota representing habitat created by wildfire, prescribed fire, and MPB infestations (Table 1). All wildfire sites burned in June or July (hereafter we use the term wildfire and summer wildfire synonymously) and all prescribed fire sites were treated during September or October (hereafter we use the term prescribed fire and fall prescribed fire synonymously). All study sites were composed primarily of monotypic ponderosa pine forest (*Pinus ponderosa*) forest, with quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*) occurring less frequently (Hoffman and Alexander, 1987).

2.2. Capture and radio-telemetry

We collected Black-backed Woodpecker home range and resource selection data by fitting VHF radio-transmitters to adult birds. We initially targeted Black-backed Woodpeckers for capture by playing audio recordings of territorial calls at potential study sites. Once found, we captured woodpeckers with mist nets, hoop nets, and net guns. Mist nets were used with limited success only during the 2009 and 2010 breeding seasons and were quickly abandoned in favor of the more efficient hoop net and net gun capture approach (Lehman et al., 2011). Hoop nets were an efficient capture method only during the breeding season when woodpeckers were actively attending cavities. Alternatively, the net gun allowed capture away from nest cavities and outside the breeding season. Once captured, we weighed all birds and attached a small (3.0–3.3 g) transmitter (Rappole and Tipton, 1991). Black-backed Woodpeckers captured during the course of this study weighed an average of 75 g, so transmitters weighed <5% of an average adult bird's mass (Fair et al., 2010). We fit all birds with a unique combination of colored leg bands and a uniquely numbered U.S. Fish and Wildlife Service aluminum leg band. As VHF radio-transmitter batteries died, we attempted to recapture previously marked individuals and replace transmitters. We supplemented recaptured birds with unmarked birds that were captured opportunistically.

We located woodpeckers at least 2 times weekly to ensure $\geqslant$30 telemetry locations necessary to estimate home range size before transmitters failed (Seaman et al., 1999). All telemetry locations were spaced $\geqslant$4 h apart. We assumed spacing telemetry locations $\geqslant$4 h apart was adequate to ensure independence between successive locations because woodpeckers could (and did) traverse even the largest home range during this time interval. We located woodpeckers via homing and all trees physically occupied by woodpeckers (hereafter 'used' trees) were visually confirmed. During the nesting period, we excluded all telemetry observations made at the nest cavity to address resource selection patterns beyond the nest cavity and to ensure home range size estimates were not biased because of repeated observations at the nest cavity. Whenever woodpeckers were located, we recorded spatial coordinates (Universal Transverse Mercator Zone 13N, NAD 1983) using a hand-held GPS unit and flagged the tree for future vegetation sampling.

2.3. Estimating home range size

We collected home range data on Black-backed Woodpeckers between April 2008 and August 2011, and again between May 2012 and August 2012. We only included woodpeckers in the home range analysis if we obtained $\geqslant$30 telemetry locations (Seaman et al., 1999) during the 12-month period from April 1

Table 1
Study sites used to evaluate home range size and resource selection of Black-backed Woodpeckers in the Black Hills, South Dakota, USA.

Site	Habitat	Coordinates	Size (Ha)[a]	Month/year disturbed[b]	Years included in study
Box elder	Wildfire	44°9′N, 103°24′W	129	July 2007	2008, 2009
4-Mile	Wildfire	43°41′N, 103°26′W	955	June 2007	2008–2011
Bullock	Rx Fire	44°0′N, 103°30′W	486	September 2008	2010–2012
Bitter	Rx Fire	43°58′N, 103°26′W	304	October 2010	2012
Headquarters west	Rx Fire	43°34′N, 103°30′W	255	September 2009	2011
American elk	Rx Fire	43°61′N, 103°49′W	1376	October 2010	2012
Norbeck	MPB	43°50′N, 103°30′W	>213[c]	1998	2008
Bear mountain	MPB	43°51′N, 103°45′W	>48[c]	Before 1995	2008–2011
East slate Creek	MPB	43°58′N, 103°44′W	>1303[d]	Before 1995	2008–2011
Deerfield Lake	MPB	44°00′N, 103°49′W	>169[c]	Before 1995	2008
Medicine Mountain	MPB	43°52′N, 103°42′W	>1748[d]	Before 1995	2009–2011

[a] Size of MPB infestations calculated from FHP Aerial Detection Surveys, available at <http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/?cid=fsbdev3_041629> (accessed February 13, 2013). This is an estimate of the minimum total area impacted by MPBs in each study site in a given year.
[b] The first year MPB infestations were detected in FHP Aerial Detection Surveys. Note there is no aerial detection data prior to 1995.
[c] Calculated from 2008 FHP Aerial Detection Survey.
[d] Calculated from 2010 FHP Aerial Detection Survey.

through March 31. We classified the number of years post-fire based on this 12 month period, with the 1st year post-fire occurring the 1st April following a burn. For example, we considered telemetry locations gathered in the 4-Mile study site between April 1, 2008 and March 31, 2009 as 1-year post-fire (4-Mile burned in June 2007). We began the 12-month period on April 1 because this is the approximate date woodpeckers begin excavating cavities (recognizing that Black-backed Woodpeckers make territorial settlement decisions year-round, C.T. Rota, *personal observation*). We clumped winter and summer telemetry locations during the same 12-month period together because there was no clear difference in space use between seasons and because of small sample sizes during winter months ($n = 3$ wildfire winter home ranges and $n = 3$ prescribed fire winter home ranges). We did not attempt to classify the age of MPB infestations because infestations were not one discrete disturbance and woodpeckers often used infestations of several different ages.

