ABUNDANCE OF BLACK-BACKED WOODPECKERS AND OTHER BIRDS IN RELATION TO DISTURBANCE AND FOREST STRUCTURE IN THE BLACK HILLS AND BEAR LODGE MOUNTAINS OF SOUTH DAKOTA AND WYOMING

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by

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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

ABUNDANCE OF BLACK-BACKED WOODPECKERS AND OTHER BIRDS IN RELATION TO DISTURBANCE AND FOREST STRUCTURE IN THE BLACK HILLS AND BEAR LODGE MOUNTAINS OF SOUTH DAKOTA AND WYOMING

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ABSTRACT

Natural disturbances, such as wildfire and mountain pine beetle (*Dentroctonus ponderosae*, hereafter MPB) infestations, are two sources of large-scale disturbance that can significantly alter forest structure in the Black Hills. The Black Hills has recently experienced one of the largest MPB outbreaks in the last 100 years, along with varying levels of wildfires throughout the forest, gives us a unique opportunity to study how birds respond to these disturbances. Three-toed Woodpecker (*Picoides dorsalis*), Brown Creeper (*Certhia americana*), Red-breasted Nuthatch (*Sitta canadensis*), and White-winged Junco (*Junco hyemalis aikeni*) are species of regional conservation concern or are sensitive to forest management practices in the Black Hills. The Black-backed Woodpecker (*Picoides arcticus*), was recently petitioned to be listed under the Endangered Species Act and more information on their population size in the region is needed. Our objectives were to 1) map abundance of Black-backed Woodpeckers and provide an estimate of population size in the region and 2) to determine densities of our five focal species in relation to vegetation characteristics and disturbance in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming. We located 124 and 115 transects, containing 1,232 and 1,138 sampling points, in 2015 and 2016, respectively. We visited each point 3 times from late-March to late-June in 2015 and 2016. We characterized vegetation around each point using GIS derived landscape variables and simple point-level measurements.

The global abundance model received the most support for Black-backed Woodpeckers. There was a negative relationship of Black-backed Woodpecker abundance with latitude, percent cover of dead trees, and green trees and a positive relationship with percent cover of beetle killed trees, and 1- to 2-, 3-, and 4- to 5-year-old wildfires. Abundance of Black-backed Woodpeckers was most strongly related to percent cover of beetle killed trees and wildfires that had burned within the last 5 years. Mean density was 0.00528 birds/ha and 0.00626 birds /ha and an estimated 2,920 (LCL: 1,449; UCL: 5,917) and 3,439 (LCL: 1,739; UCL: 6,908) individual Black-backed Woodpeckers in the Black Hills in 2015 and 2016, respectively. Our abundance model can be used with previously published demographic rates for the species in the Black Hills to assess future viability of Black-backed Woodpeckers and provide information on the levels of disturbance needed to maintain a viable Black-backed Woodpecker population in the future.

At a smaller scale, Black-backed Woodpeckers, Brown creepers, and Red-breasted Nuthatch had mixed responses to 1- to 5-year-old wildfires. With the exception of American Three-toed Woodpeckers, all species were positively related to percent cover of beetle killed trees. Brown Creepers, White-winged Juncos, and Red-breasted Nuthatches had mixed responses to percent overstory canopy cover. White-winged Juncos also had a positive association with percent ground vegetation and Brown Creepers were strongly linked with the white spruce (*Picea glauca*) vegetation type. American Three-toed Woodpeckers, which are thought to occupy spruce forest in the Black Hills, did not show a strong relationship with any covariates. Management that maintains or permits some level of disturbance and heterogeneity within stands and at the landscape-level will benefit the diverse needs of birds. Continued monitoring of these species across a variety of habitat types will improve understanding about their responses to disturbances and the effects of management practices in the Black Hills.

THESIS FORMAT

Thesis chapters were formatted as independent manuscripts intended for peer-reviewed journal submission. As such, similar content is conveyed in the introductions and methods of each chapter, and a list of citations and supplemental data follows each chapter. We provide analyses of factors related to Black-backed Woodpecker abundance in both chapter one and two. In chapter one we only consider factors measured with GIS in a 78.5 ha circle that would allow us to map abundance across the entire study area, whereas in the second we consider vegetation characteristic measured in the field and factors measured with GIS in a 16.28 ha hexagon. I used plural nouns throughout to include co-authors.

CHAPTER 1

ABUNDANCE OF BLACK-BACKED WOODPECKERS (*Picoides arcticus*) IN THE BLACK HILLS OF SOUTH DAKOTA AND WYOMING

ABSTRACT

Black-backed Woodpeckers (*Picoides arcticus*) are rare residents of northern conifer forests and are almost always associated with disturbances, such as fire and beetle infestation. The Black Hills population of Black-backed Woodpeckers has been petitioned to be considered a Distinct Population Segment under the Endangered Species Act and more information on their population size in the region is needed. Our objective was to map abundance of Black-backed Woodpeckers in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming and provide a population estimate for Black-backed Woodpeckers in the region. We located 124 and 115 transects, containing 1,232 and 1,138 sampling points, in 2015 and 2016, respectively. We conducted 5-minute point count surveys from late-March to late-June and visited each point three times to estimate detection probability. We characterized vegetation around each point using GIS derived landscape variables that included: percent cover of green trees, beetle killed trees, dead trees, and year since wildfire. We detected 362 Black-backed Woodpeckers across both years. We fit three-level hierarchical time-removal models that simultaneously estimated abundance, availability, and detection probability in R package "unmarked" using *gmultmix* and ranked models using Akaike Information Criterion. The global abundance model received the most support. Abundance was negatively related to percent cover of dead trees and green trees and a positively related to percent cover of beetle killed trees, and percent area of 1- to 2-, 3-, and 4- to 5-year-old wildfires. Abundance of Black-backed Woodpeckers varied the greatest across present cover of beetle killed trees and wildfires that had burned within the last five years. Mean density was 0.00528 birds/ha in 2015 and 0.00626 birds /ha in 2016. An estimated

2,920 (LCL: 1,449; UCL: 5,917) and 3,439 (LCL: 1,739; UCL: 6,908) individual Black-backed Woodpeckers, which is equivalent to 1,460 and 1,720 pairs of Black-backed Woodpeckers, in the Black Hills in 2015 and 2016, respectively. Our study is the most extensive survey of Black-backed Woodpecker abundance in the region and sets the stage for future analyses of the species population viability in the region.

INTRODUCTION

Natural disturbances play an important role in shaping landscapes and bird distributions across western North America (Hejl 1992, Hejl 1994). Fire has been a natural disturbance in the Black Hills which has shaped the vegetation community resulting in decreased understory growth and stand densities (Brown and Cook 2006). For much of the 20th century, however, fire has largely been suppressed due to potential human conflicts and the loss of marketable timber (Nix 2012). These changes in the occurrence of natural fire regimes have altered the composition and structure of western forests resulting in less early successional post-fire habitat, which affects bird communities (Hejl 1992, Hejl 1994). Mountain pine beetle (*Dentroctonus ponderosae*, hereafter MPB) infestations are currently a source of large scale disturbance in the Black Hills (Shinneman and Baker 1997). Historically, MPB populations occur at endemic levels with periodic outbreaks every 20 years lasting 6-18 years (Graham et al. 2016). MPB outbreaks span hundreds of thousands of hectares and kill 60-90% of the trees, which affects the structure, composition, and function of stands (Raffa et al. 2008). The habitats created by these disturbances contain temporary food resources which are exploited by organisms for a short time following the disturbance. Thus, these habitats are ephemeral and require species that depend on them to constantly move among episodically disturbed habitat patches.

Black-backed Woodpeckers (*Picoides arcticus*) are almost completely restricted to disturbed ephemeral habitats. Black-backed Woodpeckers occupy unburned, late successional forests (Setterington et al. 2000, Huot and Ibarzabal 2006, Tremblay et al. 2009, Fogg et al. 2014, Mohren et al. 2014), in low densities throughout their range, but are strongly associated with burned forests (Murphy and Lehnhausen 1998, Hoyt and Hannon 2002, Hutto 2008, Rota et al. 2014a), as well as habitats created by beetle infestations (Goggans et al. 1989, Bonnot et al. 2008, Bonnot et al. 2009, Rota et al. 2014a, Rota et al. 2014b). These disturbances produce standing dead and dying trees that are important foraging resources due to the abundance of wood-boring (Cerambycidae and Buprestidae) and bark (Scolytidae) beetles which are the main source of food for Black-backed Woodpeckers (Goggans et al. 1989, Murphy and Lehnhausen 1998, Powell et al. 2002).

Black-backed Woodpeckers rapidly colonize disturbed areas due to the large quantity of food present. However, after 2- to 3-years the beetle larvae emerge from host trees and habitat quality declines (Murphy and Lehnhausen 1998, Rota et al. 2014a). Bonnot et al. (2009) found that Black-backed Woodpeckers selected territories based more on food availability than nest-site availability in MPB outbreaks in the Black Hills. Black-backed Woodpeckers mostly disappear from these disturbances after four years, coinciding with the emergence of the beetles (Harris 1982). Rota et al. (2014b) saw a dramatic increase in the home range size of Black-backed Woodpeckers between year two and three post-wildfire and larger home ranges in MPB infestations compared to early post-wildfire habitats; both are thought to be attributed to the diminishing food resources between years and different habitat types. Therefore, Black-backed Woodpeckers rely on a patchwork of recently burned, beetle killed, and undisturbed forests due to the ephemeral nature of their habitat (Hutto 1995, Rota et al. 2014a).

Black-backed Woodpeckers nest in burned forest as early as two weeks after a fire (Villard and Schieck 1997) and are common to abundant the first two years post disturbance (Harris 1982, Murphy and Lehnhausen 1998, Rota et al. 2014b). Nesting success is high in recently burned stands (Saab and Dudley 1998, Saab et al. 2007, Vierling et al. 2008, Nappi and Drapeau 2009, Rota et al. 2014a) and population growth is positive, suggesting these areas are population sources for Black-backed Woodpeckers (Rota et al. 2014a). In the absence of fire, Black-backed Woodpeckers are attracted to beetle-killed forests. However, Black-backed Woodpeckers have lower fledging rates, juvenile survival, nesting success, and population growth in MPB infestations compared to wildfire habitat (Rota et al. 2014a). Despite the negative population growth and lower demographic rates Black-backed Woodpeckers exhibit in MPB infestations, this habitat likely harbors some value to the species and ultimately may keep Black-backed Woodpecker populations from declining precipitously when fire habitats are unavailable (Rota et al. 2014a).

Black-backed Woodpeckers are uncommon to rare over broad landscapes because of their dependence on disturbance, the ephemeral nature of high quality habitat, fire suppression, and salvage logging throughout their range (Saab and Powell 2005). Furthermore, the population of Black-backed Woodpeckers in the Black Hills of South Dakota may be genetically isolated with little to no interchange with other populations (Pierson et al. 2010). The Black-backed Woodpecker is a “Sensitive Species” in Region 2 of the U.S. Forest Service because of concerns about population viability (USDA Forest Service 2005). It is a “Species of Local Concern” due to limited habitat in the Black Hills (Allen et al. 2002) and as a “Management Indicator Species” to reflect major issues and challenges to public land management (USDA Forest Service 2005). Black-backed Woodpeckers are listed by South Dakota as locally rare, vulnerable to extinction, and a “Species of Greatest Conservation Concern” in the Black Hills ecoregion (South Dakota Department of Game, Fish and Parks 2014) and by Wyoming as a "Species of Greatest Conservation Need" (Wyoming Game and Fish Department 2017).

The Black Hills population of Black-backed Woodpeckers was recently petitioned for protection as a Distinct Population Segment under the Endangered Species Act (Hanson et al. 2012) and a "12-month" status review must be completed by September 30, 2017. The petition for listing the Black-backed Woodpecker in the Black Hills identified a need for more information on their population size in the region. Recent population estimates of Black-backed Woodpeckers in the Black Hills were calculated from density estimates of other areas and were far below the threshold value for an effective population size to ensure population viability (Hanson et al. 2012). Re-analysis of a population estimate by Mohren et al. (2014) suggested approximately 50% more breeding pairs than estimated by Hanson et al. (2012). Current demographic rates for Black-backed Woodpeckers in the Black Hills are available (Bonnot et al. 2008, Rota et al. 2014a); however, with contradictory abundance estimates future population viability cannot confidently be assessed. Habitat is continuously changing in the Black Hills under all land ownerships. Since the last population estimate in 2000 on Black Hills National Forest, varying levels of disturbance have affected 50-60% of the forest through wildfire and MPB infestation (USDA Forest Service 2014). The extent of change in forest structure combined with relative uncertainty of the population status and trend support the need to develop adequate monitoring techniques and species-specific surveys to obtain a population estimate that is current, reliable, and repeatable.

Our primary objective was to map abundance of Black-backed Woodpeckers in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming and provide a population estimate for Black-backed Woodpeckers in the region. We accomplished this by fitting hierarchical abundance models to data from a broad-scale survey effort, which also allowed inferences about relationships between environmental and habitat factors and the probability of detection and abundance of Black-backed Woodpeckers. A regional abundance estimate is the first step toward a better understanding of the status and viability of Black-backed Woodpeckers in the Black Hills.

STUDY AREA

Our study area included the Black Hills National Forest (BHNF) and Custer State Park (CSP) in southwest South Dakota and the Bear Lodge Mountains in northeast Wyoming (Figure 1). The BHNF and CSP are 554,627 hectares and consist of a variety of forested habitat with prairie habitat adjacent to much of the property boundaries. Elevation in the Black Hills and Bear Lodge Mountains ranges from 1065 m to 2207 m (Froiland 1990). Climate varies with latitude and elevation, and annual precipitation ranges from 46 cm to 71 cm, with the northern hills tending to receiving more (Orr 1959).

The region was dominated by Rocky Mountain coniferous forests predominantly comprised of ponderosa pine (*Pinus ponderosa*) and northern coniferous forests consisting of quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*), which occured at higher elevations and on northeast slopes (Hoffman and Alexander 1987, Walters et al. 2013). The understory was dominated by western snowberry (*Symphoricarpos occidentalis*), white coralberry (*S. albus*), juniper (*Juniperus comunis*), and kinnikinnick (*Arctostaphylos uvaursi*) (Hoffman and Alexander 1987, Severson and Thilenius 1976) along with a diversity of native and non-native grasses, sedges and forbs.

Historically natural disturbances, such as frequent fires and beetle infestations, created a unique habitat in the Black Hills and Bear Lodge Mountains. Wildfires burned more than 216,506 ha (535,000 acres) between 1909 and 2015 in the BHNF. Wildfires were common with several fires often occurring in the same year and individually ranging in size between 5 ha (13 ac) and 33,795 ha (83,510 ac) (USDA Forest Service 2013). Mountain pine beetles are endemic throughout the Black Hills and there have been many outbreaks during the last century (Allen et al. 2008). The most recent, largest, and intensive MPB epidemic in the last 100 years started in 1996 and has since affected 188,583 ha (466,000 ac), or about a quarter, of the Black Hills. In the past 4 years, 28,327 ha (70,000 ac) of the affected area was infested; however, recent evidence shows the epidemic reached its peak in 2012 and the rate of infestation was declining (Graham et al 2016). Approximately 50-60% of the BHNF has been affected by wildfires and beetle infestations since the late 1990s (USDA Forest Service 2014).

METHODS

Sampling design

We used a stratified-random sampling design for our point count surveys to ensure adequate detections of Black-backed Woodpeckers because of the widespread and scattered condition of MPB infestation and limited area of recent wildfires. We created a grid of hexagons across the study area and their center points represented potential point count sites. Each hexagon was 250m on a side, 16.28 ha (40 ac) in area, and approximately 450m from center to center (Figure 2). We *a priori* classified each hexagon as potentially low or high density habitat for Black-backed Woodpeckers; if a hexagon contained disturbance by MPB or fire it was considered high density habitat.

Color and infrared aerial photography have been used to update the status and extent of the MPB epidemic in the BHNF since 2010. We obtained the most recent infrared photography available (2014 and 2015) and classified strata representing potentially low to high density habitats for Black-backed Woodpeckers. We re-sampled the aerial photographs to create a 1-m resolution raster and then conducted a supervised classification to classify forested pixels as live trees (green trees), dead trees with needles (beetle killed trees), and dead trees with no needles (dead trees) (Figure 3). We also obtained the wildfire history for the BHNF and characterized hexagons based on the percent area in each hexagon affected by wildfire. Due to the large increase in Black-backed Woodpecker home range size between 2 and 3-year post-wildfire habitat (Rota et al. 2014b) we grouped wildfire into four categories: 1- to 2-, 3-, 4- to 5-, and 6- to 10-year-old wildfires. We then intersected the hexagon grid with the raster to determine the percent of each hexagon represented by the three classes of trees and hexagons that have had fire within the last 10 years.

We randomly selected hexagons for starting points for point count transect such that 20% occurred in potential low-density habitat and 80% in potential high-density habitat for Black-backed Woodpeckers. This design ensured we would have an adequate number of detections, even given expected low detection rates for this species (White and Giroir 2008), to fit abundance models that would enable us to estimate abundance based on vegetation conditions in each hexagon. Nevertheless we still sampled low-density habitat to ensure we sampled all available habitat conditions. Each start point was at least 100m from a road to avoid noise factors associated with roads. We laid out point transects beginning from the starting points in ArcGIS along a path that maximized sampling efficiency. Each transect contained up to 10 points because that was the estimated number of points a technician could complete in a morning. We located 124 and 115 transects, containing 1,232 and 1,138 sampling points, in 2015 and 2016, respectively (Figure 4).

Field methods

We conducted point count surveys from 1 April through 28 June 2015 and 31 March through 23 June 2016. We visited sampling points along transects three times each year, approximately one month apart, resulting in 3,696 and 3,414 point counts in 2015 and 2016, respectively. Surveys were conducted on days with minimal to no precipitation and light to moderate wind speeds and started at official sunrise and terminated approximately six hours later. We navigated to points with the aid of a Global Positing System (GPS) unit. We recorded the point number, observer, Universal Transverse Mercator (UTM) coordinates, visit number, time, date, and weather conditions (temperature, wind speed, cloud cover, and precipitation) for each survey. We recorded the time of the first detection and distance to the first detection (using a digital laser range finder) of every individual Black-backed Woodpecker heard or seen for the first five minutes of the count. We then broadcast a recorded Black-backed Woodpecker drum at the 5, 5.5, and 6.5 minute mark using a FOXPRO NX3 digital game caller (FOXPRO Inc., Lewistown, Pennsylvania, USA) and continued to listen and look for detections up to the 7-minute mark. We noted if each detection was a drum, vocalization, or visual. Broadcast calls have been shown to significantly increase detection probability for this species compared to passive point counts (Siegel et al. 2010, Saracco et al. 2011). Additionally, Black-backed Woodpeckers drum year-round and it is not considered an aggressive social behavior, whereas, other vocalizations (rattle, snarl, pik) are associated with social interactions or aggression (Tremblay et al. 2016) which would likely draw individuals to the observer (Mohren et al. 2014).

Vegetation variables

We characterized vegetation variables around each sampling point and all points across the BHNF and CSP using the classification layer mentioned above. Since Black-backed Woodpeckers home range sizes can be large (20 – 1248 ha) (Rota et al. 2014b), we decided to obtain vegetation measurements at a larger scale. Therefore, we laid out a 500 m radius buffer around each point, increasing our area of vegetation measurements from the 16.28 ha hexagon to 78.5 ha circle, which is equivalent to the average Black-backed Woodpecker home range size in a recent wildfire (Rota et al. 2014b). We intersected the buffers with the classification raster to calculate the percent cover of green trees, beetle killed trees, or dead trees and for each of the wildfire categories.

Analytical methods

We used three-level hierarchical time-removal models that simultaneously estimated abundance (λ), availability (ϕ), and detection probability (σ). This model allowed for repeated visits to a single point within a season by estimating availability, the probability that an individual is present and provides a detectable cue, and detection, the probability of the observer detecting said cue (Chandler et al. 2011). This model builds upon previous models that estimate abundance for unmarked individuals (Royle 2004), but relaxes the geographic closure assumption (i.e. no immigration or emigration during the survey period) by allowing temporary emigration. This assumption is often violated with species that have larger home ranges because they are more mobile and likely to leave the survey plot during sampling (Chandler et al. 2011). We used a model that allowed temporary emigration because Black-backed Woodpecker home ranges are 20-1248 ha in the Black Hills (Rota et al. 2014b) and would likely violate an assumption of closure over the three visits to a point in a season. We assumed the estimated abundance represented the super-population available for detection across all visits in a year, therefore the average abundance during any one visit was $\lambda \times \phi$ (Fiske and Chandler 2015).

We used a model selection approach and Akaike's Information Criterion (AIC) to assess support for *a priori* candidate models that evaluate the effects of landscape variables on Black-backed Woodpecker density. We fit models using the gmultmix function in the R package "unmarked" (Fiske and Chandler 2015). We eliminated detections at distances > 200 m because we expected detectability to decline, greater potential for errors in distance estimation, and it was consistent with recommendations to remove top 5-10% of detection distances in distance sampling (Buckland et al. 2001). Therefore, abundance estimates were for a 200-m radius plot and estimated density (birds/ha) = $\lambda \times \phi \times (\mathrm{pi} \times 200^2 \times 10000^{-1})^{-1}$. We only included Black-backed Woodpecker detections from the 5-minute passive count and assigned detections into five 1-minute intervals. We only used passive detections because we reasoned that detection probability differed before and after the playbacks and the gmultmix function did not permit detection-specific covariates that would be needed to model this scenario. We standardized all continuous covariates to a mean of zero to facilitate model convergence (Fiske and Chandler 2015). Species abundance was modeled using Poisson and negative binomial distribution.

We used a multi-stage model selection approach to evaluate *a priori* candidate models for Black-backed Woodpecker densities. We first fit candidate models for detection probability with individual and combinations of our detection covariates (day of year [doy], minutes since sunrise [min], observer [obs], visit [visit], and year [year]) with both Poisson and negative binomial distributions, resulting in 20 models total (Table 1). We selected the top-ranked model for use with abundance covariates.

We evaluated abundance covariates in three stages: landscape-level wildfire, landscape-level vegetation, and latitude and year. We first fit the top detection models with combinations of our wildfire covariates: percent cover 1- to 2-, 3-, 4- to 5-, and 6- to 10-year-old wildfires, which resulted in three models. We then fit models with all combinations of the landscape-level vegetation covariates: percent cover green trees (GT), beetle killed trees (RT), and dead trees (DS), resulting in six models. We then combined the top landscape-level fire and landscape-level vegetation models and considered models with and without year and latitude, which resulted in 14 competing models. We did not consider covariate effects on availability.