We estimated home-range size using kernel density techniques (Worton, 1989). We estimated home ranges using the 'ks' package in Program R (R Core Team, 2012), which assumes a bivariate normal density fixed kernel. We used the 'plug-in' method for calculating the bandwidth parameter (Millspaugh et al., 2006). Home range size estimates were based on 99% home range contours.

2.4. Vegetation measurements

We collected vegetation data from trees that were used by and considered available to individual Black-backed Woodpeckers. We defined the area available to each woodpecker based on the 99% home range contour. We paired each used tree with a randomly available tree, which was selected by generating uniformly distributed random points within 99% home range boundaries and then selecting the tree closest to the randomly generated point. We observed Woodpeckers using saplings, so we assumed any sapling or tree >1 cm DBH was available. At all used and available trees, we recorded DBH, whether the tree was alive, and categorized trees based on burn severity or age of MPB infestations. We classified burned trees as low severity (scorching restricted to below breast height), moderate severity (scorching above breast height but some canopy left unburned), high severity (canopy completely scorched), or unburned. We classified MPB infested trees as 'green hits' (infestations with green or yellow needles that were <1 year old), 'red hits' (infestations with red needles that were 1–2 years old) or 'gray hits' (beetle-killed trees that have lost all of their needles, generally >2 years old). We classified trees that were both burned and infested with MPBs as 'Burn/MPB' (trees were scorched and pitch tubes were evident). In addition to measuring characteristics of used and available trees, we also measured characteristics of the surrounding forest. We characterized vegetation immediately surrounding the used or available tree using a 10 basal area factor prism (variable-radius plots) to identify trees to include in measurements. These data were used to calculate basal area and proportion of dead trees. We collected vegetation data from home ranges used by woodpeckers from May 2010 to August 2011 and from May 2012 to August 2012. Consequently, we collected vegetation data in 3–4 year post-wildfire and 2–4 year post-prescribed fire habitat.

2.5. Modeling resource selection

We used a random-effects discrete choice model within a Bayesian framework (Cooper and Millspaugh, 1999; Thomas et al., 2006) to model the probability a woodpecker would select the used or available tree if given a choice between the 2 trees. Choice sets were thus defined as 2 trees within the home range woodpecker j; the used tree and a paired randomly available tree. We modeled the 'utility' of the used tree in the ith choice set of woodpecker j as a linear function of vegetation characteristics and individual-level regression coefficients:

$$U_{ij}^{used} = \beta_{1j}DBH_{ij}^{used} + \beta_{2j}DEAD_{ij}^{used} + \beta_{3j}BA_{ij}^{used} + \beta_{4j}LS_{ij}^{used} + \beta_{5j}MH_{ij}^{used} + \beta_{6j}GH_{ij}^{used} + \beta_{7j}RG_{ij}^{used} + \beta_{8j}BMPB_{ij}^{used} + \beta_{9j}PDEAD_{ij}^{used}$$

where DBH_{ij}^{used} is the DBH of the used tree, $DEAD_{ij}^{used}$ is a dummy variable = 1 if the used tree is dead, 0 otherwise, BA_{ij}^{used} is the basal area surrounding the used tree, LS_{ij}^{used}, MH_{ij}^{used}, GH_{ij}^{used}, RG_{ij}^{used}, $BMPB_{ij}^{used}$ are dummy variables = 1 if the used tree is categorized as low severity burn, moderate or high severity burn, green hit, red hit or gray hit, or Burn/MPB, respectively, 0 otherwise, $PDEAD_{ij}^{used}$ is the proportion of dead trees immediately surrounding the used tree, and $\beta_{1j}, \ldots, \beta_{9j}$ are the individual-level regression coefficients corresponding to woodpecker j ($j \in (1, 2, \ldots, W)$, where W is the total number of woodpeckers included in the model. We modeled the utility of each available tree (U_{ij}^{avail}) in an identical manner, substituting vegetation variables at used trees for vegetation variables at available trees. Finally, we used the utility functions defined above to model the probability of selecting the used or available tree when given a choice between the two trees, which we hereafter call relative probability. We calculated the relative probability of selecting the used tree as:

$$\psi_{ij}^{used} = \frac{\exp(U_{ij}^{used})}{\exp(U_{ij}^{used}) + \exp(U_{ij}^{avail})}.$$

Since choice-sets contained 2 trees, the relative probability of selecting the available tree is $(1 - \psi_{ij}^{used})$. Note that there is no intercept parameter in the utility function because it would cancel when calculating relative probabilities.

We modeled population-level resource selection by assuming individual-level regression coefficients for woodpecker j arise from normal population-level distributions (Thomas et al., 2006). For example, we assume

$$(\beta_{11}, \ldots \beta_{1w}) \sim N(\mu_1, \sigma_1^2).$$

Hereafter, we refer to the set of parameters governing each population-level distribution ($[\mu_1, \sigma_1^2], \ldots, [\mu_9, \sigma_9^2]$) as population-level parameters. Note that individual-level regression coefficients describe how a unit change in the value of a corresponding vegetation variable changes the 'utility' of a tree for woodpecker j, with greater utility leading to a higher relative probability of use, while population-level parameters describe the mean and variation of individual-level regression coefficients across all j woodpeckers. Hereafter, we refer to each population-level distribution by the name of the associated vegetation covariate. For example, we refer to the population-level distribution that describes the mean and variation of individual-level regression coefficients associated with tree DBH (β_1) simply as the *DBH* population-level distribution. We report the functional relation between vegetation variables and the relative probability a tree would be used with population-level mean parameters.