We ranked candidate models using AIC and evaluated goodness-of-fit for the top-ranked model using the Freeman-Tukey test with parametric bootstrap for 100 simulations (Fiske and Chandler 2015). We predicted species abundances across the ranges of supported density covariates while holding landscape-level vegetation covariates at zero and latitude at its mean, and converted abundances to densities for ease of interpretation.

To map density and estimate total abundance, we predicted Black-backed Woodpecker abundance for all points in the hexagon grid in the BHNF and CSP that were within forest boundaries and had complete areal imagery using the most supported model. We converted abundances to densities based on the plot radius, and estimated abundance in each hexagon. We summed abundances to estimate total population size and mapped hexagon densities.

RESULTS

We conducted 3,696 point counts during three visits to 1,232 points and detected 300 Black-backed Woodpeckers in 2015 and surveyed 3,414 point counts during three visits to 1,138 points and detected 310 Black-backed Woodpeckers in 2016. We obtained 362 detections from the passive count and 248 from the playback counts. We categorized vegetation for 1,222 and 1,128 points in 2015 and 2016, respectively. Vegetation measurements for sampling points were comparable to vegetation characteristics across all sampling points in the BHNF (Table 2), ranging from open habitat hit by MPB infestations or fire to closed canopy ponderosa pine stands.

Detection probability for Black-backed Woodpeckers was best described by day of year, minute, observer, and year (Table 1). The probability of detection differed across years with higher detectability in 2016 ($\beta = 0.249 \pm 0.402$) than 2015 (Table 4). Black-backed Woodpecker detections varied by observers and were negatively correlated with day of year ($\beta = -0.536 \pm 0.102$) and minute ($\beta = -0.379 \pm 0.114$) (Table 4).

The global abundance model with latitude, and percent cover of green trees, beetle killed trees, dead trees, 1- to 2-, 3-, and 4- to 5-year-old wildfires received strong support compared to all other models and there was no evidence of lack of fit for the top model ($P >$

0.10; Table 3). Density was positively related to percent cover of beetle killed trees, 1- to 2-, 3-, and 4- to 5-year-old wildfires (Table 4). Black-backed Woodpecker density increased from 0.0041–0.7759 birds/ha over a range of 0-100 percent cover of beetle killed trees (Figure 5). Black-backed Woodpecker densities ranged from 0.0041 – 0.1911, 0.0041 – 0.0610, and 0.0041 – 0.0146 birds/ha across a range of 0-100 percent cover of 1-to 2-, 3-, and 4- to 5-year-old wildfires, respectively (Figure 5).

Woodpecker density was negatively related to latitude and percent cover of green trees and dead trees (Table 4). Black-backed Woodpecker density decreased from 0.0063 – 0.0020 birds/ha and 0.0063 – 0.0030 birds/ha over a range of 0-100 percent cover of green trees and dead trees, respectively (Figure 6), but their confidence intervals overlapped zero (Table 4). Black-backed Woodpecker density decreased from 0.0106 – 0.0021 birds/ha as latitude increased from 43.51 to 44.78 (Figure 6). Black-backed Woodpeckers had higher densities in 2016 than 2015, but the confidence interval for the year effect overlapped zero (Table 4).

Abundance across all hexagons in the BHNF and CSP ranged from 0.027 – 1.820 birds/hexagon in 2015 (Figure 7) and from 0.031 – 5.371 birds/hexagon in 2016 (Figure 8). We estimated there were 2,920 (95%, LCL: 1,449; UCL: 5,917) and 3,439 (95%, LCL: 1,739; UCL: 6,908) individual Black-backed Woodpeckers in the Black Hills and Bear Lodge Mountains in 2015 and 2016, respectively. This is equivalent to 1,460 pairs in 2015 and 1,720 pairs of Black-backed Woodpeckers in 2016, assuming a 50:50 sex ratio and all individuals were paired. The estimated mean density for Black-backed Woodpeckers in the study area was 0.00528 birds/ha in 2015 and 0.00626 birds/ha in 2016.

DISCUSSION

Our study represents the largest broad-scale survey and abundance estimate of Black-backed Woodpeckers in the Black Hills and Bear Lodge Mountains of South Dakota and

Wyoming. We conducted point count surveys for Black-backed Woodpeckers across a range of vegetation types. This broad scale survey enabled us to determine how Black-backed Woodpecker densities varied across vegetation types and disturbances and fit a model that estimated population size across the entire forest.

Average density across both years of our study for all points in the BHNF and CSP was 0.00577 birds/ha. Mohren et al. (2014) reported an average 0.12 pairs/km^2 or 0.0006 birds/ha; however, their estimate was conservative by eliminating individuals that were less than 1,500-m apart and conducted after a time period of relatively low disturbance on the landscape. The current beetle epidemic began in the early 2000's and only 2,307 ha (5,700 ac) of the forest had been subjected to wildfire in the previous 4 years (Mohren et al. 2016). Prior to our study more than 8,813 ha (21,778 ac) of the BHNF and CSP had burned within the last 4 years and the peak of the most recent MPB infestation was reached around 2012 (Graham et al. 2016). Our population estimate is more than 2 times as high as Mohren et al. (2014), which is likely a result of the high levels of disturbance the forest experienced in the past 15 years. Contrasting levels of disturbance along with differences in density estimates, demonstrates the range at which Black-backed Woodpecker population size can fluctuate coinciding with different amounts of disturbance on the landscape.

The abundance of foraging resources attracts Black-backed Woodpeckers to natural disturbances like wildfire and MPB infestation. Black-backed Woodpeckers had their greatest densities at points infested by MPB compared to all other vegetation types surveyed. Black-backed woodpeckers are known to strongly respond to outbreaks of bark beetles and have shown increased densities in infested stands (Bull 1983, Bonnot et al. 2009, Drever and Martin 2007, Rota et al. 2014a) However, beetle infested areas may be sink habitats because woodpeckers experience lower nesting success, juvenile and adult survival, and negative population growth in areas affected by MPB compared to wildfire (Rota et al. 2014a). Conversely, Black-backed Woodpeckers exhibit positive population growth in wildfires and these areas are considered source habitats (Rota et al. 2014a). Densities were highest in 1- to 2-year-old wildfires compared to 3- to 5-year-old wildfires, which is consistent with previous research (Murphy and Lehnhausen 1998, Ibarzaba and Desmeules 2006, Nappi and Drapeau 2009, Saracco et al. 2011). The decline in density after 1-2 years post-wildfire is likely because of the lack of wood-boring beetles, which is the main food resource for woodpeckers (Goggans et al. 1989, Murphy and Lehnhausen 1998, Powell et al. 2002). Compared to wood-boring beetles, bark beetles are much smaller in size, usually densely aggregated, and never occur deeper than a tree's cambial layer (Powell et al. 2000), making them more accessible and possibly a more profitable food resource to woodpeckers when they are experiencing increased population sizes during beetle epidemics. While habitat created by beetle infestations may not be equal to burned forests in terms of population growth these outbreaks are likely an attractive food source and provide habitat when recently burned habitat is unavailable.

Given there availability, the majority of our sampling points in wildfires were in 3- to 4-year-old wildfires, which means there was an abundance of 1- to 2-year-old wildfires on the landscape prior to our surveys. The increased availability of recently burned habitat likely provided suitable habitat which facilitated population growth of Black-backed woodpeckers. Increased population growth would result in a large quantity of young, which then disperse searching for high quality habitats to establish territories. However, with a lack of 1- to 2-year-old wildfires available and an abundance of MPB infestation on the landscape these young individuals likely colonized MPB habitat, which could be why there were higher Black-backed Woodpecker densities in beetle outbreaks than in older burned forests. Average home range size for Black-backed Woodpeckers in MPB habitat was 307 ha, which is slightly smaller than 3-

year-old wildfires (439 ha) in the Black Hills (Rota et al. 2014b). MPB are also likely important to population persistence because large numbers of birds can reside there and may prevent the population from catastrophic declines when suitable burned habitat is unavailable (Rota et al. 2014a). Overall, Black-backed Woodpeckers prefer these disturbed habitats as average densities were 13-45 times greater in 1-2 year post-wildfire and MPB outbreaks compared to undisturbed forests.

Our mean density was slightly greater than density estimates for Black-backed Woodpeckers in Oregon. Bate (1995) observed 0.16 birds/40 ha or 0.004 birds/ha in a moderately harvested ponderosa pine stand and Dixon (1995) reported 0.15 birds/40 ha or 0.00375 birds/ha in old-growth ponderosa pine habitat (Tremblay et al. 2016). These forests had isolated outbreaks of MPB and only 1 small wildfire available, whereas, the Black Hills was going through a MPB epidemic. Arnett et al. (1997a, 1997b) observed densities in lodgepole pine stands killed by MPB of 1.99 – 5.3 birds/40 ha or 0.0497 – 0.1325 birds/ha, whereas, our mean density were slightly greater at points affected by MPB (0.1713 birds/ha). We estimated densities of 0.0082 and 0.0521 birds/ha at points with 100% coverage by 4- to 5- and 1- to 2-year-old wildfires. Model densities for Black-backed Woodpeckers ranged from 0.0013 – 0.0068 pairs/ha or 0.0007 – 0.0034 birds/ha in 1-year-old wildfires in California (Tingley et al. 2016); however, Black-backed Woodpeckers usually reach peak densities 2 years after a disturbance occurs (Murphy and Lehnhausen 1998). We grouped 1- to 2-year-old wildfires together because of the limited availability of recent wildfires and could be why our density estimates are higher. Densities in Quebec were greater and ranged 12 – 1 pair/100 ha or 0.24 – 0.02 birds/ha in 1 to 3-year post-wildfire in a mature landscape (Nappi and Drapeau 2009). Their mature landscape contained trees more than 80 years old, whereas, the BHNF has been intensively managed and is dominated by younger and smaller trees than what occurred historically (Brown and Cook

2006). Larger, old growth trees support more food resources and provide higher quality habitat (Nappi et al. 2003), which could be why our density estimates are lower for Black-backed Woodpeckers in habitat created by wildfires in the Black Hills.

Black-backed Woodpeckers, on average, occurred at low densities in areas with high percentage of green forest. Black-backed Woodpeckers occurred at low densities during periods of low forest disturbance in the Black Hills and elsewhere in undisturbed forest (Setterington et al. 2000, Huot and Ibarzabal 2006, Tremblay et al. 2009, Fogg et al. 2014, Mohren et al. 2014). Little is known about Black-backed Woodpecker adult and juvenile survival, nesting success, and habitat use in undisturbed forests. We noted Black-backed Woodpeckers in undisturbed forest throughout the Black Hills and Mohren et al. (2016) noted Black-backed Woodpeckers occurred in association with small patches of MPB killed trees within the forest. Black-backed Woodpeckers were uncommon in undisturbed forest in 1992 – 1993 and they were observed feeding on stumps of recently harvested trees (Mills et al. 2000). Throughout the BHNF Black-backed Woodpecker density also varied by latitude. Variations in Black-backed Woodpecker occupancy in green forests was best attributed to changing physiographic variables rather than habitat structure in California (Fogg et al. 2014). We observed decreases in Black-backed Woodpecker density as latitude increased, which may be related to disturbance regimes in the Black Hills. The majority of burned habitat existed in the southern hills which could explain why we observed higher Black-backed woodpecker densities in lower latitudes. Furthermore, higher latitudes in our study included the Bear Lodge Mountains of Wyoming which is isolated from the main body of the BHNF and had low levels of disturbance. Additionally, latitude could be correlated with elevation and precipitation and could affect abundance of Black-backed Woodpeckers.

The probability of detection for Black-backed Woodpeckers decreased throughout our sampling period each year. Black-backed Woodpeckers begin cavity excavation in late April, mostly by males (Tremblay et al. 2016), and the average date of the first egg occurrence in the BHNF was 29 May, with the earliest occurrence on 6 May and the latest on 21 June (unpublished data Rocky Mountain Research Station, Rapid City, SD). Both males and females spend time on the nest incubating, resulting in a lower probability of being off the nest as compared to before and after nesting. Similar to our study, Mohren et al. (2014) had greater Black-backed Woodpecker response to broadcast calls in April than March or May. Time of day also affected Black-backed Woodpecker detectability. Black-backed Woodpecker vocalizations and drumming are most readily heard 0.5 hours after sunrise, with peak detection occurring 1-2 hours later; vocalization and drumming continue throughout the day but are more variable (Goggans et al. 1989). Our surveys generally started around sunrise and detectability decreased as time of day increased. Future surveys for the species should prioritize surveys in April and conduct surveys closer to sunrise if the goal is to maximize detections of Black-backed Woodpeckers.

Broadcast calls significantly increase detection probability for Black-backed Woodpeckers compared to passive point counts (Siegel et al. 2010, Saracco et al. 2011). However, there are drawbacks to using broadcast calls when conducting point counts to estimate detectability and abundance. Broadcast calls increase the chance of individuals moving towards the observer or the same individual responding to broadcasts at consecutive points, biasing density estimates. We broadcasted Black-backed Woodpecker drums after the first 5 minutes of our survey but we did not use detections from this portion of the survey in our analysis. The probability of detection was almost certainly different for detections associated with the broadcast calls than passive detections during the first 5 minutes, and the hierarchical time-removal models that we used cannot accommodate detection specific covariates for multiple types of detections. Focusing our surveys in areas recently disturbed likely explains why our detection rates were higher than the average detection rates calculated for Black-backed Woodpeckers from recent point count surveys in BHNF (White and Giroir 2008). These higher detection rates allowed us to remove active detections from analysis and still successfully model Black-backed Woodpecker abundances.

This study sets the stage for assessing future viability and trends of Black-backed Woodpecker populations in the Black Hills. Despite higher densities in MPB infestations, this habitat ultimately does not provide Black-backed Woodpeckers with enough resources required for increased periods of population growth (Rota et al. 2014a). Furthermore, the forest can go decades without experiencing a MPB epidemic and yet Black-backed Woodpecker populations have persisted in the BHNF (Allen et al. 2001, Rota et al. 2013). Forest disturbances, specifically 1-2 year post-wildfire habitat, may be critical to protecting the long-term viability of Black-backed Woodpecker populations. Wildfires after 4 years in the Black Hills do not provide sufficient resources to support Black-backed Woodpeckers, as average densities in those areas were similar to densities in undisturbed forests. However, understanding Black-backed Woodpeckers habitat preferences in undisturbed forests in the Black Hills may be important when managing the species if recent wildfire habitat is unavailable in the future. Conservation of suitably large forested landscapes may be important to ensure natural disturbances periodically occur to provide habitat for Black-backed Woodpeckers. Information on demographic rates from Rota et al. (2014a) and Bonnot et al. (2008) can be used in conjunction with our population estimate to determine how frequent and large disturbances need to be over long time periods to maintain a viable Black-backed Woodpecker population in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming in the future.

LITERATURE CITED

Allen, A. A., R. Glover, P. Lynch, A. Pettersen, B. Phillips, J. Reeck, D. Reyher, K. Burns, R. Crook and Science Applications International Corporation. 2002. Process for identifying wildlife and plant species of local concern and results. Black Hills National Forest Phase II Plan Amendment. Prepared for USDA-Forest Service, Black Hills National Forest.

Allen, K. K., D. F. Long, and F. J. Cross. 2001. Evaluation of mountain pine beetle activity on the Black Hills National Forest, Biological Evaluation R2-002-02. Rapid City: U.S. Forest Service. 29 p.

Allen, K. K., and D. F. Long. 2008. Evaluation of mountain pine beetle activity in the Norbeck Area, Black Hills National Forest. USDA Forest Service, Forest Health Evaluation RCSC2-08-03. 8 p.

Arnett, E. B., B. Altman, and W. P. Erickson. 1997a. Effects of salvage logging on neotropical migratory landbirds in lodgepole pine forests of central Oregon: 1997 preliminary results. Springfield, OR: Unpublished. Report to the Weyerhaeuser Co.

Arnett, E. B., B. Altman, and W. P. Erickson. 1997b. Relationships between salvage logging and forest avifauna in lodgepole pine forests of the central Oregon Pumice Zone. Springfield, OR: Unpublished 1996 annual report to the Weyerhaeuser Co.

Bonnot, T. W., M. A. Rumble and J. J. Millspaugh. 2008. Nest success of Black-backed Woodpeckers in forests with mountain pine beetle outbreaks in the Black Hills, South Dakota. The Condor 110: 450–457.

Bonnot, T. W., J. J. Millspaugh, and M. A. Rumble. 2009. Multi-scale nest-site selection by Black-Backed Woodpeckers in outbreaks of mountain pine beetles. Forest Ecology and Management 259 (2): 220–28.

Brown, P. M., and B. Cook. 2006. Early settlement forest structure in Black Hills ponderosa pine forests. Forest Ecology and Management 223: 284–290.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford. 448 p.

Chandler, R. B., J. A. Royle, and D. I. King. 2011. Inference about density and temporary emigration in unmarked populations. Ecology 92 (7): 1429–1435.

Drever, M. C., and K. Martin. 2007. Spending time in the forest: responses of cavity-nesters to temporal changes in forest health and environmental conditions in interior British Columbia. Pages 236-251 in J. A. Bissonette and I. Storch, editors. Temporal explicitness in landscape ecology: understanding wildlife responses to changes in time. Springer, New York, New York, USA.

Fiske, I., and R. Chandler. 2015. Overview of Unmarked: an R package for the analysis of data from unmarked animals. R Project for Statistical Computing. https://cran.rproject.org/web/packages-/unmarked/vignettes/unmarked.pdf.

Fogg, A. M., L. J. Roberts, and R. D. Burnett. 2014. Occurrence patterns of Black-Backed Woodpeckers in green forest of the Sierra Nevada Mountains, California, USA. Avian Conservation and Ecology 9 (2): 3.

Froiland, S. G. 1990. Natural history of the Black Hills and Badlands. Sioux Falls, SD: Center for Western Studies, Augustana College.

Goggans, R., R. D. Dixon, and C. L. Seminara. 1989. Habitat use by Three-toed and Black-backed Woodpeckers Deschutes National Forest, Oregon. Oregon Department of Fish and Wildlife Nongame Wildlife Program. USDA Deschutes National Forest Technical Report #87-3-02.

Graham, R. T., L. A. Asherin, M. A. Battaglia, T. Jain, and S. A. Mata. 2016. Mountain pine beetles: a century of knowledge, control attempts, and impacts central to the Black Hills. General Technical Report. RMRS-GTR-353. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 193 p.

Hanson, C., K. Coulter, J. Augustine, and D. Short. 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.

Harris, M. A. 1982. Habitat use among woodpeckers in forest burns. M.S. Thesis. University of Montana, Missoula. 82 p.

Hejl, S. J. 1992. The importance of landscape patterns to bird diversity: agerspective from the Northern Rocky Mountains. Northwest Environmental Journal 8: 119–137.

Hejl, S. J. 1994. Human-induced changes in bird populations in coniferous forests in western North America during the past 100 years. Studies in Avian Biology No.15: 232–246.

Hoffman, G. R., and R. R. Alexander. 1987. Forest vegetation of the Black Hills National Forest of South Dakota and Wyoming: A habitat type classification. U.S. Forest Service Research Paper. RM-276. Fort Collins, CO, USA. 54 p.

Hoyt, J. S., and S. J. Hannon. 2002. Habitat associations of Black-Backed and Three-Toed Woodpeckers in the Boreal Forest of Alberta. Canadian Journal of Forest Research 32 (10): 1881–88.

Huot, M., and J. Ibarzabal. 2006. A comparison of the age-class structure of Black-backed Woodpeckers found in recently burned and unburned boreal coniferous forest in eastern Canada. Annales Zoologici Fennici 43: 131–136.

Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in Northern Rocky Mountain (USA) conifer forests. Conservation Biology 9: 1041–1058.

Hutto, R. L. 2008. The ecological Importance of severe wildfires: some like it hot. Ecological Applications 18 (8): 1827–1834.

Hutto, R. L., and S. M. Gallo. 2006. The effects of postfire salvage logging on cavity-nesting birds. The Condor 108 (4): 817–831.

Mohren, S. R., M. A. Rumble, and S. H. Anderson. 2014. Density and abundance of Black-Backed Woodpeckers in a ponderosa pine ecosystem. The Prairie Naturalist 46 (2): 62–69.

Mohren, S. R., M. A. Rumble, C. P. Lehman, S. H. Anderson. 2016. Resource selection by Black-backed Woodpeckers (*Picoides arcticu*s) and American Three-toed Woodpeckers (*P. dorsalis*) in South Dakota and Wyoming. The Prairie Naturalist 47: 21–29.

Morissette, J. L., T. P. Cobb, R. M. Brigham, and P. C. James. 2002. The response of Boreal forest songbird communities to fire and post-fire harvesting. Canadian Journal of Forest Research 32 (12): 2169–83.

Murphy, E. C., and W. A. Lehnhausen. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. The Journal of Wildlife Management 62 (4): 1359–1372.

Nappi, A., P. Drapeau, and J.-P. L. Savard. 2004. Salvage logging after wildfire in the Boreal forest: is it becoming a hot issue for wildlife? The Forestry Chronicle 80: 67–74.

Nappi, A., and P. Drapeau. 2009. Reproductive success of the Black-Backed Woodpecker (*Picoides Arcticus*) in burned Boreal forests: are burns source habitats? Biological Conservation 142 (7): 1381–1391.

Nappi, A., and P. Drapeau. 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. Canadian Journal of Forest Research 41 (5): 994–1003.

Nix, S. 2012. Prescribed fire in forests: controlling fire in forests for ecological benefits. The New York Times Company. http://forestry.about.com/cs/forestfire/a/prescribe_burn.htm.

Orr, H. K. 1959. Precipitation and streamflow in the Black Hills. USDA, Forest Service, Rocky Mountain Forest and Range Experiment Station, Station Paper No. 44.

Pierson, J. C., F. W. Allendorf, V. Saab, P. Drapeau, and M. K. Schwartz. 2010. Do male and female Black-backed Woodpeckers respond differently to gaps in habitat? Evolutionary Applications 3 (3): 263–278.

Powell, H. D. W., S. J. Hejl, and D. L. Six. 2002. Measuring woodpecker food: a simple method for comparing wood-boring beetle abundance among fire-killed trees. Journal of Field Ornithology 73: 130–140.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58: 501–517.

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. University of Missouri, Columbia. 170 p.

Rota, C. T., J. J. Millspaugh, M. A. Rumble, C. P. Lehman, and D. C. Kesler. 2014a. The role of wildfire, prescribed fire, and mountain pine beetle infestations on the population dynamics of Black-Backed Woodpeckers in the Black Hills, South Dakota. PLoS ONE 9 (4): e94700.

Rota, C. T., M. A. Rumble, J. J. Millspaugh, C. P. Lehman, and D. C. Kesler. 2014b. Space-use and habitat associations of Black-Backed Woodpeckers (*Picoides Arcticus*) occupying recently disturbed forests in the Black Hills, South Dakota. Forest Ecology and Management 313: 161–168.

Royle, J. A. 2004. Generalized estimators of avian abundance from count survey data. Animal Biodiversity and Conservation 27 (1): 375–386.

Saab, V. A., and J. G. Dudley. 1998. Responses of cavity nesting birds to stand-replacement fire and salvage logging in ponderosa pine/Douglas-fir forests of southwestern Idaho. Research Paper RMRS-RP-11. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA. 23 p.

Saab, V. A., and H. Powell (Eds.). 2005. Fire and avian ecology in North America. Studies in Avian Biology 30: 1–193.

Saab, V. A., R. E. Russell, and J. G. Dudley. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. Condor 109: 97–108.

Saracco, J. F., R. B. Siegel, and R. L. Wilkerson. 2011. Occupancy modeling of Black-Backed Woodpeckers on burned Sierra Nevada forests. Ecosphere 2 (3): 1–17.

Setterington, M. A., I. D. Thompson, and W. A. Montevecchi. 2000. Woodpecker abundance and habitat use in mature balsam Fir forests in Newfoundland. The Journal of Wildlife Management 64 (2): 335–345.

Severson, K. E., and J. F. Thilenius. 1976. Classification of quaking aspen stands in the Black Hills and Bear Lodge Mountains. U.S. Forest Service Resource Paper. RM-166. 24 p.

Shinneman, D. J., and W. L. Baker. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. Conservation Biology 11: 1276–1288.

Siegel, R. B., J. F. Saracco, and R. L. Wilkerson. 2010. Management Indicator Species (MIS) surveys on Sierra Nevada National Forests: Black-Backed Woodpecker. The Institute for Bird Populations. 66 p.

South Dakota Game, Fish, and Parks. 2014. South Dakota wildlife action plan. http://gfp.sd.gov/wildlife/docs/WildlifeActionPlan-2014draft.pdf.

Tremblay, J., J. Ibarzabal, C. Dussault, and J. P. Savard. 2009. Habitat requirements of breeding Black-Backed Woodpeckers (*Picoides Arcticus*) in managed, unburned Boreal forest. Avian Conservation and Ecology 4 (1): 2.

Tremblay, J. A., R. D. Dixon, V. A. Saab, P. Pyle and M. A. Patten. 2016. Black-backed Woodpecker (*Picoides arcticus*), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/bkbwoo.

USDA Forest Service. 2005. Black Hills National Forest Revised 1997 Land and Resource Management Plan, Phase II Amendment. Final Environmental Impact Statement. Black Hills National Forest, Rocky Mountain Region, Custer, SD. 24 p. http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsm9_011678.pdf.

USDA Forest Service. 2013. Black Hills National Forest Large Fire History Map 1910-2012. https://fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5420893.pdf.

USDA Forest Service. 2014. Black Hills Regional Mountain Pine Beetle Strategy. 2 p. http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprd3801834.pdf.

Vierling, K. T., L. B. Lentile, and N. Nielsen-Pincus. 2008. Preburn Characteristics and Woodpecker Use of Burned Coniferous Forests. Journal of Wildlife Management 72 (2): 422–27.

Villard, P., and J. Schieck. 1997. Immediate post-fire nesting by Black-backed Woodpeckers, *Picoides arcticus*, in northern Alberta. Canadian Field Naturalist 111: 478–479.

Walters, B. F., C. W. Woodall, R. J. Piva, M. A. Hatfield, G. M. Domke, and D. E. Haugen. 2013. Forests of the Black Hills National Forest 2011. Resource Bulletin NRS-83. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 36 p.

White, C., and G. Giroir. 2008 Monitoring the birds of the Black Hills: 2008 field season report. Technical Report M-MBBH-USFS08, SDDGF08. Rocky Mountain Bird Observatory, Brighton, CO. 57 pp.

Wyoming Game and Fish Department. 2017. State wildlife action plan. Wyoming Game and Fish Department, Cheyenne. https://wgfd.wyo.gov/WGFD/media/content/PDF/Habitat/SWAP/Wyoming-SGCN.pdf.

Table 1. Number of parameters (K), AIC, ΔAIC, Akaike weight (AICwt) based on Akaik's Information Criteria, and cumulative Akaike weight (cumltvwt) for models evaluating detection (σ) covariates for Black-backed Woodpeckers in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, 2015-2016.

Model[1, 2]	K	AIC	ΔAIC	AICwt	cumltvwt
NB, σ(min+doy+obs+year)	17	3359.96	0	0.540	0.54
NB, σ(min+doy+obs)	16	3360.32	0.36	0.460	1
NB, σ(doy+obs)	15	3373.21	13.25	0.001	1
NB, σ(min+visit+obs+year)	18	3381.13	21.17	0.000	1
NB, σ(obs)	14	3421.34	61.37	0.000	1
NB, σ(doy)	5	3430.67	70.71	0.000	1
NB, σ(min)	5	3437.83	77.87	0.000	1
NB, σ(year)	5	3445.16	85.2	0.000	1
NB, σ(visit)	6	3447.42	87.45	0.000	1
NB, σ(.)	4	3449.65	89.68	0.000	1
P, σ(min+doy+obs+year)	16	3450.17	90.21	0.000	1
P, σ(min+doy+obs)	15	3450.8	90.84	0.000	1
P, σ(doy+obs)	14	3467.77	107.8	0.000	1
P, σ(min+visit+obs+year)	17	3476	116.04	0.000	1
P, σ(obs)	13	3524.24	164.28	0.000	1
P, σ(doy)	4	3535.38	175.42	0.000	1
P, σ(min)	4	3543.64	183.68	0.000	1
P, σ(year)	4	3554.16	194.19	0.000	1
P, σ(visit)	5	3558.35	198.39	0.000	1
P, σ(.)	3	3561.85	201.88	0.000	1

[1] Distributions: NB=Negative binomial and P=Poisson

[2] doy=day of year, min=minutes since sunrise, obs=observer, visit=visit, and year=year

Table 2. Descriptive statistics for landscape vegetation characteristics at sampling point locations and all points in BHNF used to predict the population of Black-backed Woodpeckers across the Black Hills and Bear Lodge Mountains in South Dakota and Wyoming, 2015 and 2016 with 78.5 ha area buffer.

Sample, Covariate	**Abbreviation**	**Mean**	**Min**	**Max**	**SD**
Sample points					
Green trees (%)	GT	38.48	0	88.52	14.21
Beetle killed trees (%)	RT	0.93	0	17.43	1.03
Dead trees (%)	DS	11.94	0	76.62	10.71
1- to 2-year-old wildfire (%)	F12	0.29	0	100	4.54
3-year-old wildfire (%)	F3	2.02	0	100	13.57
4- to 5-year-old wildfire (%)	F45	2.05	0	100	13.75
6- to 10-year-old wildfire (%)	F610	0.34	0	100	4.20
Latitude	lat	44.06	43.51	44.75	0.29
BHNF					
Green trees (%)	GT	35.59	0	88.52	16.23
Beetle killed trees (%)	RT	0.92	0	17.43	1.02
Dead trees (%)	DS	11.70	0	76.62	10.71
1- to 2-year-old wildfire (%)	F12	0.02	0	89.78	0.99
3-year-old wildfire (%)	F3	0.45	0	100	6.12
4-to 5-year-old wildfire (%)	F45	0.47	0	100	6.31
6- to 10-year-old wildfire (%)	F610	0.48	0	100	6.05
Latitude	lat	44.06	43.51	44.79	0.28

Table 3. Number of parameters (K), AIC, ΔAIC, Akaike weight (AICwt) based on Akaik's Information Criteria, and cumulative Akaike weight (cumltvwt) for final model combinations evaluating abundance covariates and estimating Black-backed Woodpecker abundance (λ), availability (ϕ), and detection (σ) in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, 2015 and 2016.

Model[1,2]	K	AIC	ΔAIC	AICwt	cumltvwt
λ(lat+GT+RT+DS+F12+F3+F45+yr)ϕ(.)σ(min+doy+obs+year)	25	3226.1	0	0.98	0.98
λ(GT+RT+DS+F12+F3+F45)ϕ(.)σ(min+doy+obs+year)	23	3233.86	7.76	0.02	1
λ(F12+F3+F45)ϕ(.)σ(min+doy+obs+year)	20	3258.92	32.82	0.00	1
λ(F12+F3+F45+F610)ϕ(.)σ(min+doy+obs+year)	21	3259.58	33.48	0.00	1
λ(F12+F3)ϕ(.)σ(min+doy+obs+year)	19	3266.65	40.56	0.00	1
λ(lat+GT+RT+DS)ϕ(.)σ(min+doy+obs+year)	21	3278.22	52.12	0.00	1
λ(GT+RT+DS)ϕ(.)σ(min+doy+obs+year)	20	3279.1	53	0.00	1
λ(RT+DS)ϕ(.)σ(min+doy+obs+year)	19	3281.4	55.3	0.00	1
λ(DS)ϕ(.)σ(min+doy+obs+year)	18	3296.47	70.37	0.00	1
λ(GT+RT)ϕ(.)σ(min+doy+obs+year)	19	3312.13	86.04	0.00	1
λ(lat)ϕ(.)σ(min+doy+obs+year)	18	3316.12	90.03	0.00	1
λ(GT)ϕ(.)σ(min+doy+obs+year)	18	3322.47	96.37	0.00	1
λ(RT)ϕ(.)σ(min+doy+obs+year)	18	3349.68	123.59	0.00	1

[1] doy=day of year, min=minutes since sunrise, obs=observer, visit=visit, and year=year

[2] lat=latitude, GT=green trees, RT=beetle killed trees, DS=dead trees, F12=1- to 2-year-old wildfire, F3=3-year-old wildfire, F45=4- to 5-year-old wildfire, yr=year

Table 4. Coefficients (Coeff), standard errors (SE), and 95% confidence limits (LCL, UCL) for covariates in the most supported abundance model for Black-backed Woodpeckers in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, 2015-2016.

Covariate	Coeff	SE	LCL	UCL
Intercept	0.331	0.324	-0.304	0.967
lat	-0.262	0.099	-0.456	0.068
GT	-0.100	0.095	-0.285	0.086
RT	0.286	0.056	0.177	0.396
DS	-0.032	0.094	-0.215	0.151
F12	0.155	0.031	0.094	0.216
F3	0.307	0.047	0.215	0.400
F45	0.115	0.050	0.017	0.213
2016	0.443	0.230	-0.009	0.894

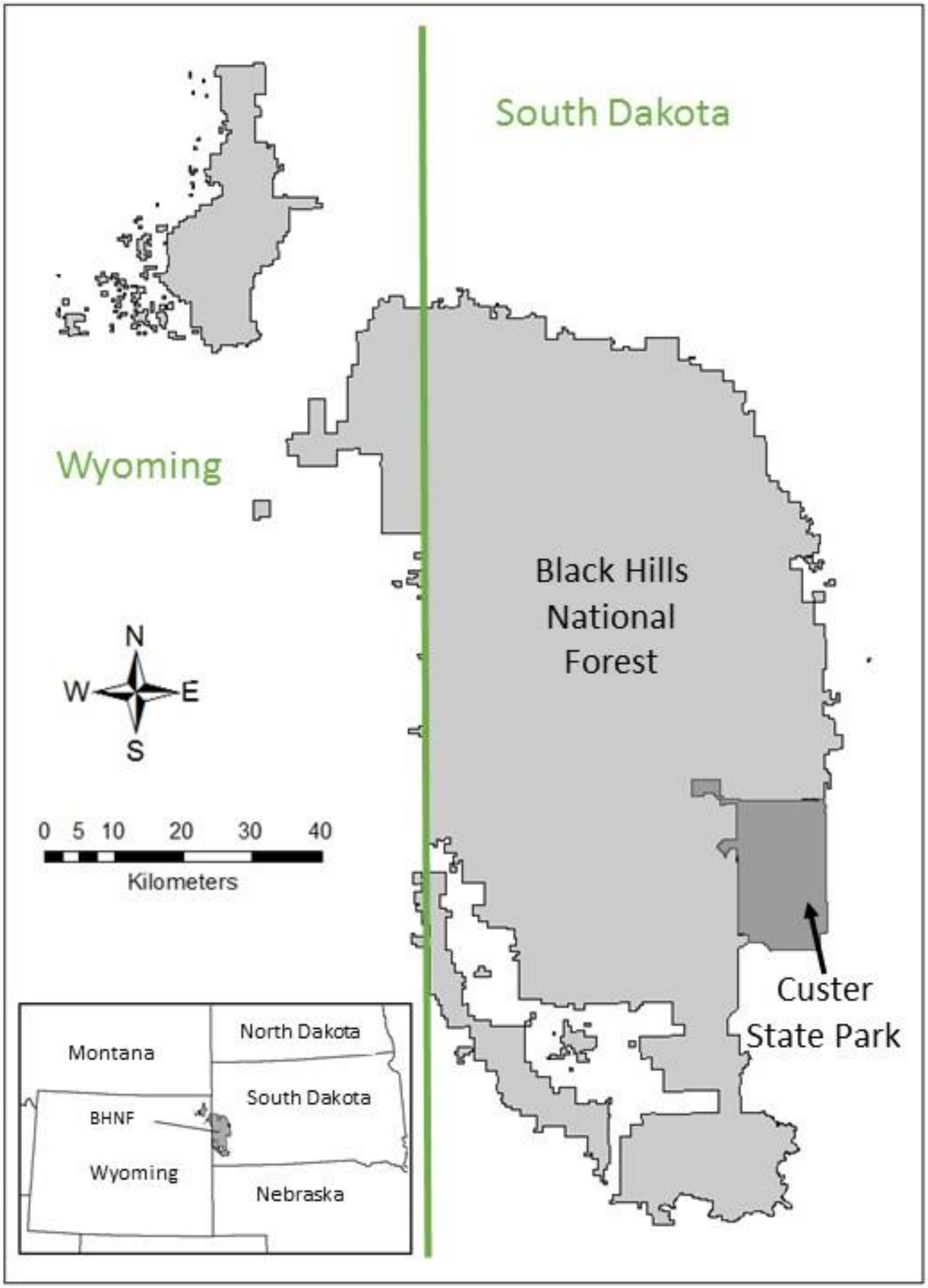


Figure 1. Study Area: Black Hills of South Dakota and Wyoming, and Bear Lodge Mountains of Wyoming.

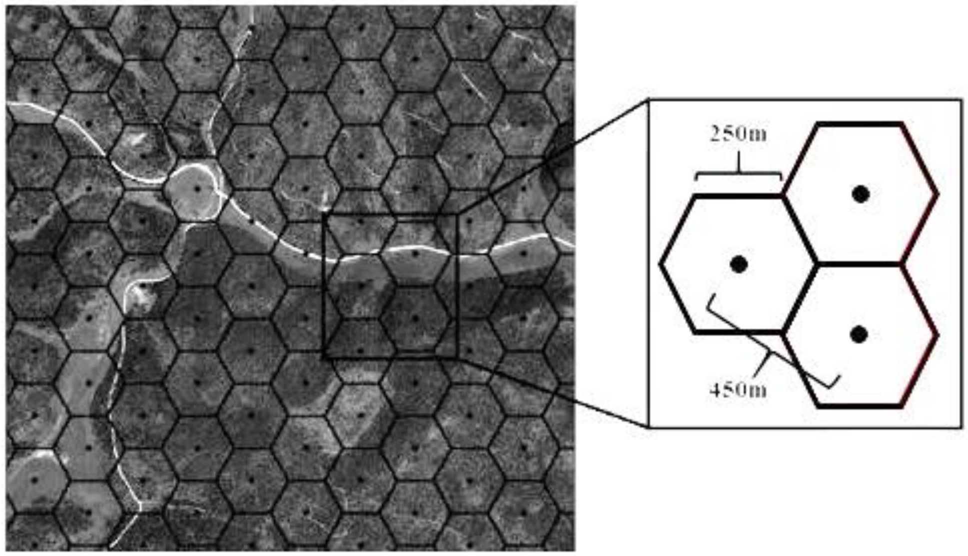


Figure 2. Hexagons (black outline) with the center point (black point) where the point count for that hexagon would take place laid over part of the Black Hills National Forest landscape.

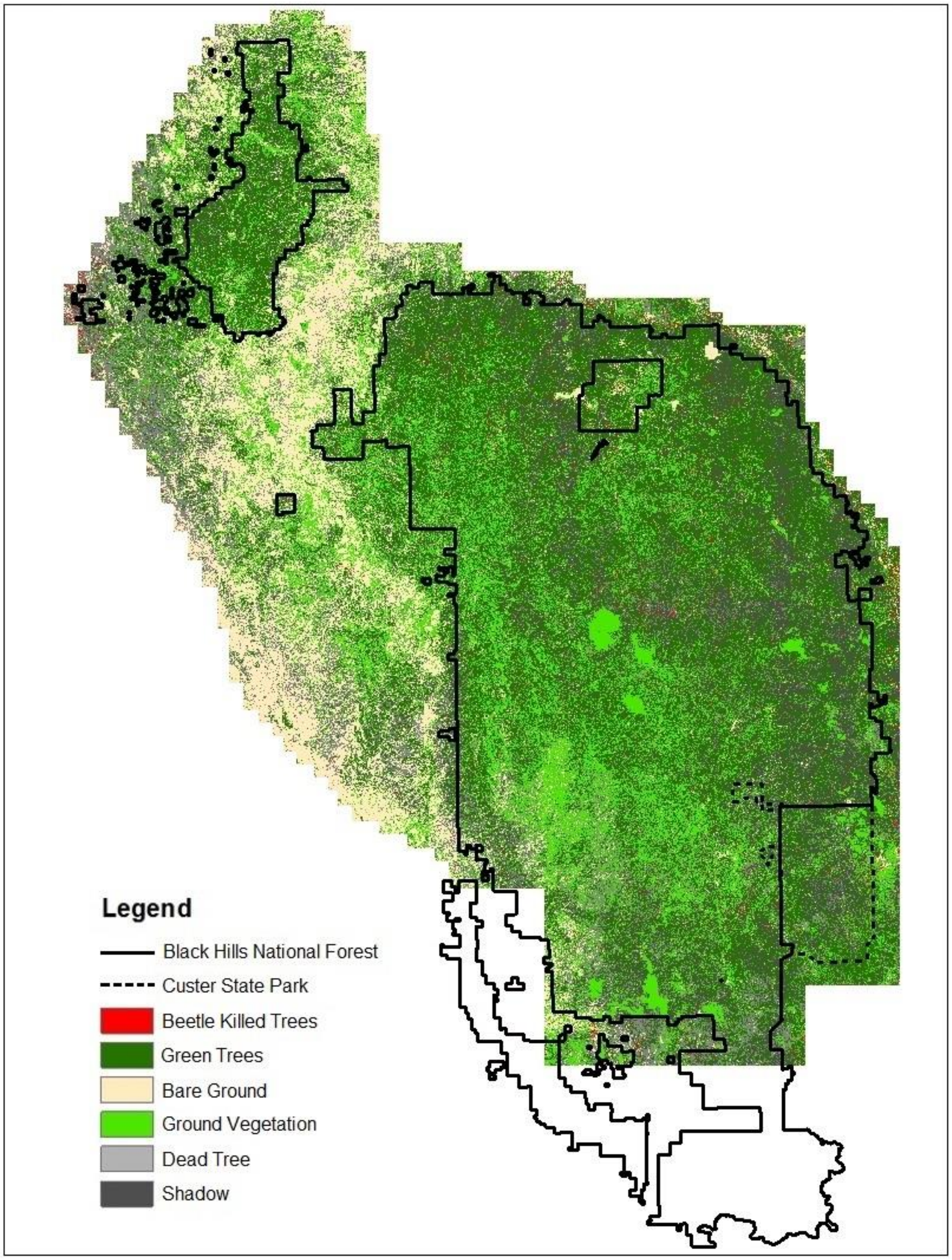


Figure 3. We classified six categories of forest vegetation on 1-m pixels from aerial photography so we could classify 16-ha hexagons as potentially low and high density to stratify sampling and for use in predicting abundance of Black-backed Woodpeckers across the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, 2015-2016.