We selected vague prior distributions for all model parameters. We assumed normal, $N(\mu = 0, \sigma^2 = 100)$ prior distributions on all population mean hyper-parameters $\mu_1, \ldots, \mu_9$ and we assumed *Uniform*(0, 10) prior distributions of all population standard deviation hyper-parameters $\sigma_1, \ldots, \sigma_9$. We assume uniform prior distributions for standard deviation hyper-parameters because the inverse gamma distribution, which is often used as a prior distribution for variance hyper-parameters, can have a strong influence on posterior distributions (Gelman, 2006).

We fit discrete choice models in WinBUGS (Gilks et al., 1994) via the R2WinBUGS interface (Sturtz et al., 2005). We simulated posterior distributions of each model parameter from 3 Markov chains. We ran each chain for 51,000 iterations, discarding the first 1000 as burn-in. There was evidence of correlation between successive draws from some Markov chains, so we kept every 50th iteration after the initial burn-in period. Estimated posterior distributions for each model parameter were thus composed of 3000 random draws. The Brooks–Gelman–Rubin convergence diagnostic (Brooks and Gelman, 1998) indicated adequate convergence for all hyperparameters ($\hat{R} = 1$).

We assessed the goodness of fit of the discrete choice model using Estrella's (1998) R^2. We calculated Estrella's R^2 as:

$$1 - \left(\frac{\log(L)}{\log(L_0)}\right)^{-\left(\frac{2}{N}\right)\log(L_0)}$$

where $\log(L)$ is the log-likelihood of the fully parameterized model, $\log(L_0)$ is the likelihood of a null model with all coefficients = 0, and N is the total number of choice sets ($N = 1104$). Since there were only two choices per choice-set, the null model assumes each tree is selected with 50% probability. Values of Estrella's $R^2 = 0$ indicate the discrete choice model predicts use at random, while values of $R^2 = 1$ indicates perfect fit.

3. Results

3.1. Home range size

We collected ⩾30 telemetry locations over at least 1 12-month period for 70 individual Black-backed Woodpeckers. We collected ⩾30 telemetry locations over 2 12-month periods for 4 individual woodpeckers, so we analyzed a total of 74 different home ranges. Estimated home range size was highly variable among woodpeckers (minimum estimated home range size = 20 ha, maximum estimated home range size = 1248 ha, Table 2). Average estimated home range size was the smallest in 1-year post-wildfire habitat and was slightly larger in 2-year post-wildfire and post-prescribed fire habitat. We rarely observed Black-backed Woodpeckers in 1-year post prescribed fire habitat, so we were unable to estimate home range size in this disturbance category. Home range size was largest in ⩾3-year post-fire habitats (both wildfire and prescribed fire). Home range size in MPB infestations were intermediate between 1–2 year post-fire habitats and ⩾3 year post-fire habitats.

3.2. Resource selection

We modeled resource selection from 1104 pairs of used and available trees (hereafter called resource selection data) collected from 29 Black-backed Woodpeckers: 5 woodpeckers were in habitat created by wildfire, 8 were in habitat created by MPB infestations, and 16 were in habitat created by prescribed fire. On average, resource selection data were collected over a period of 118 days for a single bird (range = 41–434 days). Because we often obtained multiple locations from a bird in a single day, 42% of telemetry locations used to model resource selection were 1 of 2 locations collected from a single bird in 1 day and 3% of telemetry locations used to model resource selection were 1 of 3 locations collected from a single bird in 1 day. The remaining 55% of all telemetry locations used to model resource selection represented the only location from a single bird in 1 day. We collected resource selection data in 3–4 year post-wildfire habitat and 2–4 year post-prescribed fire habitat. The mean posterior distribution of Estrella's $R^2 = 0.68$ (95% credible interval = [0.66, 0.70]). This mean value of 0.68 indicates performance that is better than random, so we assume an adequate goodness-of-fit for the discrete choice model.

The relative probability a Black-backed Woodpecker used a tree was influenced by characteristics of both the tree and the surrounding forest. The relative probability of using a tree was positively associated with DBH ($\bar{\mu}_1 = 0.81$, 95% CI = [0.61, 1.03]; Figs. 1, 2a) and was greater for dead trees than for live trees ($\bar{\mu}_2 = 1.78$, 95% CI = [1.16, 2.53]; Fig. 2b). Within burned forests (both wildfire and prescribed fire), Black-backed Woodpeckers exhibited the greatest relative probability of using trees that were both burned and infested with MPBs ($\bar{\mu}_8 = 2.46$, 95% CI = [1.02, 4.18]), followed by intermediate relative probabilities of using

Table 2
Mean and range of estimated home range size (ha) of Black-backed Woodpeckers occupying habitat created by wildfire, prescribed fire, and mountain pine beetle (MPB) infestations in the Black Hills, South Dakota, USA. Home ranges in wildfire and prescribed fire are further broken down by number of years post-fire. Home range size estimates represent the area contained within 99% contours, estimated using fixed kernel techniques.