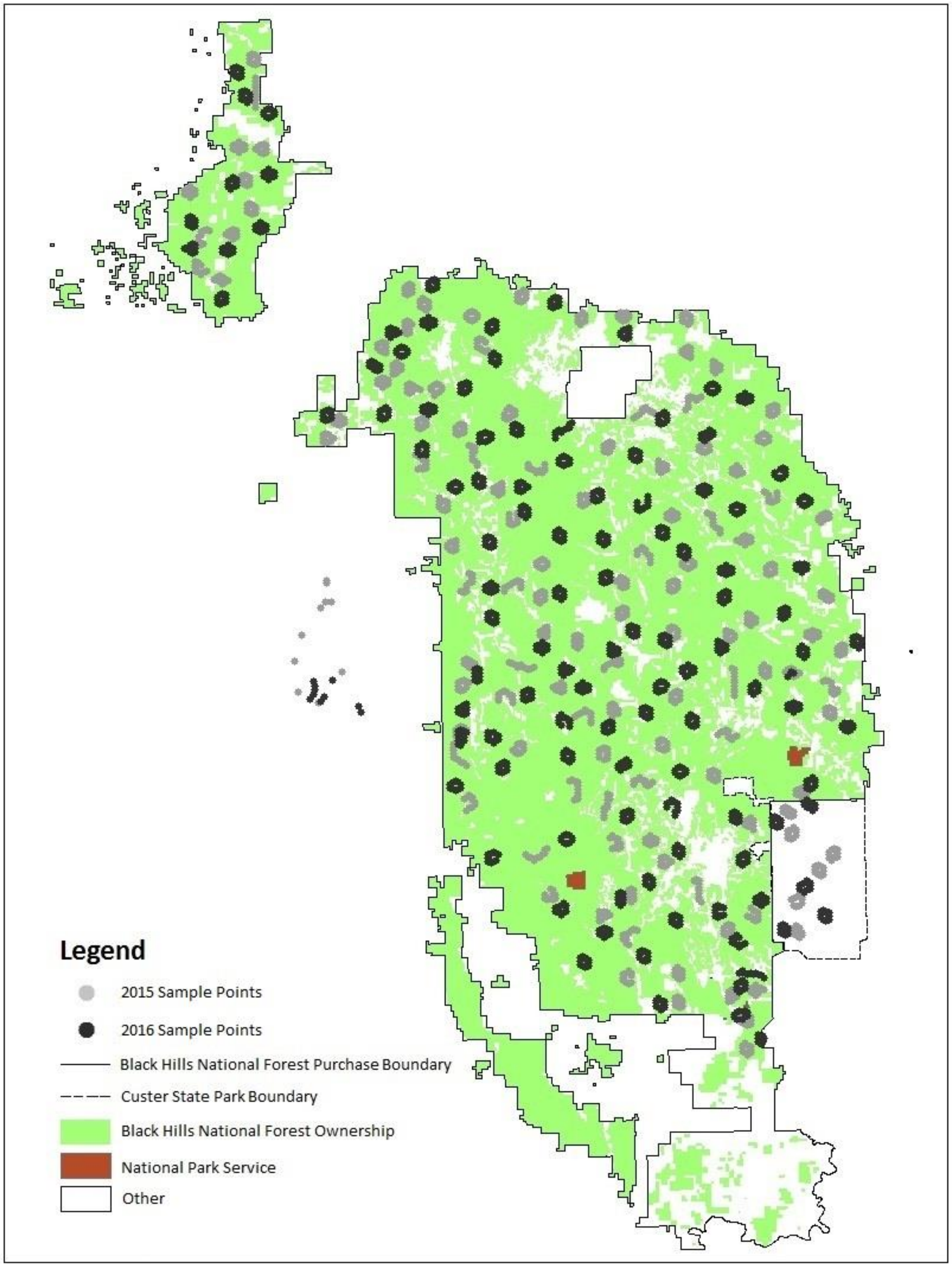


Figure 4. Black-backed Woodpecker sample point locations (N = 2370) for 2015 (light grey circles) and 2016 (dark grey circles) in the Black Hills National Forest and Custer State Park, South Dakota and Wyoming between end of March and end of June.

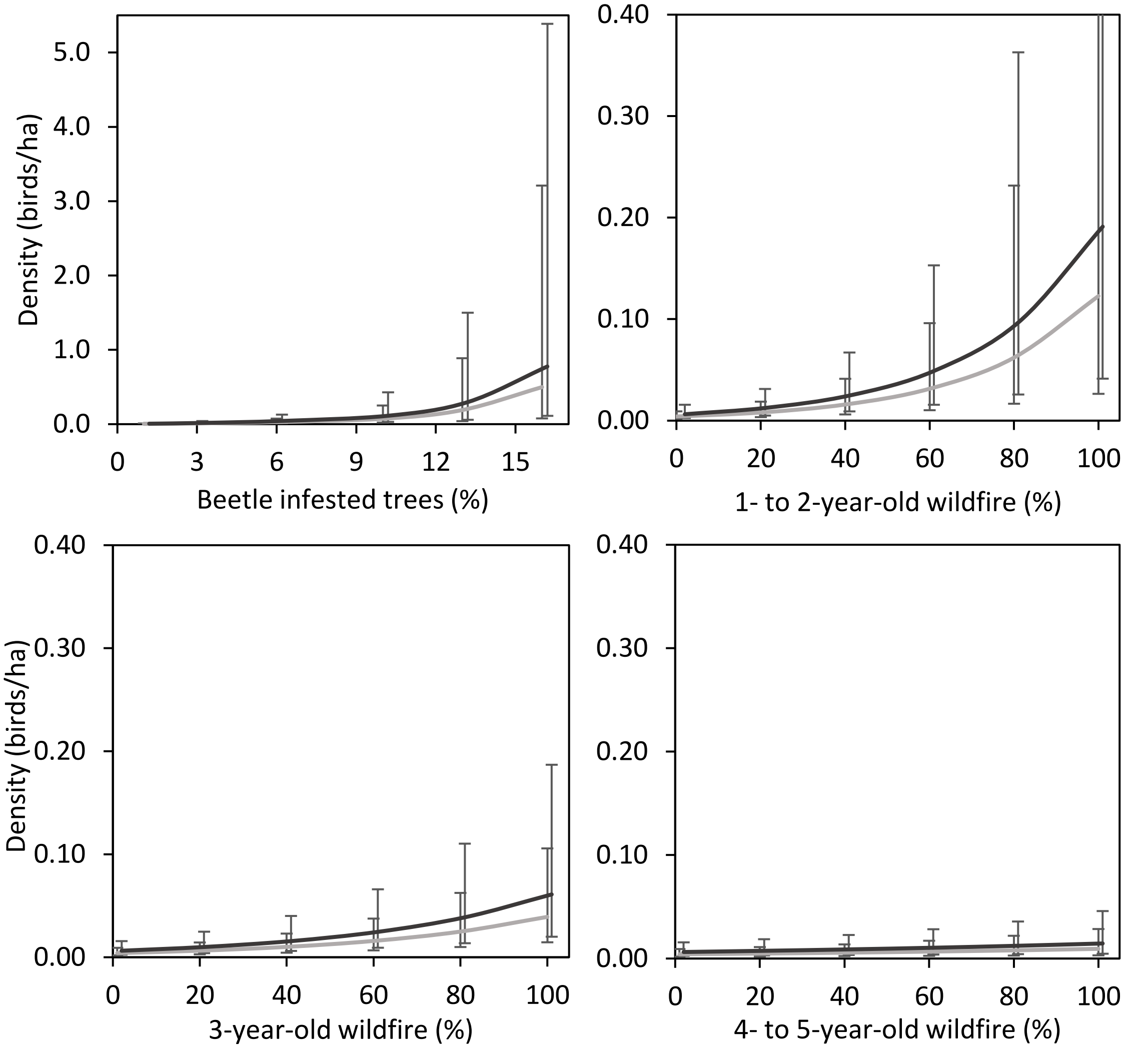


Figure 5. Predicted density and SE of Black-backed Woodpeckers across percentages of beetle killed trees, 1- to 2-year-old wildfires, 3-year-old wildfires, and 4- to 5-year-old wildfires in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, March-June 2015 (light grey) and 2016 (dark grey).

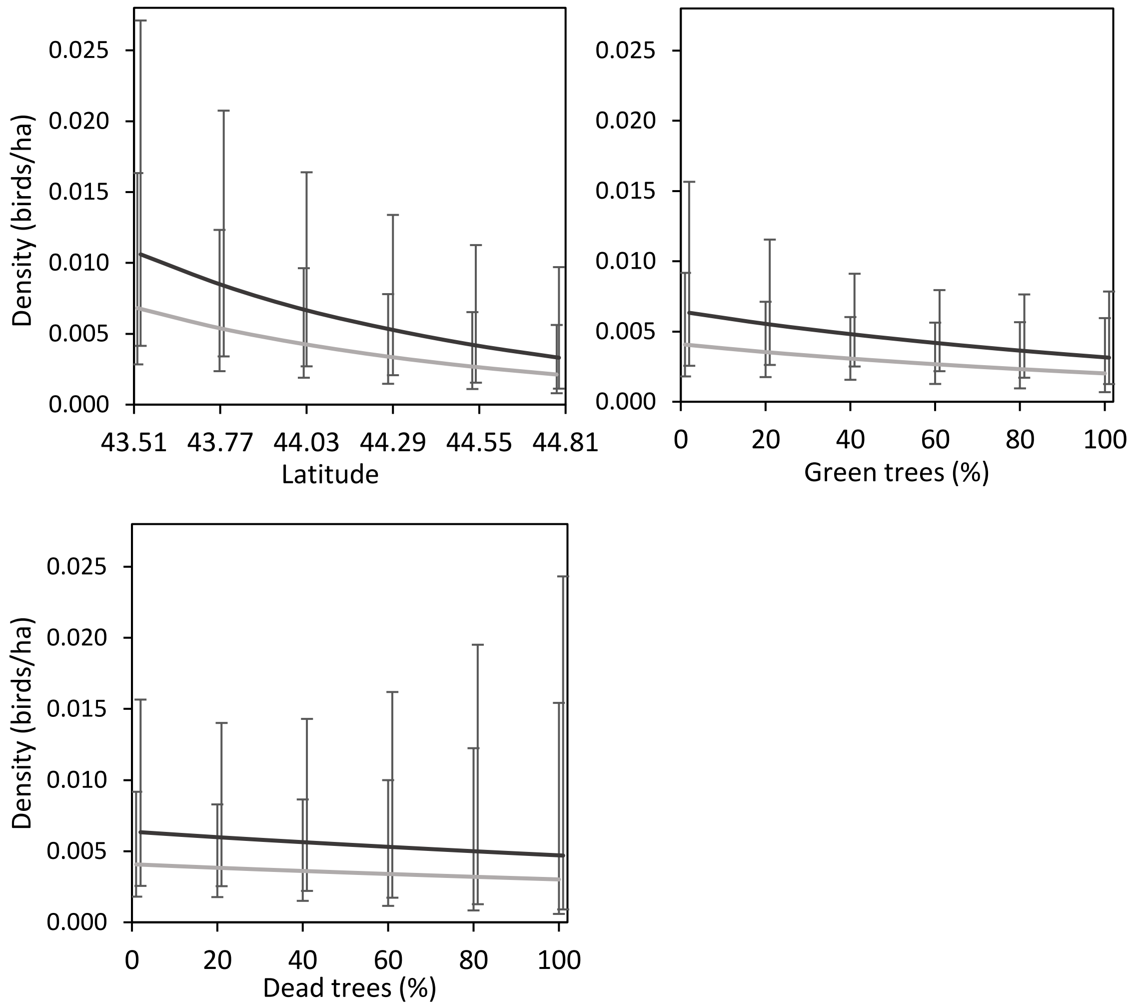


Figure 6. Predicted density and SE of Black-backed Woodpeckers across a gradient of latitude and percentages for green trees and dead trees in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, March-June 2015 (light grey) and 2016 (dark grey).

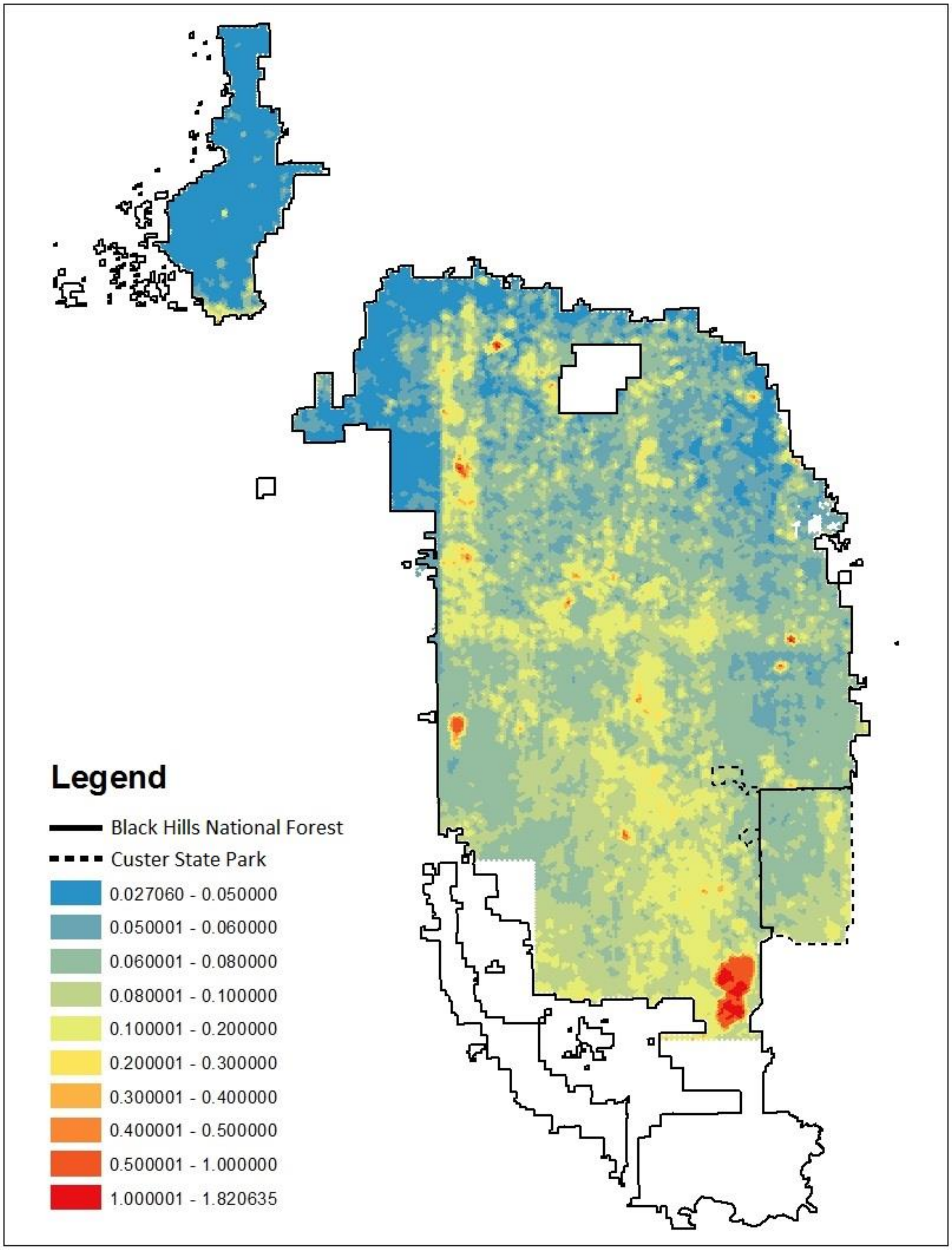


Figure 7. Abundance (birds/hexagon) across all hexagons in the Black Hills National Forest and Custer State Park in South Dakota and Wyoming, 2015.

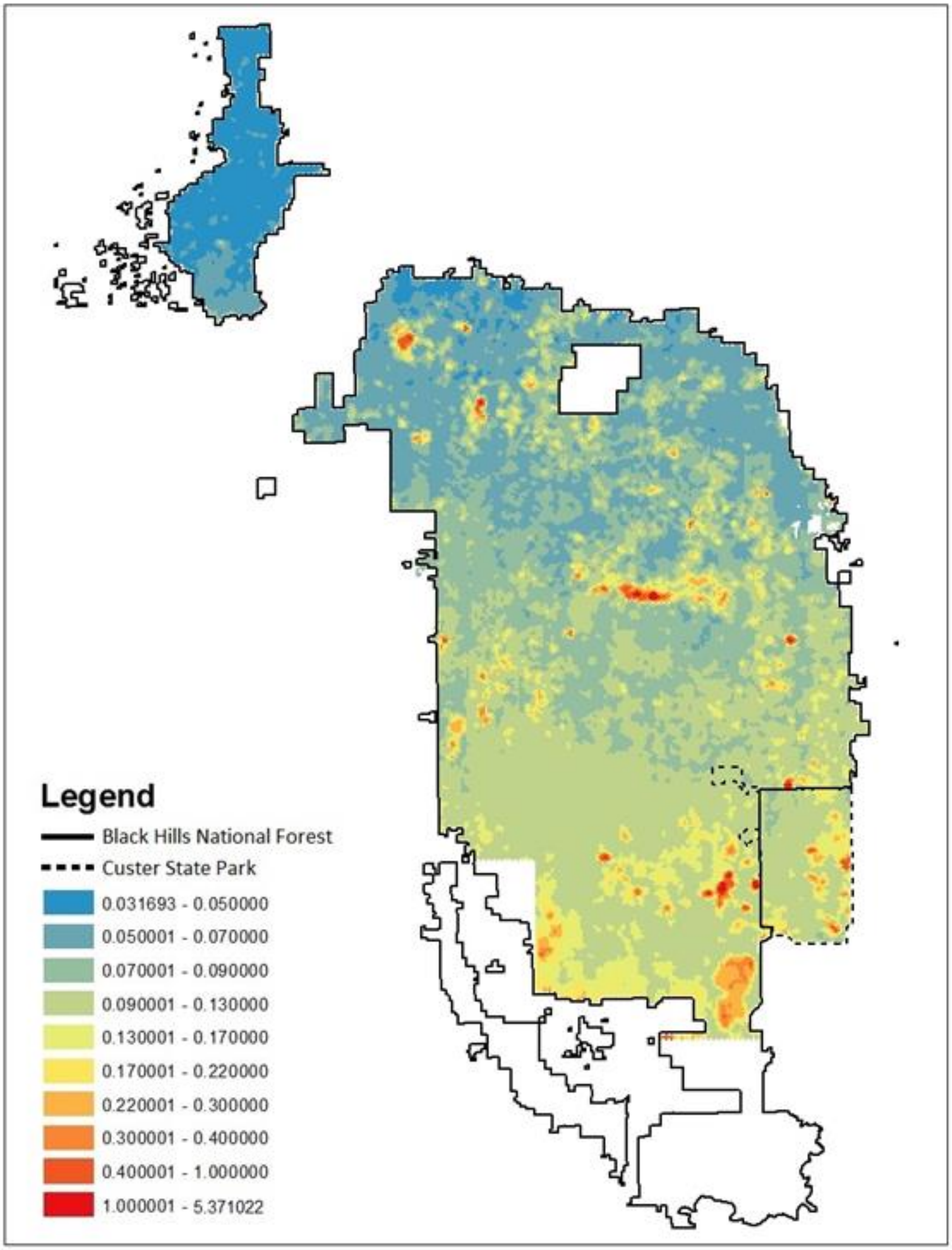


Figure 8. Abundance (birds/hexagon) across all hexagons in the Black Hills National Forest and Custer State Park in South Dakota and Wyoming, 2016.

CHAPTER 2

HABITAT ASSOCIATIONS AND ABUNDANCE OF BIRDS IN THE BLACK HILLS AND BEAR LODGE MOUNTAINS OF SOUTH DAKOTA AND WYOMING

ABSTRACT

The Black Hills is a unique environment for both eastern and western birds because of its geographic location and changes in elevation and climate conditions. Human activity and natural disturbances, such as wildfire and mountain pine beetle (*Dentroctonus ponderosae*) infestation, have recently altered forest structure in the Black Hills. Therefore, there is a need for more information on relationships between avian abundance and forest structure and disturbance. Our objective was to determine densities of American Three-toed Woodpecker (*Picoides dorsalis*), Black-backed Woodpecker (*Picoides arcticus*), Brown Creeper (*Certhia americana*), Red-breasted Nuthatch (*Sitta canadensis*), and White-winged Junco (*Junco hyemalis aikeni*) in relation to vegetation characteristics and disturbance at the point- and landscape-level in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming. We conducted 1,222 and 1,128 point counts, visiting each point three times, from late-March to late-June, across a gradient of forest structure and disturbance types. We estimated densities using three-level hierarchical time-removal models that simultaneously estimated abundance, availability, and detection probability. Black-backed Woodpeckers were positively related to percent area 1- to 3-year-old wildfires and Brown creepers were positively associated with percent area in 4- to 5-year-old wildfires; however, Red-breasted Nuthatches were negatively related to percent area in 3- to 5-year-old wildfires. With the exception of American Three-toed Woodpeckers, species were positively related to percent cover of beetle killed trees. Brown Creepers, White-winged Juncos, and Red-breasted Nuthatches had mixed responses to percent overstory canopy cover. White-winged Juncos also had a positive association with percent ground vegetation at the

point- and landscape-level, whereas, Brown Creepers were strongly linked with white spruce (*Picea glauca)* vegetation type. American Three-toed Woodpeckers, which are thought to occupy spruce forest in the Black Hills, did not show a strong relationship with any covariates. Maintaining some areas of natural disturbances along with heterogeneity of vegetation characteristics within stands and at the landscape-scale will benefit the diverse needs of birds in the Black Hills. Continued monitoring of these species along with further understanding of the breeding benefits these disturbances, specifically beetle infestations, provide are needed.

INTRODUCTION

Often described as the "Island in the Plains" the Black Hills is a predominantly ponderosa pine (*Pinus ponderosa*) forest isolated from similar habitats in the Rocky Mountains by mixed-grass prairies and shrub-steppe ecosystems (Raventon 1994, Boldt and Van Deusen 1974). Natural disturbances and human activity play a significant role in altering forest structure in the Black Hills. Historically, the forest consisted of open stands containing large trees to few dense stands with frequent low intensity ground fires (Brown and Cook 2006). Human settlement in the Black Hills has resulted in fire suppression, altering the occurrence of natural fire regimes; thus, forests contain younger, smaller trees and are denser than they are thought to have been historically (Fule´ et al. 1997, Brown and Cook 2006). Insect outbreaks, such as Mountain pine beetle (*Dentroctonus ponderosae*, hereafter MPB), are another disturbance that alters stand structure in the Black Hills. MPB populations occur at endemic levels with periodic outbreaks every 20 years lasting 6-18 years (Graham et al. 2016), resulting in a widespread loss of trees significantly altering structure, composition, and function of forests (Raffa et al. 2008).

The Black Hills is the most heavily and intensively managed forest in the Rocky Mountain region of the Forest Service (Alexander and Edminster 1981). It is managed for multiple uses including wildlife, grazing, and recreation, but timber production is an important goal (USDA

Forest Service 2005). Timber harvest in the Black Hills began with human settlement in the late 1800s. Almost all of the managed forest has been cut over once, with some areas receiving multiple partial cuts. This management has resulted in a landscape dominated by second-growth forest containing small, scattered old-growth stands (Boldt and Van Deusen 1974, Alexander and Edminster 1981, Shepperd and Battaglia 2002). Currently, shelterwood logging is used for timber harvest throughout the forest, but post-fire salvage logging and sanitation logging after fire or MPB infestations are commonly used to mitigate economic losses (Boldt and Van Deusen 1974, Nappi et al. 2004).

The Black Hills creates a unique environment for many species, but the bird community is unusual in that both eastern and western species are present (Dykstra et al. 1997, Mills et al. 2000). Black Hills bird composition can be significantly altered by timber harvest or natural disturbances. More species had greater abundances in forests recently burned by wildfire than other vegetation type in the Black Hills (Beason et al. 2006). Relationships between bird abundance and richness with MPB infestations vary for avian foraging guilds in British Columbia (Drever et al. 2009), but recent long-term monitoring efforts in the Black Hills did not assess bird response to beetle outbreaks (White and Giroir 2008). In Saskatchewan, resident species, canopy and cavity nesters, and insectivorous bird species are least likely to be detected in areas where salvage logging had taken place after a disturbance (Morissette et al. 2002). Other studies have shown lower nesting densities of cavity nesters in areas of recent post-fire salvage logging (Saab and Dudley 1998, Hutto and Gallo 2006, Saab et al. 2007). In the Black Hills species richness did not change between unharvest and harvested stands, but rather species composition was different in the two types of forest structure (Dykstra et al. 1997). Given this range of responses among species to disturbances and management, it is unclear how birds are responding to changes in forest structure in the Black Hills.

Birds are often excellent indicators of ecosystem health and can be easily monitored. Furthermore, there are many species in the Black Hills that are of conservation concern and sensitive to natural disturbances and forest management practices. One species, the Black-backed Woodpecker was recently petitioned to be listed as an endangered or threatened species under the Endangered Species Act (Hanson et al. 2012). The American Three-toed Woodpecker is a rare permanent resident of the Black Hills and listed as a "Species of Greatest Conservation Need" in South Dakota (South Dakota Department of Game, Fish and Parks 2014). Brown Creepers are reportedly sensitive to a variety of forest management practices and an important indicator of forest health (Wiggins 2005) and are a "Management Indicator Species" in Region 2 of the U.S. Forest Service (USDA Forest Service 2005). The White-winged Junco (*Junco hyemalis aikeni*) is a subspecies of the Dark-eyed Junco (*Junco hyemalis*) and is generally common to abundant in most wooded habitats of the Black Hills (Mills et al. 2000), but is a "Species of Greatest Conservation Need" in South Dakota because it is endemic to the Black Hills region (South Dakota Department of Game, Fish and Parks 2014). The Red-breasted Nuthatch (*Sitta canadensis*) is abundant and their population is generally stable in the Black Hills, but they require high snag densities, which could be impacted by forest management practices (Mills et al. 2000).

More information on absolute abundance of these species in relation to forest structure, disturbance, and landscape composition would better inform conservation and management in the region. The Black Hills recently experienced one of the largest MPB outbreaks in the last 100 years (Graham et al. 2016) and varying levels of wildfire throughout the forest, which provides a unique opportunity to study how species are responding to these disturbances. Our objective was to determine densities of five focal species in relation to vegetation characteristics and disturbance at the point- and landscape-level in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming.

STUDY AREA

Our study area included 554,627 hectares of the Black Hills National Forest (BHNF) and Custer State Park (CSP) in southwest South Dakota and the Bear Lodge Mountains in northeast Wyoming (Figure 1). The southern portion of the area receives less rainfall, contains a more grassy understory, and pine forests integrated with native mixed-grass prairies to form a unique landscape. Conversely, the northern Black Hills receives more rainfall and supports a denser under and mid-story and has a more widespread deciduous component (Driscoll et al. 2000, Shepperd and Battaglia 2002). This gradient of habitat types throughout the Black Hills supports a wide diversity of avian species.

Most of the Black Hills is dominated by ponderosa pine with quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*) occurring less frequently and mostly in northern, wetter portions of the forest (Hoffman and Alexander 1987, Walters et al. 2013). Understory vegetation is comprised of western snowberry (*Symphoricarpos occidentalis*), white coralberry (*S. albus*), juniper (*Juniperus comunis*), and kinnikinnick (*Arctostaphylos uvaursi*) (Hoffman and Alexander 1987, Severson and Thilenius 1976) along with a diversity of native and non-native grasses, sedges and forbs.

Wildfires in the Black Hills have ranged in size from 5 ha (13 ac) to 33,795 ha (83,510 ac) and have burned more than 19,836 ha (49,018 ac) in the past 10 years (USDA Forest Service 2013). The Black Hills is currently on the back end of the largest, and intensive MPB epidemic in the last 100 years (Graham et al 2016). Approximately 188,583 ha (466,000 ac, about a quarter) of the Black Hills has been affected since the outbreak began in 1996, but recent evidence shows the epidemic reached its peak in 2012 and the rate of infestation is declining (Graham et al 2016). Roughly 50-60% of the BHNF has been affected by natural disturbances since the late 1990s, creating unique vegetation patterns throughout the forest.

METHODS

Sampling design

We used a stratified-random sampling design for our point count surveys because of the widespread and scattered MPB infestation and limited area of recent wildfires. We generated a grid of hexagons across the BHNF and CSP and the center point of each hexagon represented a potential point count site (Figure 2). Each hexagon was 16.28 ha (40 ac) in area and approximately 450m from center to center. The status and extent of the MPB epidemic in the BHNF has been mapped annually using color and infrared aerial photography since 2010. We obtained the most recent infrared photography available (2014 and 2015) and re-sampled it to create a 1-m resolution raster. We conducted a supervised classification to classify forested pixels as live trees (green trees), dead trees with needles (beetle killed trees), and dead trees with no needles (dead trees), bare ground, ground vegetation, and shadow (Figure 3). We acquired the most recent wildfire history for the BHNF and calculated the percent area in each hexagon affected by fire. We categorized wildfire as burned 1- to 2-, 3-, 4- to 5-, and 6- to 10-years ago and then intersected the hexagon grid with the raster to calculate the percent of each hexagon represented by each class.

We randomly selected starting points for point-transects points such that 20% occurred in undisturbed habitat and 80% occurred in disturbed habitat. We sampled disturbed points in greater proportion to their availability to ensure we had sufficient detections to fit abundance models of uncommon species, such as the Black-backed Woodpecker, which were more likely to occur in disturbed habitat. To avoid noise factors associated with roads we picked starting points that were at least 100m off a road. We laid out the remaining 9 points in a transect from starting points in ArcGIS along a path that maximized sampling efficiency. Transects contained a maximum of 10 points because that was the estimated number of points a technician could complete in a morning. We placed 124 transects (1,232 sampling points) and 115 transects (1,138 sampling points) in 2015 and 2016, respectively (Figure 4).

Avian surveys

We surveyed abundance of five focal species (Table 1) from 1 April through 28 June 2015 and 31 March and 23 June 2016. We conducted 5-minute point counts at sampling points three times each year, approximately one month apart, resulting in 3,696 and 3,414 point counts in 2015 and 2016, respectively. Surveys were conducted on days with minimal or no precipitation and light to moderate wind speeds. Surveys began at official sunrise and terminated approximately six hours later. We navigated to each point using a Global Positioning System (GPS) unit. For each survey we recorded the point number, observer, Universal Transverse Mercator (UTM) coordinates, visit number, time, date, and weather conditions (temperature, wind speed, cloud cover, and precipitation). We recorded the time of the first detection, distance to the individual (using a digital laser range finder), and detection type (e.g. drum, song, call, or visual) of each individual. Observers were trained in bird species identification and distance estimation prior to the start of the field season.

Vegetation variables

We measured basal area, dominant tree species, dominant size class, overstory canopy cover, and understory vegetation at each sampling point. We measured basal area, dominant tree species, and dominant size class in April, overstory canopy cover in May, and understory vegetation in June. We estimated basal area with a 10-factor prism. We identified the dominant tree species and dominant size class based on trees within an 11.3 m radius. We classified dominant tree species as aspen, hardwood, ponderosa pine, spruce, and none to minimize the number of categories and aid with model convergence. We classified dominant tree size class as: none, sapling (<12.5 cm DBH), pole timber (12.5-27.5 cm DBH), and saw timber (>27.5 cm DBH). We measured percent canopy cover as the mean of four readings with a concave spherical densitometer at the point in each of the cardinal directions (Sharpe et al. 1976). We estimated the percentage of grass/forb cover and woody vegetation within an 11.3 m radius and allowed the sum to exceed 100 because vegetation categories could be multi-layered.

Analytical methods

We used three-level hierarchical time-removal models that simultaneously estimated abundance (λ), availability (ϕ), and detection probability (σ). This model permits repeated visits to a single point within a season by estimating availability, the probability that an individual is present and provides a detectable cue, and detection, the probability of the observer detecting said cue (Chandler et al. 2011). Simpler models that estimate abundance for unmarked individuals included a geographical closure assumption (i.e. no immigration or emigration during the survey period (Royle 2004), which is often violated by species that have larger home ranges because they are more mobile and likely to leave the survey plot during sampling (Chandler et al. 2011). Two of our focal species, Black-backed Woodpeckers and American Three-toed Woodpeckers, have large home ranges in the Black Hills and would likely violate this closure assumption across three visits to a point (Goggans et al. 1989, Rota et al. 2014b). Therefore, we used a model that relaxes this assumption and allows for temporary emigration. We assumed the estimated abundance represented the super-population available for detection across all visits in a year, therefore the average abundance during any one visit was $\lambda \times \phi$ (Fiske and Chandler 2015).

We used a model selection approach and Akaike's Information Criterion (AIC) to assess support for *a priori* candidate models that measure the effects of point-level and landscape-level vegetation variables on densities for each of our five focal species. We fit models using the gmultmix function in the R package "unmarked" (Fiske and Chandler 2015). We assigned species detections into five 1-minute intervals and modeled species abundance using a Poisson or negative binomial distribution. We truncated observations for each focal species by removing the top 5-10% of detection distances per recommendations in distance sampling (Buckland et al. 2001) to remove extreme values and define the sampled area for each species. We estimated density as: birds/ha = $\lambda \times \phi \times (pi \times r^2 \times 10000^{-1})^{-1}$, where r was the species-specific truncation distance. We standardized all continuous covariates to a mean of zero to facilitate model convergence (Fiske and Chandler 2015).

We used a multi-stage model selection approach to evaluate *a priori* candidate models for each focal species. We first fit candidate models for detection probability with singular and multiple combinations of detection covariates (day of year [doy], minutes since sunrise [min], observer [obs], visit [visit], and year [year]) with both Poisson and negative binomial distributions, which resulted in 20 competing models. We selected the top-ranked model for use with abundance covariates.

We evaluated abundance covariates in four stages: landscape-level wildfire, landscape-level vegetation cover, point-level vegetation, and with and without latitude and year. We *a priori* constructed three landscape-level wildfire, seven landscape-level vegetation, and 11 point-level vegetation models for all species except the white-winged junco, which differed slightly by having six landscape-level vegetation and 13 point-level vegetation models. Landscape-level wildfire covariates included: percent area burned 1- to 2-years ago, 3-years ago, 4- to 5-years ago, and 6- to 10-years ago. Landscape-level vegetation covariates were percent cover green trees (GT), beetle killed trees (RT), dead trees (DT), and ground vegetation (GV). Point-level vegetation measurements were basal area (ba), dominant tree species (dt), dominant size class (sc), overstory canopy cover (cc), percent grass/forb cover (gr), and percent woody vegetation (wo). The most-supported models from each category were then combined and evaluated with and without year and latitude. If the top ranking detection model was the most-supported model in a category we did not include any covariates from that category in the final combination stages. This approach resulted in 24 competing models specific to each species, except white-winged juncos which had 25 competing models. We did not model covariate effects on a bird's availability for detection (ϕ).

Candidate models for each species were ranked using AIC and we evaluated goodness-of-fit for the top-ranked model using the Freeman-Tukey test with parametric bootstrap for 100 simulations (Fiske and Chandler 2015). We predicted species abundance from the most-supported model or model averaged predictions if there were competing models with ΔAIC < 2; however, we did not include models that incorporated additional uninformative parameters to a more supported model (Arnold 2010). We predicted species abundance for all focal species across the ranges of supported density covariates while holding landscape-level covariates at zero and latitude and point-level vegetation at their mean, expect for dominant tree species and size class which we held at ponderosa pine and saw timber, respectively. We only interpreted relationships of covariates when confidence limits did not overlap zero, except where specifically noted. We converted abundance to densities for ease of interpretation.

RESULTS

We assessed vegetation characteristics at 1,222 and 1,128 sampling points in 2015 and 2016, respectively. Vegetation at sampling points ranged from grassy meadows or open habitat with disturbances to closed canopy ponderosa pine stands (Table 2). We had 41-5,848 detections per species and we fit abundance models for all five focal species (Table 1, Appendix

A1). There was no evidence of lack of fit for the most-supported model of any species based on goodness-of-fit tests ($P > 0.10$).

Top detection models were similar for some species and differed for others (Table 3). Detection probability for Black-backed Woodpeckers and American Three-toed Woodpeckers was related to day of year, minute, observer, and year. Detection probability of Brown creeper was related to day of year and minute and detection probability for White-winged Junco and Red-breasted Nuthatch was related to minute, visit, observer, and year. The negative binomial distribution was supported for modeling abundance of all species except Red-breasted Nuthatch, for which the Poisson model had more support.

Landscape-level wildfire covariates were supported for Black-backed Woodpeckers, Brown Creepers, and Red-breasted Nuthatches (Table 3). Black-backed Woodpeckers and Brown Creepers were positively related to percent area of 1- to 3-year-old and 4- to 5-year-old wildfires, respectively, while Red-breasted Nuthatches were negatively related to percent area of 3- to 5-year-old wildfires (Appendix A1). Black-backed Woodpecker densities increased 0.0027 – 0.0324 birds/ha and 0.0027 – 0.0214 birds/ha across the range of percent area 1- to 2-year-old and 3-years-old wildfires, respectively (Figure 5). Brown Creepers density increased from 0.075-0.119 birds/ha as percent area of 4- to 5-year-old wildfires increased (Figure 5). However, Red-breasted Nuthatches densities decreased from 0.20-0.08 birds/ha and 0.20-0.11 birds/ha across the range of percent area 3-year-old and 4- to 5-year-old wildfires, respectively.

The supported landscape-level vegetation covariates varied among species, but almost all focal species had a strong positive relationship to percent cover of beetle killed trees (Appendix A1). Black-backed Woodpeckers densities increased from 0.0027-0.0425 birds/ha across a range of 0-16 percent cover of beetle killed trees (Figure 6). Similarly, Brown Creepers (0.075-0.347 birds/ha), White-winged Juncos (0.21-0.53 birds/ha), and Red-breasted Nuthatch

(0.20-0.29 individual/ha) densities also increased as percent cover of beetle killed trees increased from 0-16 (Figure 6). Conversely, percent cover of dead trees had a negative effect on abundances of two of our focal species (Appendix A1). Red-breasted Nuthatch densities decreased from 0.20-0.12 birds/ha as percent cover of dead trees increased (Figure 7). American Three-Toed Woodpeckers also responded negatively to percent cover of dead trees, but confidence intervals contained zero (Appendix A1). White-winged Juncos were the only species to show a strong association with percent cover of ground vegetation and green trees. White-winged Junco densities increased from 0.21-0.38 and 0.21-0.33 birds/ha when percent ground vegetation and green trees increased, respectively (Figure 7).

There was weaker support for point-level vegetation covariates and many confidence intervals overlapped zero for all of our focal species (Appendix A1). However, Brown Creepers had the highest densities when the dominant tree type was spruce (0.15 birds/ha) and increased densities from 0.024-0.081 birds/ha when overstory canopy cover ranged from 0-80 percent (Figure 8). White-winged Junco density increased slightly when percent grass/forb cover increased from 0-100 percent (0.19-0.23 birds/ha), but densities decreased as overstory canopy cover increased from 40-100 percent (0.22-0.15 birds/ha) (Figure 8). Lastly, densities for Red-breasted Nuthatches ranged from 0.15-0.19 birds/ha as percent overstory canopy cover increased from 0-80 percent (Figure 8).

Abundance of Black-backed Woodpecker and Red-breasted Nuthatches were related to latitude (Appendix A1). Black-backed Woodpecker density decreased from 0.0048-0.0013 birds/ha, whereas, Red-breasted Nuthatches density increased from 0.14-0.31 birds/ha as latitude ranged 43.51-44.76 (Figure 9). Year was included in all of the top models for Black-backed Woodpeckers, Red-breasted Nuthatches, and White-winged Juncos, but confidence intervals encompassed zero for Black-backed Woodpeckers and White-winged Juncos (Appendix A1).

DISCUSSION

Wildfires can significantly alter forest structure creating unique habitat that attracts many plant and animal species. Abundance of Black-backed Woodpecker, Brown Creepers, and Red-breasted Nuthatch were positively related to the presence of wildfire in the Black Hills. Black-backed Woodpeckers are known to be strongly associated with burned habitats (Hutto 2008). Black-backed Woodpeckers have higher fledgling rates, juvenile survival, nesting success, and positive population growth in wildfire habitat as compared to MPB infestations and prescribed burns (Rota et al. 2014a). Black-backed Woodpeckers likely had a stronger positive response to percent cover of 1- to 2-year-old wildfires than 3-year-old wildfires because of a decline in availability of their main food resource, wood-boring beetles (Goggans et al. 1989, Murphy and Lehnhausen 1998, Powell et al. 2002). Furthermore, Black-backed Woodpeckers did not have a strong association with 4- to 5-year-old wildfires suggesting these areas are not beneficial. Despite their strong association with mature, old-growth forests (Sallabanks et al. 2006), Brown Creepers have been shown to be more abundant in burned compared to unburned areas (Morissette et al. 2002). In our surveys Brown Creepers had a strong positive relation to percent cover by 4- to 5-year-old wildfires. Previous surveys in the Black Hills have shown Brown Creeper detections to be 2 times greater in 4- to 5-year-old wildfires than any other year surveyed, but detections for the species were extremely low (<10) (Panjabi 2005, Hutton et al. 2006). Brown Creepers need large, loose pieces of bark to nest, which is more predominant on trees as year since burn increases (Poulin et al. 2013). Red-breasted Nuthatches prefer to forage in the canopy of live trees (Ghalambor and Martin 1999) and are generally thought to avoid burned areas all together (Bock and Lynch 1970, Raphael and White 1984).

Majority of the wildfires we surveyed were in high intensity fires, which greatly reduces canopy cover and is likely why we see a negative association with Red-breasted Nuthatch and habitats created by wildfires.

MPB outbreaks are another source of natural disturbance that can also have a significant effect on avian biodiversity by altering nesting, roosting, and foraging resources (Martin et al. 2006). All of our focal species, except American Three-toed Woodpecker, had a positive association with percent cover of beetle killed trees. Black-backed Woodpeckers, Brown Creepers, and White-winged Juncos showed their highest densities in hexagons with a modest percentage of beetle killed trees. MPB outbreaks provide a pulse in resource availability, such as food and nest sites, leading to increased population abundances, which can be followed by sharp decreases when resources are depleted (Ostfeld and Keesing, 2000). Increased down trees and grass growth is likely why we and others found a positive association between juncos abundance and MPB outbreaks (Saab et al. 2014). Brown Creepers were also positively related to percent cover by beetle killed trees, but past research shows a mixed response by this species to MPB outbreaks (Saab et al. 2014). Nuthatches also had a positive relationship with percent cover of beetle killed trees, which is consistent with previous research that observed increased nesting and positive population growth for the species in beetle infestations (Norris and Martin 2008). Black-backed Woodpeckers are known to rapidly colonize beetle outbreaks due to the increase in resources (Goggans et al. 1989, Bonnot et al. 2008, Bonnot et al. 2009, Rota et al. 2014a). However, they have slightly negative population growth, decreased nesting success, and lower demographic rates in beetle infestations compared to wildfires (Rota et al. 2014a). Other research has shown an increase in woodpecker abundances in areas of MPB outbreak as compared to pre-outbreak levels, but saw no change in fecundity (Edworthy et al. 2010). Recent bird surveys between 2000 and 2007 looked at a variety of habitats in the Black Hills, but did not assess bird response in beetle infested forests (White and Giroir 2008). While these areas may look attractive due to the increased resource availability, the breeding benefits this habitat provides to our focal species is unclear. Further research on how species nesting success and population size are responding to MPB infestations is needed to determine the value this disturbance provides to other birds species in the Black Hills.

White-winged Juncos were the only ground nesting species and the only species associated with greater percent cover by ground vegetation and green trees at the landscape-level scale. White-winged Juncos were also positively associated with ground vegetation at the landscape-level and grass/forbs cover at the point-level. Clawges et al. (2008) found that juncos were significantly associated with 0.5-2.0 m vegetation cover in pine-dominated stands of the Black Hills. Juncos rely on understory cover for nesting and foraging (Holmes and Robinson 1988), which explains the strong association with ground vegetation cover at the point- and landscape-level. Juncos were positively related to percent cover of green trees at the landscape level, but negatively related to overstory canopy cover at the point-level. Juncos are primarily a forest and forest edge species that are widespread and abundant in the Black Hills (Mills et al. 2000). Their increased abundance with increased percent cover of green trees at the landscape-scale is likely a reflection of their preference for forested habitat. However, at the point-level juncos prefer a more open canopy allowing more understory vegetation to grow and provide suitable nesting and foraging habitat. Previous studies in the BHNF have also reported decreased junco abundances as overstory canopy cover increases above 40% (Mills et al. 2000).

Only three of five focal species had strong associations with point-level vegetation characteristics. Brown creepers densities peaked at 80% point-level overstory canopy cover. Brown Creepers prefer dense, mature stands of ponderosa pine, displaying some of the highest densities when canopy cover is > 70% (Mills et al. 2000, Anderson and Crompton 2002). They also showed a strong relationship with spruce habitat in our study, this coincides with previous research that showed higher Brown Creeper densities in spruce compared to any other habitat surveyed (Panjabi 2003). While only 4% of our sampling points were in spruce forests this habitat is largely untouched in the Black Hills because it is not managed for timber. This habitat produces large diameter old-growth trees which are conducive to Brown Creepers foraging and nesting preferences (Weikel and Hayes 1999, Poulin et al. 2008). At the point-level, Red-breasted Nuthatch density was highest between 60-80% overstory canopy cover. Mills et al. (2000) repeatedly observed nuthatches select mature and multi-storied ponderosa pine stands with moderate to high canopy cover. Other studies in the Black Hills also showed nuthatch densities to be highest in late-successional pine habitat (Beason et al. 2006). While our woodpecker species included point-level covariates in their top models all confidence intervals overlapped zero. Their lack of association with point-level variables could be a reflection of their larger home range sizes, meaning they are more dependent on variables at the landscape-level because they encompasses vegetation characteristics at a broader scale. Furthermore, our point-level measurements only encompass a small area around each point, which we are assuming represents vegetation characteristics of the entire hexagon; however, majority of birds detected occur outside that immediate area, which could be why we didn't see more relationships with point-level vegetation characteristics.

Two species, Black-backed Woodpeckers and Red-breasted Nuthatches, showed opposite, but strong responses to latitude. Black-backed Woodpeckers density decreased as latitude increased in the Black Hills. The majority of burned habitat existed in the southern hills which could be why we see higher densities in lower latitudes. Furthermore, higher latitudes in our study included the Bear Lodge Mountains of Wyoming which is isolated from the main body of the forest and has less natural disturbance than the main portion of the BHNF and CSP.