Habitat	Mean	Min	Max	n[a]
MPB	307	67	790	27
Prescribed fire				
2-year	143	44	339	13
3-year	519	150	1248	5
4-year	164	–	–	1
Wildfire				
1-year	70	30	187	11
2-year	88	20	226	10
3-year	439	37	825	5
4-year	408	399	416	2

[a] The number of home ranges collected in each category.

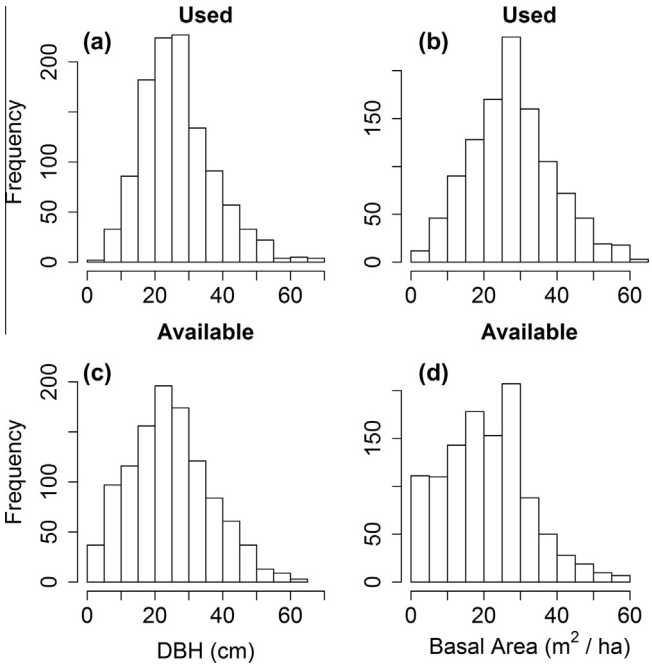

Fig. 1. Histograms showing the distribution of diameter at breast height(a and c) and basal area(b and d) at trees used and available to Black-backed Woodpeckers in the Black Hills, South Dakota.

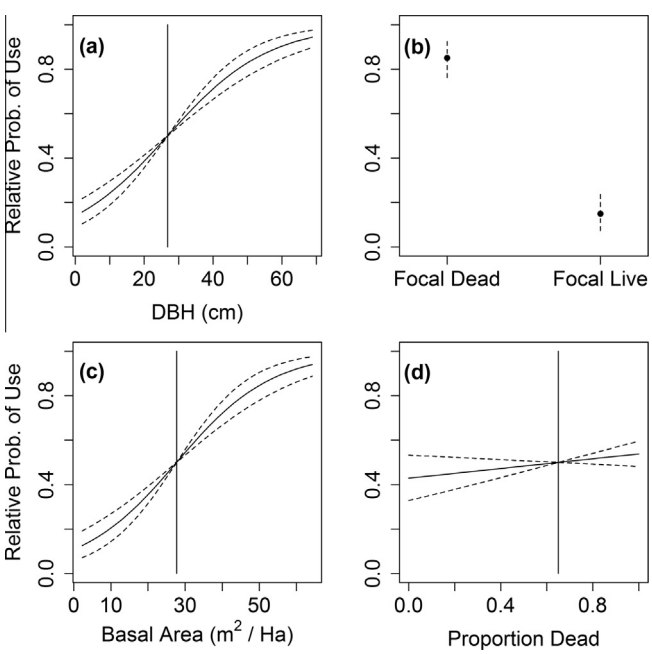

Fig. 2. Estimated relative probability (±95% credible intervals) of a Black-backed Woodpecker using a tree as a function of (a) tree diameter at breast height (DBH), (b) whether a tree is alive or dead, (c) basal area surrounding tree, and (d) proportion of dead trees surrounding the tree. All figures assume a woodpecker is faced with two choice sets. For continuous predictors (DBH, basal area, proportion dead, panels a, c, and d, respectively), one choice set is always represented by the value of the vertical line and the other choice set is represented as the value of the *x*-axis. Figure (b) assumes a woodpecker is faced with a choice of a dead or live tree. There is no variation around the vertical lines because, under the assumptions of the discrete choice model, Woodpeckers will always choose 1 of 2 identical trees with 50% probability.

trees that burned at moderate/high severity ($\bar{\mu}_5 = 2.08$, 95% CI = [1.43, 2.78]) and trees that burned at low severity ($\bar{\mu}_4 = 1.45$, 95% CI = [0.81, 2.10]; Fig. 3a). The relative probability of using an unburned tree was almost 0 when any category of burned tree was available. Within MPB infestations, Black-backed Woodpeckers exhibited the greatest relative probability of using green hit trees ($\bar{\mu}_6 = 3.66$, 95% CI = [1.80, 6.90]), followed by intermediate relative probabilities of using trees that were both burned and infested with MPB infestations and trees that were infested with MPBs >1 year ($\bar{\mu}_7 = 2.34$, 95% CI = [1.41, 3.46]; Fig. 3b). As with woodpeckers occupying burned forests, the relative probability of using an undisturbed tree was almost 0 when any category of MPB infested tree was available.

Black-backed Woodpeckers also exhibited selection at the level of the forest immediately surrounding a tree. The relative probability of using a tree increased as the basal area of the surrounding forest increased ($\bar{\mu}_3 = 0.89$, 95% CI = [0.65, 1.16]; Figs. 1, 2c). The relative probability of using a tree also increased slightly as the proportion of dead trees in the surrounding stand increased ($\bar{\mu}_9 = 0.44$, 95% CI = [−0.20, 1.10]; Fig. 2d), though 95% credible intervals of the *PDEAD* population-level distribution mean overlapped 0.

4. Discussion

Our evaluation of Black-backed Woodpecker resource selection revealed consistent selection for several vegetation characteristics within the home range of individual birds, regardless of the disturbance type occupied by individual woodpeckers. Across all disturbance types, Black-backed Woodpeckers were most likely to use larger, disturbance-killed trees in relatively high basal area stands. Further, the clear influence of several vegetation characteristics on relative probabilities of use indicates that Black-backed Woodpeckers use of trees within a home range is not driven by a few specific resources, but is instead driven by a suite of vegetation characteristics.

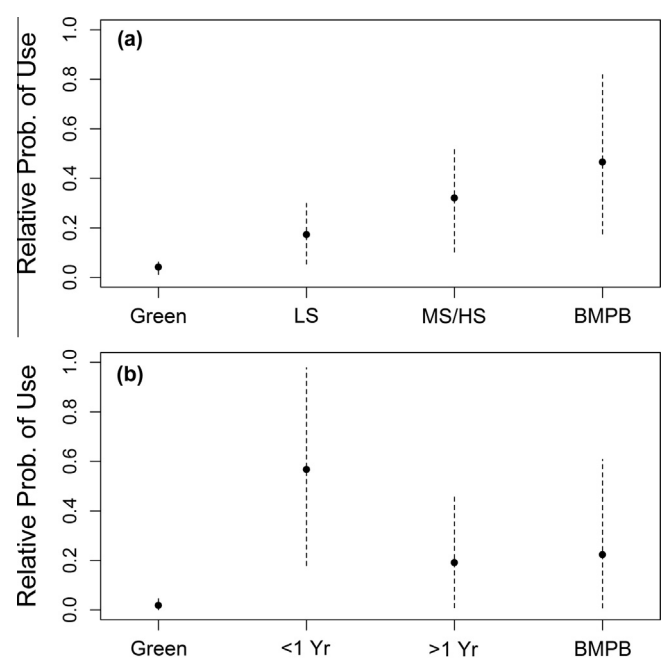

Fig. 3. Estimated relative probability of a Black-backed Woodpecker using a tree as a function of disturbance categories typical to (a) burned forest and (b) mountain pine beetle (MPB) infestations. Green refers to trees not disturbed by either fire or MPBs, LS refers to trees burned at low severity, MS/HS refers to trees burned at moderate or high severity, <1 year refers to trees infested with MPBs <1 year, >1 year refers to trees infested with MPBs for ⩾1 year, and BMPB refers to trees that are both burned and infested with mountain pine beetles. In both disturbance types, Black-backed Woodpeckers are assumed to be faced with a choice set of 4 trees, one of each disturbance category listed on the *x*-axis.

Variation in population-level responses to vegetation characteristics and home range size are likely driven by underlying variation in food resources. At the most basic level, the consistently high relative probability of Black-backed Woodpeckers using disturbance-killed trees of any category probably reflects the food resources harbored in these trees. Black-backed Woodpeckers also exhibited consistently high relative probability of using the largest diameter trees available, which is likely a result of higher beetle abundance in large diameter trees (Nappi et al., 2003; Saint-Germain et al., 2004). Finally, Black-backed Woodpeckers exhibited consistently high probability of using trees situated in relatively high basal area stands. While this may reflect conditions that lead to high tree mortality following fire or MPB infestations (Negrón et al., 2008), high basal area stands may also contain high densities of beetle-rich trees. Variation in home range size may also reflect variation in food resources between disturbance types. Wood-boring beetles of the families Cerambycidae and Buprestidae are strongly attracted to fire-killed trees (Costello et al., 2011; Saint-Germain et al., 2004) and the larvae of these beetles are the primary prey items of Black-backed Woodpeckers occupying recently burned forest (Murphy and Lehnhausen, 1998). Wood-boring beetle larvae are much larger than MPB larvae and likely provide a greater food resource. This potentially greater food resource in recently burned forest may explain why home range sizes were consistently smaller in 1–2 year post-wildfire habitat relative to home ranges in habitat created by MPB infestations and ⩾3 year post-fire forest.

Black-backed Woodpeckers only consistently occupied habitat created by wildfires the first 2 years following disturbance. We rarely observed Black-backed Woodpeckers occupying 1-year post prescribed fire habitat and were unable to estimate home range size in this disturbance category. The rare occurrence of Black-backed Woodpeckers in 1-year post prescribed fire habitat may occur because of a difference in timing of disturbance, since all of our wildfire study sites burned during June or July and all of our prescribed fire study sites were treated in September of October. Indeed, Vierling (2004) failed to detect Black-backed Woodpecker nests the first year following the Jasper wildfire in the Black Hills, which burned in late August 2000. This suggests that the timing of fire, rather than whether a fire is wild or prescribed, may play the biggest role in determining whether Black-backed Woodpeckers occupy burned forest the first post-fire breeding season.

Differences between the timing of wildfire and prescribed fire in our study may have affected the ability of wood-boring beetles to colonize post-fire forests. Many species of wood-boring beetles are capable of detecting compounds in smoke (Schütz et al., 1999), but may be unable to rapidly colonize burns if they occur in the fall months when beetles are inactive. This is consistent with recent surveys (M.A.R., *unpublished data*) indicating abundant wood-boring beetle activity the first autumn following a summer wildfire, but little wood-boring beetle activity the first autumn following a fall wildfire. This is also consistent with Rota (2013), who found Black-backed Woodpeckers successfully captured nearly twice as many wood-boring beetles in habitat created by summer wildfire relative to fall prescribed fire.