Conversely, Red-breasted Nuthatch density increased as latitude increased. We also observed the highest densities for this species in northern latitudes. Previous studies in the BHNF have also seen the highest Red-breasted Nuthatch abundances in the northern hills (White and Giroir 2008). The northern hills contains more late successional pine habitat with a deciduous component providing an abundance of live trees and increased canopy cover that Red-breasted Nuthatches prefer (Shepperd and Battaglia 2002). In addition, latitude could be correlated with elevation and precipitation, which could have an effect on abundances of these species.

American Three-toed Woodpeckers did not show a strong association with any vegetation variables in our study. Panjabi (2003) only observed American Three-toed Woodpeckers in spruce forests; however, Mohren et al. (2016) observed them in aspen and ponderosa pine stands in the Black Hills. While dominant tree species was included in the top model for American Three-toed Woodpeckers we did not see a strong association with any specific tree species. Furthermore, they have been known to exploit burns in other parts of their range (Bock et al. 1978, Hoffman 1997, Hoyt and Hannon 2002), but recent surveys did not record any American Three-toed Woodpeckers in burned habitats of the Black Hills (Panjabi 2003). Although we had low detections of American Three-toed Woodpeckers we did observe them in burned ponderosa pine stands.

Our large-scale surveys efforts enabled us to predict avian density over a variety of habitat types across the BHNF and CSP. Many of our focal species are considered sensitive to forest management practices and one, the Black-backed Woodpecker, was recently petitioned to be listed as an endangered or threatened species. Because habitat relationships varied among our focal species, there is potential to adversely affect some species while managing for others. Maintaining some areas of natural disturbances along with heterogeneity of vegetation characteristics within stands and at the landscape-scale will benefit the diverse needs of avian species in the Black Hills. Forests that have been subjected to wildfires within the last 5 years will supply Black-backed woodpeckers with newly burned habitat, providing opportunity for population growth, and also give Brown Creepers 4- to 5-year-old wildfires they prefer. Also retaining a mixture of canopy cover between 40–80% will allow for increased grass/shrub cover for ground-nesters like White-winged Juncos, but also provide closed canopy conditions, which Red-breasted Nuthatches favor. Additionally, conserving spruce forests provides large-diameter old-growth trees for several species such as, the Brown Creeper and American Three-toed Woodpecker. Spruce forests are largely untouched, since they are not managed for timber harvest, creating a unique habitat for species in an overall highly managed forest. However, information on species diversity and habitat use of these spruce forests is needed to entirely understand the potential benefits this habitat provides. Continued research and monitoring for avian species across a variety of vegetation types in the Black Hills would improve understanding about their responses to disturbances and the effects of management practices throughout the BHNF and CSP.

LITERATURE CITED

Alexander, R. R., and C. B. Edminster. 1981. Management of ponderosa pine in even aged stands in the Black Hills. USDA Forest Service General Technical Report RM-228. 10 p.

Anderson, S. H., and B. J. Crompton. 2002. The effects of shelterwood logging on bird community composition in the Black Hills, Wyoming. Forest Science 48 (2): 365–372.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of Wildlife Management 74 (6): 1175–78.

Beason, J., K. Hutton, A. Panjabi, R. Sparks, and D. Hanni. 2006. Monitoring the birds of the Black Hills: 2005 field season report. Technical Report M-MBBHO5-01. Rocky Mountain Bird Observatory, Brighton, CO. 113 p.

Bock, C. E., and J. F. Lynch. 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. The Condor 72 (2): 182–89.

Boldt, C. E., and J. L. Van Deusen. 1974. Silviculture of ponderosa pine in the Black Hills: the status of our knowledge. Research paper RM-124. Rocky Mountain Forest and Range Experiment Station, U.S. Forest Service, Ft. Collins, Colorado. 48 p.

Bonnot, T. W., M. A. Rumble and J. J. Millspaugh. 2008. Nest success of Black-backed Woodpeckers in forests with mountain pine beetle outbreaks in the Black Hills, South Dakota. The Condor 110: 450–457.

Bonnot, T. W., J. J. Millspaugh, and M. A. Rumble. 2009. Multi-scale nest-site selection by Black-Backed Woodpeckers in outbreaks of mountain pine beetles. Forest Ecology and Management 259 (2): 220–28.

Brown, P. M., and B. Cook. 2006. Early settlement forest structure in Black Hills ponderosa pine forests. Forest Ecology and Management 223: 284–290.

Chandler, R. B., J. A. Royle, and D. I. King. 2011. Inference about density and temporary emigration in unmarked populations. Ecology 92 (7): 1429–1435.

Clawges, R., K. Vierling, L. Vierling, and E. Rowell. 2008. The use of airborne lidar to assess avian species diversity, density, and occurrence in a pine/aspen forest. Remote Sensing of Environment 112 (5): 2064–2073.

Drever, M. C., J. R. Goheen, and K. Martin. 2009. Species-energy theory, pulsed resources, and regulation of avian richness during a mountain pine beetle outbreak. Ecology 90 (4): 1095–1105.

Driscoll, D. G., G. R. Hamade, and S. J. Kenner. 2000. Summary of precipitation data for the Black Hills area of South Dakota, water years 1931–1998: USGS Open file report 00-329. 163 p.

Dykstra, B. L., M. A. Rumble, and L. D. Flake. 1997. Effects of timber harvesting on birds in the Black Hills of South Dakota and Wyoming, USA. 12 p. http://www.treesearch.fs.fed.us/pubs/22156.

Edworthy, A. B., M. C. Drever, and K. Martin. 2011. Woodpeckers increase in abundance but maintain fecundity in response to an outbreak of mountain pine bark beetles. Forest Ecology and Managemen*t* 261 (2): 203–210.

Fiske, I., and R. Chandler. 2015. Overview of Unmarked: an R package for the analysis of data from unmarked animals. R Project for Statistical Computing. https://cran.rproject.org/web/packages-/unmarked/vignettes/unmarked.pdf.

Fulé, P. Z., W. W. Covington, M. M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecological Applications 7: 895–908.

Gentry, D. J., and K. T. Vierling. 2008. Reuse of woodpecker cavities in the breeding and non-breeding seasons in old burn habitats in the Black Hills, South Dakota. The American Midland Naturalist 160 (2): 413–29.

Ghalambor, C. K., and T. E. Martin. 1999. Red-breasted Nuthatch (*Sitta canadensis*). Account 459 in A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.

Goggans, R., R. D. Dixon, and C. L. Seminara. 1989. Habitat use by Three-toed and Black-backed Woodpeckers Deschutes National Forest, Oregon. Oregon Department of Fish and Wildlife Nongame Wildlife Program. USDA Deschutes National Forest Technical Report #87-3-02.

Graham, R. T., L. A. Asherin, M. A. Battaglia, T. Jain, and S. A. Mata. 2016. Mountain pine beetles: a century of knowledge, control attempts, and impacts central to the Black Hills. General Technical Report RMRS-GTR-353. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 193 p.

Hanson, C., K. Coulter, J. Augustine, and D. Short. 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.

Hoffman, N. J. 1997. Distribution of Picoides woodpeckers in relation to habitat disturbance within the Yellowstone area. Thesis. Bozeman: Montana State University. 85 p.

Hoffman, G. R., and R. R. Alexander. 1987. Forest vegetation of the Black Hills National Forest of South Dakota and Wyoming: A habitat type classification. U.S. Forest Service Research Paper. RM-276. Fort Collins, CO, USA. 54 p.

Holmes, R. T. and S. K. Robinson. 1988. Spatial patterns, foraging tactics, and diets of ground-foraging birds in a northern hardwoods forest. Wilson Bulletin 100 (3): 377−394.

Hoyt, J. S. and S. J. Hannon. 2002. Habitat associations of Black-Backed and Three-Toed Woodpeckers in the Boreal Forest of Alberta. Canadian Journal of Forest Research 32 (10): 1881–88.

Hutto, R. L., and S. M. Gallo. 2006. The effects of postfire salvage logging on cavity-nesting birds. The Condor 108 (4): 817–831.

Hutto, R. L. 2008. The ecological Importance of severe wildfires: some like it hot. Ecological Applications 18 (8): 1827–1834.

Hutton, K., J. Beason, G. Girior, A. Panjabi, R. Sparks, and D. Hanni. 2006. Monitoring the birds of the Black Hills: 2006 Field Season Report. Tech. Rep. MMBBH06-01. Rocky Mountain

Bird Observatory, Brighton, CO. 71 p.

Martin, K., A. Norris, and M. Drever. 2006. Effects of bark beetle outbreaks on avian biodiversity in the British Columbia interior: Implications for critical habitat management. BC Journal of Ecosystems and Management 7 (3): 10–24.

Mills, T. R., M. A. Rumble, and L. D. Flake. 2000. Habitat of birds in ponderosa pine and aspen/birch in the Black Hills, South Dakota. Journal of Field Ornithology 71 (2): 187–206.

Mohren, S. R., M. A. Rumble, C. P. Lehman, and S. H. Anderson. 2016. Resource selection by Black-Backed Woodpeckers (*Picoides Arcticus*) and American Three-Toed Woodpeckers (*P. Dorsalis*) in South Dakota and Wyoming. The Prairie Naturalist 47: 21–29.

Morissette, J. L., T. P. Cobb, R. M. Brigham, and P. C. James. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. Canadian Journal of Forest Research 32 (12): 2169–83.

Murphy, E. C., and W. A. Lehnhausen. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. The Journal of Wildlife Management 62 (4): 1359–1372.

Nappi, A., P. Drapeau, and J.-P. L. Savard. 2004. Salvage logging after wildfire in the Boreal forest: is it becoming a hot issue for wildlife? The Forestry Chronicle 80: 67–74.

Norris, A. R., and K. Martin. 2008. Mountain Pine Beetle Presence Affects Nest Patch Choice of Red-Breasted Nuthatches. Journal of Wildlife Management 72 (3): 733–37.

Ostfeld, R.S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution. 15: 232–237.

Panjabi, A. 2003. Monitoring the birds of the Black Hills: Year 2. Annual Report submitted to Black Hills National Forest. Rocky Mountain Bird Observatory, Brighton, CO. 96 p.

Panjabi, A. 2005. Monitoring the birds of the Black Hills: Year 4. Annual Report submitted to Black Hills National Forest. Rocky Mountain Bird Observatory, Brighton, CO. 67 p.

Poulin, J. F., M. A. Villard, M. Edman, P. J. Goulet, and A. M. Eriksson. 2008. Thresholds in nesting habitat requirements of an old forest specialist, the Brown Creeper (*Certhia americana*), as conservation targets. Biological Conservation 141: 1129–1137.

Poulin, J. F., E. D'Astous, M. A. Villard, S. J. Hejl, K. R. Newlon, M. E. McFadzen, J. S. Young, and C. K. Ghalambor. 2013. Brown Creeper (*Certhia americana*), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/brncre.

Powell, H. D. W., S. J. Hejl, and D. L. Six. 2002. Measuring woodpecker food: a simple method for comparing wood-boring beetle abundance among fire-killed trees. Journal of Field Ornithology 73: 130–140.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58: 501–517.

Raphael, M. G., and M. White. 1984. Use of snags by cavity-nesting Birds in the Sierra Nevada. Wildlife Monographs 86: 3–66.

Raventon, E. 1994. Island in the plains: A Black Hills natural history. Boulder, CO: Johnson Books. 272 p.

Rota, C. T., J. J. Millspaugh, M. A. Rumble, C. P. Lehman, and D. C. Kesler. 2014a. The role of wildfire, prescribed fire, and mountain pine beetle infestations on the population dynamics of Black-Backed Woodpeckers in the Black Hills, South Dakota. PLoS ONE 9 (4): e94700.

Rota, C. T., M. A. Rumble, J. J. Millspaugh, C. P. Lehman, and D. C. Kesler. 2014b. Space-use and habitat associations of Black-Backed Woodpeckers (Picoides Arcticus) occupying recently disturbed forests in the Black Hills, South Dakota. Forest Ecology and Management 313: 161–168.

Royle, J. A. 2004. Generalized estimators of avian abundance from count survey data. Animal Biodiversity and Conservation 27 (1): 375–386.

Saab, V. A., and J. G. Dudley. 1998. Responses of cavity nesting birds to stand-replacement fire and salvage logging in ponderosa pine/Douglas-fir forests of southwestern Idaho. Research Paper RMRS-RP-11. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA. 23 p.

Saab, V. A., R. E. Russell, and J. G. Dudley. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. Condor 109: 97–108.

Saab, V. A., Q. S. Latif, M. M. Rowland, T. N. Johnson, A. D. Chalfoun, S. W. Buskirk, J. E. Heyward, and M. A. Dresser. 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests. Forest Science 60 (3): 539–559.

Sallabanks, R., J. B. Haufler, and C. A. Mehi. 2006. Influence of forest vegetation structure on avian community composition in west-central Idaho. Wildlife Society Bulletin 34: 1079–1093.

Severson, K. E., and J. F. Thilenius. 1976. Classification of quaking aspen stands in the Black Hills and Bear Lodge Mountains. U.S. Forest Service Res. Paper. RM-166. 24 p.

Sharpe, G. W., C. W. Hendee, and S. W. Allen. 1976. Introduction to forestry. McGraw-Hill Books Co. New York, N. Y. 544 p.

Shepperd, W. D., and M. A. Battaglia. 2002. Ecology, silviculture, and management of Black Hills ponderosa pine forests. USDA Forest Service, General Technical Report RMRS-GTR-97. 119 p.

South Dakota Game, Fish, and Parks. 2014. South Dakota wildlife action plan. http://gfp.sd.gov/wildlife/docs/WildlifeActionPlan-2014draft.pdf.

USDA Forest Service. 2005. Black Hills National Forest Revised 1997 Land and Resource Management Plan, Phase II Amendment. Final Environmental Impact Statement. Black Hills National Forest, Rocky Mountain Region, Custer, SD. 24 p. http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsm9_011678.pdf.

USDA Forest Service. 2013. Black Hills National Forest Large Fire History Map 1910-2012. https://fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5420893.pdf.

Walters, B. F., C. W. Woodall, R. J. Piva, M. A. Hatfield, G. M. Domke, and D. E. Haugen. 2013. Forests of the Black Hills National Forest 2011. Resource Bulletin NRS-83. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 36 p.

Weikel, J. M., and J. P. Hayes. 1999. The foraging ecology of cavity-nesting birds in young forests of the northern Coast Range of Oregon. Condor 101: 58–66.

White, C., and G. Giroir. 2008 Monitoring the birds of the Black Hills: 2008 field season report. Technical Report M-MBBH-USFS08, SDDGF08. Rocky Mountain Bird Observatory, Brighton, CO. 57 p.

Wiggins, D. 2004. American Three-toed Woodpecker (*Picoides dorsalis*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. http://www.fs.fed.us/r2/projects/scp/assessments/americanthreetoedwoodpecker.pdf.

Table 1. Number of detections of bird species across all sampling points in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, 2015 and 2016.

Common name	Scientific name	Detections
American Three-toed Woodpecker [a b]	*Picoides dorsalis*	41
Black-backed Woodpecker [* † a b c]	*Picoides arcticus*	362
Brown Creeper [†]	*Certhia americana*	558
Red-breasted Nuthatch	*Sitta canadensis*	5848
White-winged Junco [a b]	*Junco hyemalis aikeni*	2639

* U.S. Forest Service "Sensitive Species"

† U.S. Forest Service "Management Indicator Species"

[a] South Dakota "Species of Concern" in the Black Hills ecoregion

[b] South Dakota "Species of Conservation Need"

[c] Wyoming "Species of Conservation Need"

Table 2. Descriptive statistics for point- and landscape-level characteristics at sampling point locations for a study of bird abundance in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, 2015 and 2016. Proportions of observations are reported for classes of categorical variables in lieu of means.

Covariate	**Abbreviation**	**Mean**	**Min**	**Max**
Year (2015/2016)	yr	.52/.48		
Latitude	lat	44.08	43.51	44.75
1-to 2-year-old wildfire (%)	F12	0.30	0.00	100.00
3-year-old wildfire (%)	F3	2.05	0.00	100.00
4- to 5-year-old wildfire (%)	F45	2.14	0.00	100.00
6- to 10-year-old wildfire (%)	F610	0.29	0.00	100.00
Green trees (%)	GT	38.96	0.00	96.00
Beetle killed trees (%)	RT	0.96	0.00	16.00
Dead trees (%)	DS	12.02	0.00	75.00
Ground vegetation (%)	GV	26.05	0.00	97.00
Basal area ft^2/acre	ba	69.30	0.00	330.00
Dominant tree species (Aspen/HARDW/None/POPI/Spruce)	dt	.04/.02/.07/.82/.04		
Dominant size class (None/SAPL/POLE/SAWT)	sc	.06/.24/.14/.55		
Point-level canopy cover (%)	cc	57.92	0.00	100.00
Grass vegetation (%)	gr	60.17	0.00	100.00
Woody vegetation (%)	wo	32.87	0.00	100.00

Table 3. Number of parameters (K), ΔAIC, and P-value from Freeman-Tukey goodness-of-fit test for the top-ranked abundance (λ) availability (ϕ) and detection (σ) model predicting species abundance for 5 focal species in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming. Multiple models presented where supported and predictions were model-averaged.

Species	Most-supported model(s)	K	ΔAIC	P
American Three-toed Woodpecker	λ(DS+ba+dt+sc)ϕ(.)σ(min+doy+obs+year)	27	0	0.495
	λ(ba+dt+sc)ϕ(.)σ(min+doy+obs+year)	26	1.51	--
Black-backed Woodpecker	λ(lat+yr+F12+F3+F45+RT+DS+dt)ϕ(.)σ(min+doy+obs+year)	29	0	0.485
Brown Creeper	λ(F12+F3+F45+RT+dt+cc2+sc)ϕ(.)σ(min+doy)	20	0	0.545
Red-breasted Nuthatches	λ(lat+yr+F12+F3+F45+F610+RT+DS+GT+ba+dt+cc2+sc)ϕ(.)σ(min+visit+obs+year)	37	0	0.267
White-winged Junco	λ(yr+RT+GV+GT+ba+dt+gr+cc2)ϕ(.)σ(min+visit+obs+year)	31	0	0.139

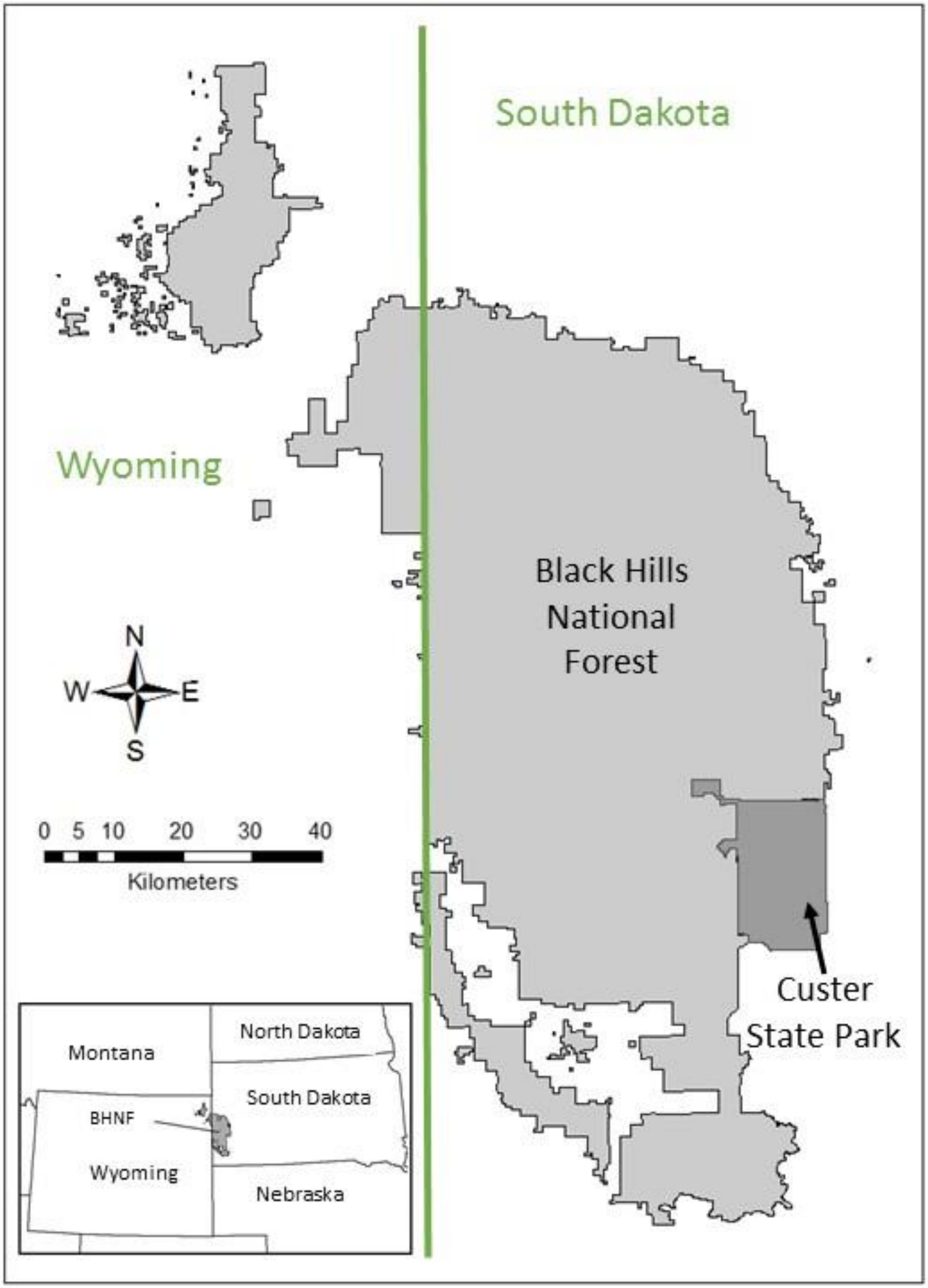


Figure 1. Study Area in which we surveyed bird abundance and measured vegetation in the Black Hills of South Dakota and Wyoming, and Bear Lodge Mountains of Wyoming.