Woodpeckers occupying post-fire habitat (both wildfire and prescribed fire) were most likely to use trees that were both burned and infested with MPBs relative to their availability. This finding may be a result both of the age of post-wildfire habitat we evaluated and low relative abundance of wood-boring beetles in habitat created by prescribed fire. We only modeled resource selection of woodpeckers that occupied 3–4 year post-wildfire habitat. This timing coincided with a large increase in average home range size in post-wildfire habitat that likely coincided with most wood-boring beetle larvae emerging as adults (Murphy and Lehnhausen, 1998). Woodpeckers in these older post-wildfire habitats were observed foraging in MPB infestations along the periphery of burn boundaries, which is similar to observations made by Dudley and Saab (2007) in 6–8 year post-wildfire habitat. In wildfire study sites, the woodpeckers may need to forage on MPB infestations along burn peripheries as wood-boring beetle abundance declines ⩾3 years post-fire, which may account for the apparent preference for trees that were burned and infested with MPBs. In habitat created by prescribed fire, autumn burns may prevent the immediate colonization of wood-boring beetles in fire-killed trees. Therefore, trees that burned at moderate and high severity in prescribed fire study sites may have relatively low wood-boring beetle abundance relative to post-wildfire habitat of the same age. Lack of wood-boring beetle resources may thus require Black-backed Woodpeckers to spend more time foraging on trees that are infested with MPBs along burn peripheries.

4.1. Management implications

Our evaluation of habitat-specific home range size clearly demonstrates that summer wildfire is the most efficient disturbance agent for creating Black-backed Woodpecker habitat. Habitat created by summer wildfire supported smaller home ranges relative to all disturbance types and supported Black-backed Woodpeckers for more years relative to habitat created by fall prescribed fire. The core of any Black-backed Woodpecker conservation strategy should thus focus on maintaining a mosaic of 1–2 year post-summer wildfire habitat. We recognize fire management policy is unlikely to allow summer wildfires to remain unsuppressed, particularly in densely populated regions like the Black Hills, and we do not advocate such an approach. However, ignitions of summer wildfires are inevitable, and management strategies that allow summer wildfires to burn safely within a network of treated forest patches may allow maintenance of a mosaic of early post-wildfire habitat. Safety nets could include road systems in combination with mechanically treated patches and prescribed fire treatments. After summer wildfires do occur, retaining patches of 1–2 year post-summer wildfire forest that are at least 200 ha (the largest estimated home range size in this habitat) should provide high-quality habitat. Ideally, patches of recently burned forest should support more than 1 breeding pair of Black-backed Woodpeckers, which can be accomplished by exempting at least 50% of the area of summer wildfires >400 ha from salvage logging.

Results from resource selection analysis suggest that woodpeckers are more likely to use burned patches with certain structural characteristics. Black-backed Woodpeckers demonstrated consistently high relative probability of using trees ⩾27 cm DBH (the mean DBH of all used trees) in stands ⩾27.8 m^2 basal area/ha (the mean basal area surrounding used trees). On average, trees ⩾27 cm DBH constituted 11.1 m^2/ha (approximately 40%) of the basal area surrounding used trees. Across all habitats, Black-backed Woodpeckers exhibited the greatest probability of using disturbed trees of any category relative to undisturbed trees and dead trees relative to live trees. Trees burned at moderate and high severity were more likely to be used than trees burned at low severity and undisturbed trees, and increased burn severity resulted in greater tree mortality. Ideally, recently burned forest should thus be composed of ⩾27 m^2 basal area/ha of trees that burned at moderate and high severity, since these stands will likely contain the greatest number of standing dead trees. Additionally, at least 40% of the basal area of these stands should ideally be composed of trees ⩾27 cm DBH.

We do not advocate the use of fall prescribed burns as a tool for creating Black-backed Woodpecker habitat in the Black Hills. Not only did we fail to detect many woodpeckers in 1-year post-prescribed fire habitat, but Rota (2013) also reported declining population growth rates of Black-backed Woodpeckers occupying habitat created by prescribed fire. However, we do not completely

discount the utility of prescribed fire as a management tool if applied differently. More research regarding the mechanisms leading to delayed Black-backed Woodpecker colonization of habitat created by prescribed fire may increase the utility of this tool for creating woodpecker habitat. For example, spring burns may allow rapid colonization of prescribed fire sites by wood-boring beetles, allowing Black-backed Woodpeckers to immediately occupy habitat created by prescribed fire. Additionally, prescribed fire could also be used as a tool to allow greater tolerance of summer wildfires. Prescribed fire has repeatedly been shown to reduce the severity of subsequent wildfires in ponderosa pine forests (Pollet and Omi, 2002; Prichard and Kennedy, 2012; Wagle and Eakle, 1979), which may provide managers greater control over naturally ignited wildfires within previously treated areas. Thus, naturally ignited summer wildfires could potentially be allowed to burn in sections of forest that have been previously treated with prescribed fire.