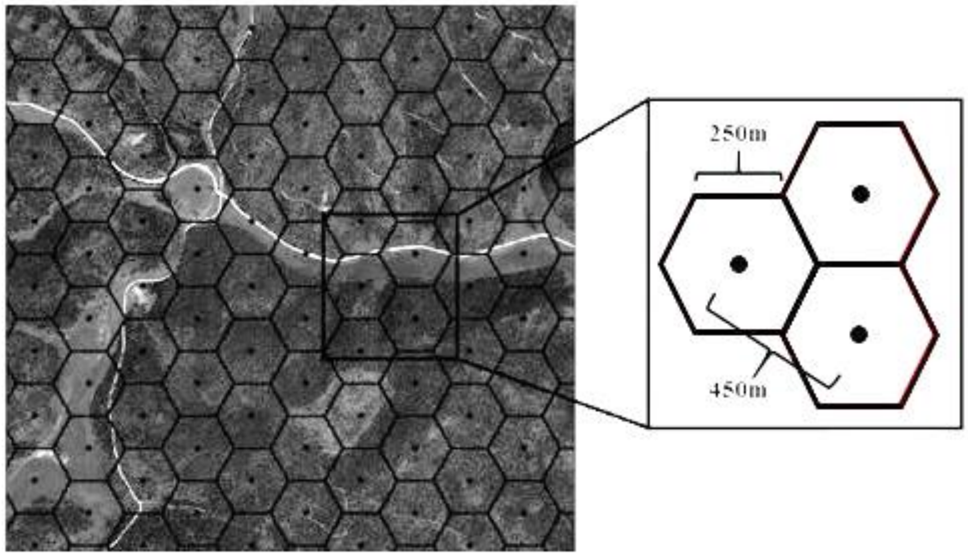


Figure 2. Examples of hexagons (black outline) and center points (black point) from which we selected bird survey points in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming.

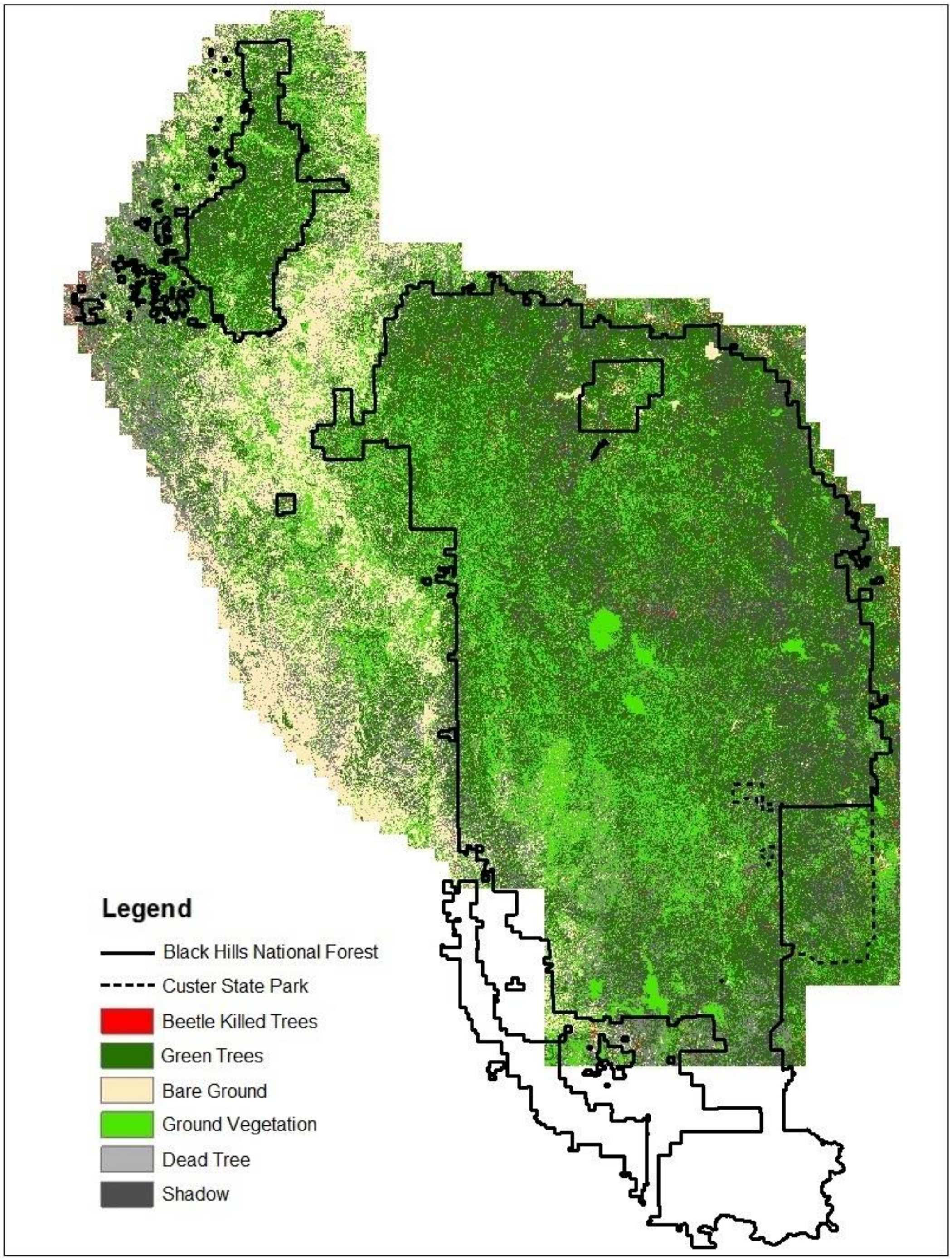


Figure 3. We classified six categories of forest vegetation on 1-m pixels from aerial photography and measured the percent cover of each category in 16-ha hexagons for use as covariates in bird abundance models in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, 2015-2016.

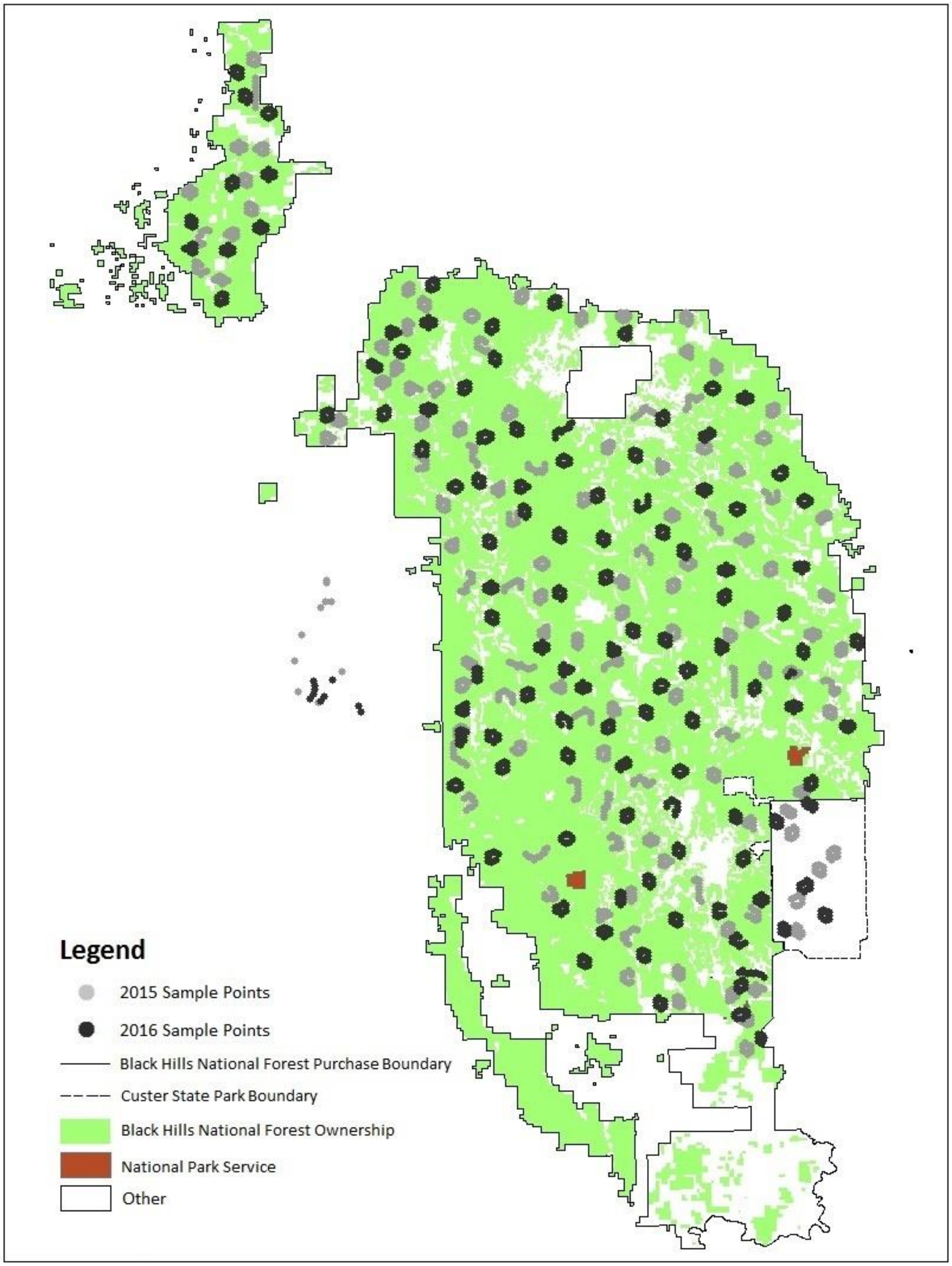


Figure 4. Sampling point locations (N = 2370) for 2015 (light grey circles) and 2016 (dark grey circles) for a study of bird abundance in the Black Hills National Forest and Custer State Park, South Dakota and Wyoming between end of March and end of June.

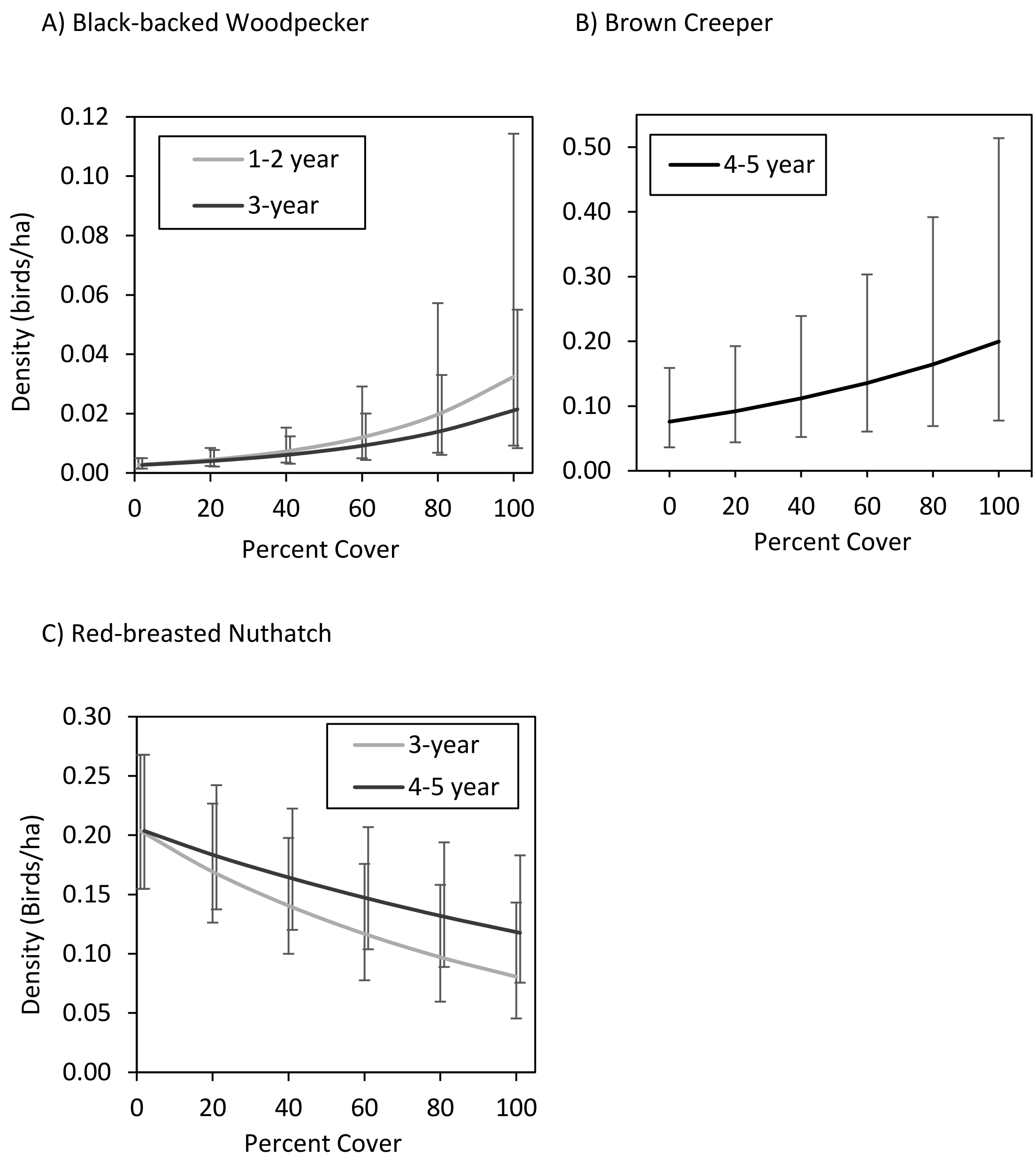


Figure 5. Predicted densities and SE of bird species across ranges of percent cover in a 16.28-ha hexagon of different years since burned wildfire classes in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, March-June 2015 and 2016.

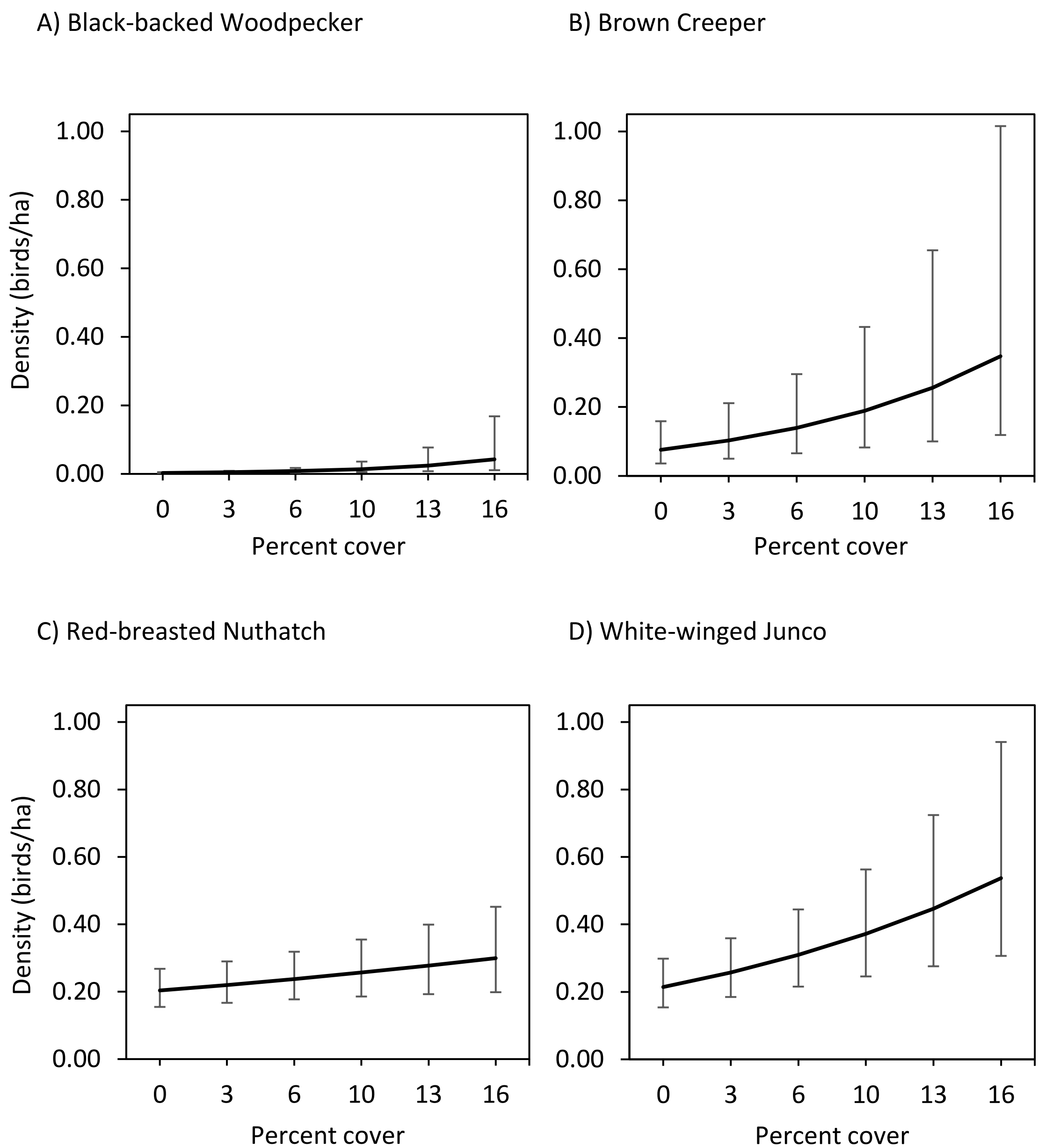
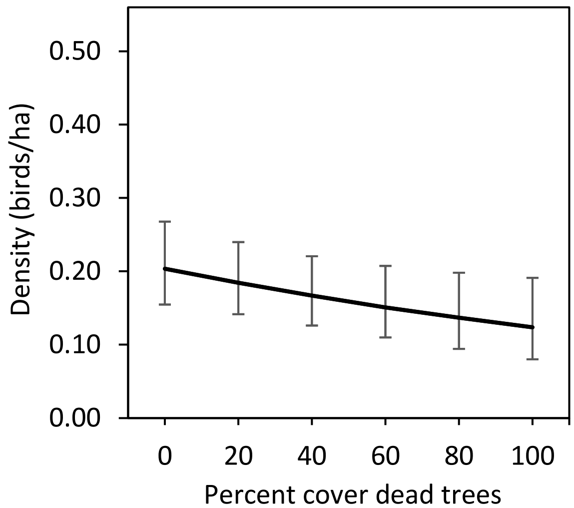


Figure 6. Predicted densities and SE of bird species across a gradient of percent cover of beetle infested (red top) pine trees in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming., March-June, 2015 and 2016.

A) Red-breasted Nuthatch



B) White-winged Junco

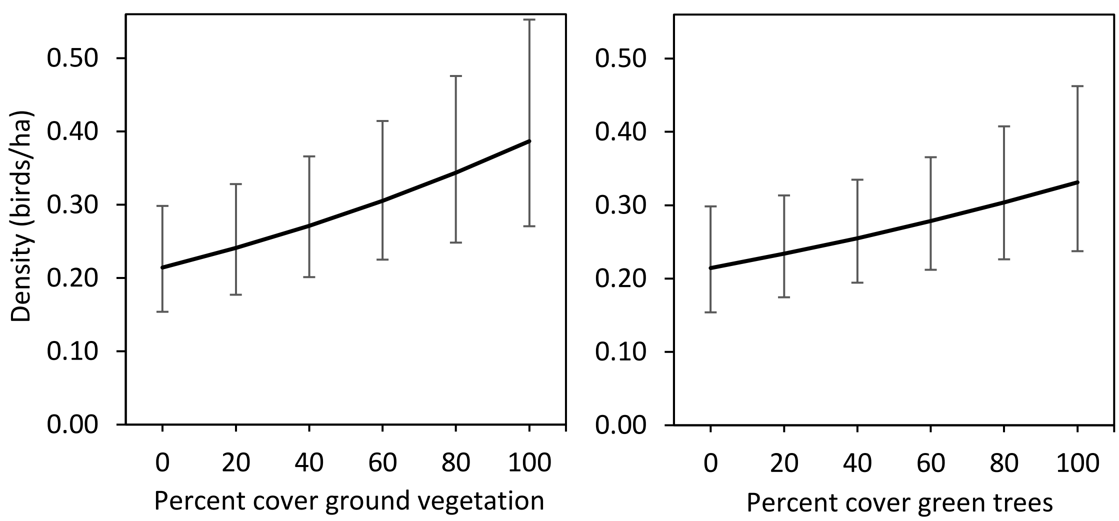


Figure 7. Predicted densities and SE of bird species across a gradient of landscape-level nt cover measurements in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, March-June, 2015 and 2016.

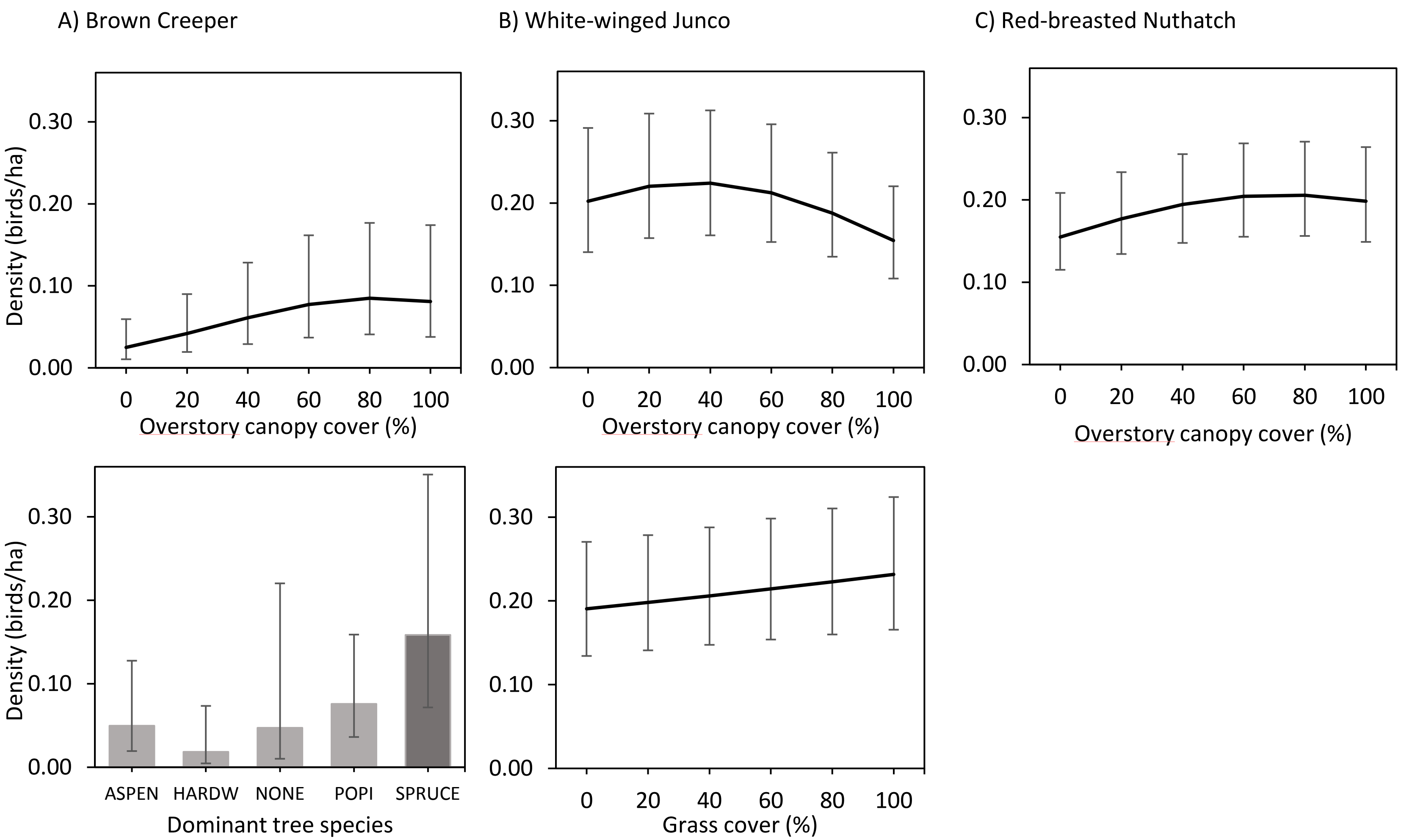


Figure 8. Predicted densities and SE of bird species across a gradient of point-level vegetation measurements in the Black Hills and Bear lodge Mountains of South Dakota and Wyoming, March-June, 2015 and 2016.

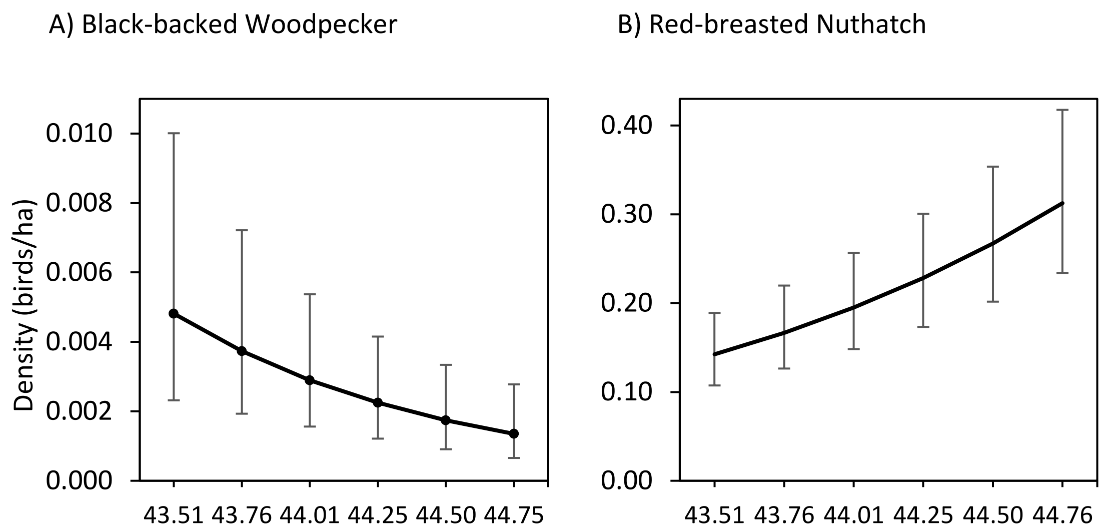


Figure 9. Predicted densities and SE of bird species across a gradient of latitude in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, March-June, 2015 and 2016.

APPENDIX

Table A1. Coefficients (Coeff), standard errors (SE), and 95% confidence limits (LCL, UCL) for covariates in species density models with informative parameters and < 2 ΔAIC in the Black Hills of South Dakota and Wyoming, March-June, 2015 and 2016.

Species, Covariate	Coeff	SE	LCL	UCL
American Three-toed Woodpecker (1)				
Intercept	-8.472	52.837	112.033	95.089
DS	-0.465	0.268	-0.990	0.060
ba	0.285	0.218	-0.142	0.712
dtHARDW	8.642	52.762	-94.772	112.056
dtNONE	7.750	52.810	-95.758	111.258
dtPOPI	8.120	52.750	-95.270	111.510
dtSPRUCE	10.298	52.752	-93.096	113.692
scSAPL	-1.550	2.628	-6.701	3.601
scPOLE	-1.619	2.621	-6.756	3.518
scSAWT	-1.159	2.601	-6.257	3.939
American Three-toed Woodpecker (2)				
Intercept	-7.378	30.896	-67.934	53.178
ba	0.305	0.221	-0.128	0.738
dtHARDW	7.595	30.774	-52.722	67.912
dtNONE	6.590	30.849	-53.874	67.054
dtPOPI	6.865	30.752	-53.409	67.139
dtSPRUCE	9.207	30.755	-51.073	69.487
scSAPL	-1.355	2.544	-6.341	3.631
scPOLE	-1.436	2.537	-6.409	3.537
scSAWT	-1.000	2.516	-5.931	3.931
Black-backed Woodpecker				
Intercept	-0.198	0.522	-1.220	0.824
lat	-0.293	0.092	-0.473	-0.112
yr2016	0.661	0.151	0.364	0.957

Species, Covariate	Coeff	SE	LCL	UCL
F12	0.133	0.031	0.072	0.194
F3	0.288	0.047	0.196	0.381
F45	0.070	0.056	-0.040	0.180
RT	0.235	0.057	0.123	0.346
DS	0.075	0.084	-0.090	0.239
dtHARDW	-1.038	1.106	-3.204	1.129
dtNONE	0.453	0.494	-0.515	1.421
dtPOPI	0.248	0.444	-0.623	1.118
dtSPRUCE	0.234	0.576	-0.895	1.363
Brown Creeper				
Intercept	1.946	0.844	0.292	2.498
F12	0.018	0.043	-0.066	0.126
F3	-0.137	0.090	-0.314	0.268
F45	0.139	0.049	0.043	0.144
RT	0.129	0.042	0.047	0.124
cc	0.263	0.062	0.141	0.185
cc2	-0.151	0.063	-0.274	0.186
dtHARDW	-0.991	0.662	-2.289	1.960
dtNONE	-0.051	0.744	-1.509	2.201
dtPOPI	0.423	0.300	-0.166	0.889
dtSPRUCE	1.159	0.348	0.477	1.031
scSAPL	-0.472	0.713	-1.870	2.110
scPOLE	-0.463	0.711	-1.855	2.103
scSAWT	-0.498	0.710	-1.889	2.101
Red-breasted Nuthatch				
Intercept	1.620	0.255	1.120	2.119
lat	0.181	0.019	0.143	0.219
yr2016	0.458	0.040	0.379	0.538
F12	-0.007	0.018	-0.043	0.028
F3	-0.129	0.036	-0.199	-0.059
F45	-0.079	0.025	-0.128	-0.029

Species, Covariate	Coeff	SE	LCL	UCL
F610	-0.036	0.021	-0.077	0.005
RT	0.033	0.015	0.004	0.061
DS	-0.056	0.024	-0.103	-0.009
GT	0.023	0.021	-0.017	0.064
ba	0.026	0.021	-0.015	0.067
cc	0.048	0.022	0.005	0.091
cc2	-0.046	0.019	-0.082	-0.009
dtHARDW	-0.013	0.113	-0.234	0.208
dtNONE	-0.230	0.216	-0.653	0.194
dtPOPI	0.076	0.074	-0.069	0.220
dtSPRUCE	0.169	0.099	-0.025	0.363
scSAPL	-0.200	0.213	-0.618	0.218
scPOLE	-0.132	0.213	-0.549	0.286
scSAWT	-0.146	0.212	-0.561	0.269
White-winged Junco				
Intercept	2.909	0.177	2.561	3.257
yr2016	0.353	0.061	0.234	0.473
RT	0.078	0.022	0.035	0.121
GV	0.102	0.030	0.044	0.160
GT	0.066	0.030	0.007	0.125
ba	-0.066	0.035	-0.135	0.003
cc	-0.119	0.036	-0.189	-0.048
cc2	-0.075	0.028	-0.129	-0.021
dtHARDW	-0.018	0.205	-0.420	0.384
dtNONE	-0.188	0.161	-0.503	0.127
dtPOPI	0.061	0.125	-0.183	0.306
dtSPRUCE	-0.070	0.175	-0.412	0.273
gr	0.058	0.026	0.007	0.110

Table A2. Number of parameters (K), AIC, ΔAIC, Akaike weight (AICwt) based on Akaike's Information Criteria, and cumulative Akaike weight (cumltvwt) for all final model combinations evaluating species density (λ), availability (ϕ), and detection (σ) for 5 focal species in the Black Hills National Forest, March-June, 2015-2016.

Species, model	K	AIC	ΔAIC	AICwt	cumltvwt
American Three-toed Woodpecker					
λ(DS+ba+dt+sc)ϕ(.)σ(min+doy+obs+year)	27	529.44	0.00	0.36	0.36
λ(ba+dt+sc)ϕ(.)σ(min+doy+obs+year)	26	530.95	1.51	0.17	0.53
λ(yr+DS+ba+dt+sc)ϕ(.)σ(min+doy+obs+year)	28	531.44	2.00	0.13	0.67
λ(cc)ϕ(.)σ(min+doy+obs+year)	19	532.56	3.12	0.08	0.74
λ(DS)ϕ(.)σ(min+doy+obs+year)	19	532.69	3.25	0.07	0.81
λ(lat+yr+DS+ba+dt+sc)ϕ(.)σ(min+doy+obs+year)	29	533.38	3.94	0.05	0.86
λ(RT+DS)ϕ(.)σ(min+doy+obs+year)	20	534.42	4.98	0.03	0.89
λ(cc+cc2)ϕ(.)σ(min+doy+obs+year)	20	534.52	5.08	0.03	0.92
λ(.)ϕ(.)σ(min+doy+obs+year)	18	535.02	5.58	0.02	0.95
λ(ba)ϕ(.)σ(min+doy+obs+year)	19	535.72	6.28	0.02	0.96
λ(RT+DS+GT)ϕ(.)σ(min+doy+obs+year)	21	536.08	6.64	0.01	0.97
λ(RT)ϕ(.)σ(min+doy+obs+year)	19	536.55	7.11	0.01	0.98
λ(GT)ϕ(.)σ(min+doy+obs+year)	19	537.00	7.56	0.00	0.99
λ(RT+GT)ϕ(.)σ(min+doy+obs+year)	20	538.53	9.09	0.00	1.00
λ(sc)ϕ(.)σ(min+doy+obs+year)	21	539.85	10.41	0.00	1.00

Species, model	K	AIC	ΔAIC	AICwt	cumltvwt
λ(ba+sc)ϕ(.)σ(min+doy+obs+year)	22	540.19	10.75	0.00	1.00
Black-backed Woodpecker					
λ(lat+yr+F12+F3+F45+RT+DS+dt)ϕ(.)σ(min+doy+obs+year)	29	3314.36	0.00	1.00	1.00
λ(lat+F12+F3+F45+RT+DS+dt)ϕ(.)σ(min+doy+obs+year)	28	3331.80	17.45	0.00	1.00
λ(F12+F3+F45+RT+DS+dt)ϕ(.)σ(min+doy+obs+year)	27	3341.21	26.86	0.00	1.00
λ(F12+F3+F45)ϕ(.)σ(min+doy+obs+year)	21	3362.51	48.16	0.00	1.00
λ(F12+F3+F45+F610)ϕ(.)σ(min+doy+obs+year)	22	3362.79	48.43	0.00	1.00
λ(RT+DS)ϕ(.)σ(min+doy+obs+year)	20	3375.41	61.06	0.00	1.00
λ(F12+F3)ϕ(.)σ(min+doy+obs+year)	20	3375.71	61.35	0.00	1.00
λ(RT+DS+HT)ϕ(.)σ(min+doy+obs+year)	21	3377.40	63.05	0.00	1.00
λ(DS)ϕ(.)σ(min+doy+obs+year)	19	3382.06	67.71	0.00	1.00
λ(RT+HT)ϕ(.)σ(min+doy+obs+year)	20	3439.71	125.35	0.00	1.00
λ(HT)ϕ(.)σ(min+doy+obs+year)	19	3443.46	129.11	0.00	1.00
λ(dt)ϕ(.)σ(min+doy+obs+year)	22	3447.50	133.15	0.00	1.00
λ(ba+dt+sc)ϕ(.)σ(min+doy+obs+year)	26	3452.69	138.33	0.00	1.00
λ(dt+sc)ϕ(.)σ(min+doy+obs+year)	25	3453.29	138.93	0.00	1.00
λ(cc+dt+sc)ϕ(.)σ(min+doy+obs+year)	26	3454.32	139.96	0.00	1.00
λ(ba+cc+dt+sc)ϕ(.)σ(min+doy+obs+year)	27	3454.67	140.32	0.00	1.00
λ(RT)ϕ(.)σ(min+doy+obs+year)	19	3456.12	141.76	0.00	1.00
λ(sc)ϕ(.)σ(min+doy+obs+year)	21	3457.50	143.14	0.00	1.00

Species, model	K	AIC	ΔAIC	AICwt	cumltvwt
λ(ba+sc)ϕ(.)σ(min+doy+obs+year)	22	3458.13	143.77	0.00	1.00
λ(.)ϕ(.)σ(min+doy+obs+year)	18	3461.76	147.41	0.00	1.00
λ(cc)ϕ(.)σ(min+doy+obs+year)	19	3463.13	148.78	0.00	1.00
λ(ba)ϕ(.)σ(min+doy+obs+year)	19	3463.68	149.32	0.00	1.00
λ(cc2)ϕ(.)σ(min+doy+obs+year)	20	3465.00	150.64	0.00	1.00
Brown Creeper					
λ(F12+F3+F45+RT+cc2+dt+sc)ϕ(.)σ(min+doy)	20	5058.40	0.00	0.49	0.49
λ(yr+F12+F3+F45+RT+cc2+dt+sc)ϕ(.)σ(min+doy)	21	5059.00	0.61	0.36	0.86
λ(lat+yr+F12+F3+F45+RT+cc2+dt+sc)ϕ(.)σ(min+doy)	22	5060.91	2.51	0.14	1.00
λ(cc2+dt+sc)ϕ(.)σ(min+doy)	15	5068.80	10.40	0.00	1.00
λ(ba+cc2+dt+sc)ϕ(.)σ(min+doy)	16	5069.86	11.46	0.00	1.00
λ(cc2)ϕ(.)σ(min+doy)	8	5082.93	24.54	0.00	1.00
λ(cc)ϕ(.)σ(min+doy)	7	5088.40	30.00	0.00	1.00
λ(ba+dt+sc)ϕ(.)σ(min+doy)	14	5092.50	34.10	0.00	1.00
λ(dt)ϕ(.)σ(min+doy)	10	5096.22	37.83	0.00	1.00
λ(dt+sc)ϕ(.)σ(min+doy)	13	5101.43	43.03	0.00	1.00
λ(ba)ϕ(.)σ(min+doy)	7	5102.13	43.73	0.00	1.00
λ(RT)ϕ(.)σ(min+doy)	7	5104.22	45.83	0.00	1.00
λ(RT+GT)ϕ(.)σ(min+doy)	8	5105.65	47.25	0.00	1.00
λ(RT+DS+GT)ϕ(.)σ(min+doy)	9	5107.62	49.22	0.00	1.00

Species, model	K	AIC	ΔAIC	AICwt	cumltvwt
λ(F12+F3+F45)ϕ(.)σ(min+doy)	9	5107.89	49.49	0.00	1.00
λ(ba+sc)ϕ(.)σ(min+doy)	10	5107.93	49.54	0.00	1.00
λ(F12+F3+F45+F610)ϕ(.)σ(min+doy)	10	5108.33	49.93	0.00	1.00
λ(F12+F3)ϕ(.)σ(min+doy)	8	5110.21	51.81	0.00	1.00
λ(.)ϕ(.)σ(min+doy)	6	5113.02	54.62	0.00	1.00
λ(DS)ϕ(.)σ(min+doy)	7	5114.75	56.36	0.00	1.00
λ(GT)ϕ(.)σ(min+doy)	7	5114.89	56.49	0.00	1.00
λ(sc)ϕ(.)σ(min+doy)	9	5117.79	59.39	0.00	1.00
Red-breasted Nuthatch					
λ(lat+yr+F12+F3+F45+F610+RT+DS+GT+ba+cc2+dt++sc)ϕ(.)σ(min+visit+obs+year)	37	28564.13	0.00	1.00	1.00
λ(yr+F12+F3+F45+F610+RT+DS+GT+ba+cc2+dt+sc)ϕ(.)σ(min+visit+obs+year)	36	28647.31	83.19	0.00	1.00
λ(F12+F3+F45+F610+RT+DS+GT+ba+cc2+dt+sc)ϕ(.)σ(min+visit+obs+year)	35	28752.89	188.76	0.00	1.00
λ(RT+DS+GT)ϕ(.)σ(min+visit+obs+year)	21	28823.03	258.9	0.00	1.00
λ(RT+GT)ϕ(.)σ(min+visit+obs+year)	20	28866.61	302.49	0.00	1.00
λ(GT)ϕ(.)σ(min+visit+obs+year)	19	28870.70	306.57	0.00	1.00
λ(DS)ϕ(.)σ(min+visit+obs+year)	19	28952.88	388.75	0.00	1.00
λ(DS+GT)ϕ(.)σ(min+visit+obs+year)	20	28954.83	390.71	0.00	1.00
λ(F12+F3+F45+F610)ϕ(.)σ(min+visit+obs+year)	22	28965.92	401.79	0.00	1.00
λ(F12+F3+F45)ϕ(.)σ(min+visit+obs+year)	21	28968.70	404.58	0.00	1.00
λ(ba+cc2+dt+sc)ϕ(.)σ(min+visit+obs+year)	28	28991.72	427.59	0.00	1.00

Species, model	K	AIC	ΔAIC	AICwt	cumltvwt
λ(cc2+dt+sc)ϕ(.)σ(min+visit+obs+year)	27	28992.80	428.67	0.00	1.00
λ(F12+F3)ϕ(.)σ(min+visit+obs+year)	20	29006.67	442.55	0.00	1.00
λ(cc2)ϕ(.)σ(min+visit+obs+year)	20	29014.08	449.95	0.00	1.00
λ(cc)ϕ(.)σ(min+visit+obs+year)	19	29017.47	453.34	0.00	1.00
λ(ba+dt+sc)ϕ(.)σ(min+visit+obs+year)	26	29025.70	461.57	0.00	1.00
λ(dt+sc)ϕ(.)σ(min+visit+obs+year)	25	29026.85	462.72	0.00	1.00
λ(dt)ϕ(.)σ(min+visit+obs+year)	22	29036.92	472.79	0.00	1.00
λ(ba+sc)ϕ(.)σ(min+visit+obs+year)	22	29048.49	484.37	0.00	1.00
λ(sc)ϕ(.)σ(min+visit+obs+year)	21	29052.19	488.06	0.00	1.00
λ(ba)ϕ(.)σ(min+visit+obs+year)	19	29073.37	509.24	0.00	1.00
λ(.)ϕ(.)σ(min+visit+obs+year)	18	29090.70	526.57	0.00	1.00
λ(RT)ϕ(.)σ(min+visit+obs+year)	19	29092.12	527.99	0.00	1.00
White-winged Junco					
λ(yr+RT+GV+GT+ba+cc2+dt+gr)ϕ(.)σ(min+visit+obs+year)	31	16778.88	0.00	0.68	0.68
λ(lat+yr+RT+GV+GT+ba+cc2+dt+gr)ϕ(.)σ(min+visit+obs+year)	32	16780.39	1.52	0.32	1.00
λ(RT+GV+GT+ba+cc2+dt+gr)ϕ(.)σ(min+visit+obs+year)	30	16810.17	31.29	0.00	1.00
λ(ba+cc2+dt+gr)ϕ(.)σ(min+visit+obs+year)	27	16834.00	55.13	0.00	1.00
λ(ba+cc2+dt+gr+wo)ϕ(.)σ(min+visit+obs+year)	28	16834.70	55.83	0.00	1.00
λ(cc2+gr+wo)ϕ(.)σ(min+visit+obs+year)	23	16839.56	60.68	0.00	1.00
λ(ba)ϕ(.)σ(min+visit+obs+year)	20	16842.59	63.71	0.00	1.00

Species, model	K	AIC	ΔAIC	AICwt	cumltvwt
λ(cc2)σ(min+visit+obs+year)	21	16842.74	63.86	0.00	1.00
λ(ba+dt+wo)ϕ(.)σ(min+visit+obs+year)	25	16844.17	65.29	0.00	1.00
λ(cc)ϕ(.)σ(min+visit+obs+year)	20	16852.23	73.36	0.00	1.00
λ(RT+GV+GT)ϕ(.)σ(min+visit+obs+year)	22	16853.28	74.40	0.00	1.00
λ(GV+GT)ϕ(.)σ(min+visit+obs+year)	21	16857.70	78.82	0.00	1.00
λ(gr+wo)ϕ(.)σ(min+visit+obs+year)	21	16865.19	86.31	0.00	1.00
λ(gr)ϕ(.)σ(min+visit+obs+year)	20	16865.79	86.91	0.00	1.00
λ(GV)ϕ(.)σ(min+visit+obs+year)	20	16871.68	92.81	0.00	1.00
λ(RT)ϕ(.)σ(min+visit+obs+year)	20	16871.95	93.08	0.00	1.00
λ(GT)ϕ(.)σ(min+visit+obs+year)	20	16874.57	95.70	0.00	1.00
λ(sc)ϕ(.)σ(min+visit+obs+year)	22	16876.73	97.86	0.00	1.00
λ(.)ϕ(.)σ(min+visit+obs+year)	19	16877.44	98.57	0.00	1.00
λ(F12+F3)ϕ(.)σ(min+visit+obs+year)	21	16877.51	98.63	0.00	1.00
λ(wo)ϕ(.)σ(min+visit+obs+year)	20	16879.15	100.27	0.00	1.00
λ(F12+F3+F45)ϕ(.)σ(min+visit+obs+year)	22	16879.47	100.60	0.00	1.00
λ(F12+F3+F45+F610)ϕ(.)σ(min+visit+obs+year)	23	16880.98	102.10	0.00	1.00
λ(dt)ϕ(.)σ(min+visit+obs+year)	23	16883.20	104.33	0.00	1.00