We also do not believe MPB infestations require specific management action targeted toward Black-backed Woodpeckers. Home ranges in habitat created by MPBs were large relative to 1–2 year post-wildfire habitat. Assuming relatively large home ranges coincide with relatively low-quality habitat (e.g., Anich et al., 2010), this may suggest that MPB infestations have low value to Black-backed Woodpeckers relative to recently burned forest. This notion is supported by parallel work demonstrating that mean population growth rates of Black-backed Woodpeckers may be negative in MPB infestations (Rota, 2013). Additionally, Black-backed Woodpeckers have historically persisted in the Black Hills, despite decades without widespread MPB infestations (Allen et al., 2001; Rota, 2013). Finally, the spatial extent of the current MPB infestation in the Black Hills, SD, coupled with an inability to fully treat the entire infestation (USDA, 2011), suggests there is unlikely to be a shortage of MPB infested habitat for Black-backed Woodpeckers in the foreseeable future.

Our study is the first to simultaneously compare resource selection and home range size of Black-backed Woodpeckers occupying habitat created by wildfire, prescribed fire, and MPB infestations. Our study suggests that although Black-backed Woodpeckers may exploit vegetation characteristics in a similar manner across all disturbance types, woodpeckers occupying 1–2 year post-wildfire forests have smaller spatial requirements. Thus, while Black-backed Woodpeckers are clearly exploiting the ongoing MPB epidemic in the Black Hills ecoregion, we believe long-term conservation strategies should focus on ensuring a network of 1–2 year post summer wildfire patches.

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References

Allen, K., Long, D., Cross, F., 2001. Evaluation of mountain pine beetle activity on the Black Hills National Forest. USDA Forest Service Biological, Evaluation R2-02-02.
Anich, N.M., Benson, T.J., Bednarz, J.C., 2010. Factors influencing home-range size of Swainson's warblers in eastern Arkansas. Condor 112, 149–158.
Bock, C.E., Lynch, J.F., 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. Condor 72, 182–189.
Bonnot, T.W., Rumble, M.A., Millspaugh, J.J., 2008. Nest success of black-backed woodpeckers in forests with mountain pine beetle outbreaks in the Black Hills, South Dakota. Condor 110, 450–457.
Bonnot, T.W., Millspaugh, J.J., Rumble, M.A., 2009. Multi-scale nest-site selection by black-backed woodpeckers in outbreaks of mountain pine beetles. For. Ecol. Manage. 259, 220–228.
Brooks, S.P., Gelman, A., 1998. General methods for monitoring convergence of iterative simulations. J. Comput. Graph. Stat. 7, 434–455.
Cooper, A.B., Millspaugh, J.J., 1999. The application of discrete choice models to wildlife resource selection studies. Ecology 80, 566–575.
Costello, S.L., Negrón, J.F., Jacobi, W.R., 2011. Wood-boring insect abundance in fire-injured ponderosa pine. Agric. For. Entomol. 13, 373–381.
Dudley, J.G., Saab, V.A., 2007. Home range size of black-backed woodpeckers in burned forests of southwestern Idaho. West. N. Am. Nat. 67, 593–600.
Dudley, J.G., Saab, V.A., Hollenbeck, J.P., 2012. Foraging-habitat selection of Black-backed Woodpeckers in forest burns of southwestern Idaho. Condor 114, 348–357.
Estrella, A., 1998. A new measure of fit for equations with dichotomous dependent variables. J. Bus. Econ. Stat. 16, 198–205.
Fair, J.M., Paul, E., Jones, J., 2010. Guidelines to the Use of Wild Birds in Research. Ornithological Council, Washington, DC.
Gelman, A., 2006. Prior distributions for variance parameters in hierarchical models (Comment on Article by Browne and Draper). Bayesian Anal. 1, 515–534.
Gilks, W.R., Thomas, A., Spiegelhalter, D.J., 1994. A language and program for complex Bayesian modelling. J. R. Stat. Soc. Ser. D 43, 169–177.
Goggans, R., Dixon, R.D., Seminara, C.L., 1989. Habitat use by three-toed and black-backed woodpeckers. USDA Deschutes National Forest Technical, Report #87-3-02.
Hanson, C.T., North, M.P., 2008. Postfire woodpecker foraging in salvage-logged and unlogged forests of the Sierra Nevada. Condor 110, 777–782.
Hanson, C., Coulter, K., Augustine, J., Short, D., 2012. Petition to list the Black-backed Woodpecker (*Picoides arcticus*) as Threatened or Endangered under the federal Endangered Species Act. <http://www.biologicaldiversity.org/species/birds/black-backed_woodpecker/pdfs/BBWO_FESA_Petition.pdf> (accessed May 2013).
Hobson, K.A., Schieck, J., 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. Ecol. Appl. 9, 849–863.
Hoffman, G.R., Alexander, R.R., 1987. Forest vegetation of the Black Hills National Forest of South Dakota and Wyoming: a habitat type classification. USDA Forest Service Research Paper RM-RP-276.
Hoyt, J.S., Hannon, S.J., 2002. Habitat associations of black-backed and three-toed woodpeckers in the boreal forest of Alberta. Can. J. For. Res. 32, 1881–1888.
Hutto, R.L., 1995. Composition of bird communities following stand-replacement fires in Northern Rocky Mountain (USA) conifer forests. Conserv. Biol. 9, 1041–1058.
Hutto, R.L., 2008. The ecological importance of severe wildfires: some like it hot. Ecol. Appl. 18, 1827–1834.
Koivula, M.J., Schmiegelow, F.K.A., 2007. Boreal woodpecker assemblages in recently burned forested landscapes in Alberta, Canada: effects of post-fire harvesting and burn severity. For. Ecol. Manage. 242, 606–618.
Lehman, C.P., Kesler, D.C., Rota, C.T., Rumble, M.A., Seckinger, E.M., Juntti, T.M., Millspaugh, J.J., 2011. Netguns: a technique for capturing black-backed woodpeckers. J. Field Ornithol. 82, 430–435.
Millspaugh, J.J., Nielson, R.M., McDonald, L., Marzluff, J.M., Gitzen, R.A., Rittenhouse, C.D., Hubbard, M.W., Sheriff, S.L., 2006. Analysis of resource selection using utilization distributions. J. Wildl. Manage. 70, 384–395.
Mohren, S.R., 2002. Habitat evaluation and density estimates for the black-backed woodpecker (*Picoides arcticus*) and northern three-toed woodpecker (*Picoides tridactylus*) in the Black Hills National Forest. M.S. Thesis, University of Wyoming, Laramie.
Murphy, E.C., Lehnhausen, W.A., 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. J. Wildl. Manage. 62, 1359–1372.
Nappi, A., Drapeau, A., 2009. Reproductive success of the black-backed woodpecker (*Picoides arcticus*) in burned boreal forests: are burns source habitats? Biol. Conserv. 142, 1381–1391.
Nappi, A., Drapeau, P., 2011. Pre-fire forest conditions and fire severity as determinants of the quality of burned forests for deadwood-dependent species: the case of the black-backed woodpecker. Can. J. For. Res. 41, 994–1003.

Nappi, A., Drapeau, P., Giroux, J.-F., Savard, J.-P.L., 2003. Snag use by foraging black-backed woodpeckers (*Picoides arcticus*) in a recently burned eastern boreal forest. Auk 120, 505–511.
Nappi, A., Drapeau, P., Savard, J.-P.L., 2004. Salvage logging after wildfire in the boreal forest: is it becoming a hot issue for wildlife? Forest. Chron. 80, 67–74.
Negrón, J.F., Allen, K., Cook, B., Withrow Jr., J.R., 2008. Susceptibility of ponderosa pine, *Pinus ponderosa* (Dougl. ex Laws.), to mountain pine beetle, *Dendroctonus ponderosae* Hopkins, attack in uneven-aged stands in the Black Hills of South Dakota and Wyoming USA. For. Ecol. Manage. 254, 327–334.
Pollet, J., Omi, P., 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. Int. J. Wildland. Fire 11, 1–10.
Prichard, S., Kennedy, M., 2012. Fuel treatment effects on tree mortality following wildfire in dry mixed conifer forests, Washington State, USA. Int. J. Wildland Fire 21, 1004–1013.
R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. Bioscience 58, 501–517.
Rappole, J.H., Tipton, A.R., 1991. New harness design for attachment of radio transmitters to small passerines. J. Field Ornithol. 62, 335–337.
Rota, C.T., 2013. Not all Forests are Disturbed Equally: Population Dynamics and Resource Selection of Black-Backed Woodpeckers in the Black Hills, South Dakota. PhD Dissertation. University of Missouri, Columbia.
Russell, R.E., Royle, J.A., Saab, V.A., Lehmkuhl, J.F., Block, W.M., Sauer, J.R., 2009. Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire. Ecol. Appl. 19, 1253–1263.
Saint-Germain, M., Drapeau, P., Hebert, C., 2004. Landscape-scale habitat selection patterns of Monochamus scutellatus (Coleoptera: Cerambycidae) in a recently burned black spruce forest. Environ. Entomol. 33, 1703–1710.
Schütz, S., Weissbecker, B., Hummel, H.E., Apel, K., Schmitz, H., Bleckmann, H., 1999. Insect antenna as a smoke detector. Nature 398, 298–299.
SDGFP, 2006. South Dakota Comprehensive Wildlife Conservation Plan. South Dakota Dept. of Game, Fish and Parks Wildlife Division Report 2006-09.
Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., Gitzen, R.A., 1999. Effects of sample size on kernel home range estimates. J. Wildl. Manage. 63, 739–747.
Setterington, M.A., Thompson, I.D., Montevecchi, W.A., 2000. Woodpecker abundance and habitat use in mature balsam fir forests in Newfoundland. J. Wildl. Manage. 64, 335–345.
Sturtz, S., Ligges, U., Gelman, A., 2005. R2WinBUGS: a package for running WinBUGS. J. Stat. Softw. 12, 1–16.
Thomas, D.L., Johnson, D., Griffith, B., 2006. A Bayesian random effects discrete-choice model for resource selection: population-level selection inference. J. Wildl. Manage. 70, 404–412.
Tremblay, J.A., Ibarzabal, J., Dussault, C., Savard, J.-P.L., 2009. Habitat requirements of breeding black-backed woodpeckers (*Picoides arcticus*) in managed, unburned boreal forest. Avian Conserv. Ecol., 4.
USDA, 2011. Review of the Forest Service Response: The bark beetle outbreak in northern Colorado and southern Wyoming. USDA Forest Service, Rocky Mountain Region and Rocky Mountain Research Station.
Vierling, K. 2004. Report on woodpecker breeding in the Jasper fire. Submitted to the US Forest Service.
Wagle, R.F., Eakle, T.W., 1979. A controlled burn reduces the impact of a subsequent wildfire in a ponderosa pine vegetation type. For. Sci. 25, 123–129.
Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70, 164–168.