THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 121, 2019, pp. 1–18
DOI: 10.1093/condor/duy023

RESEARCH ARTICLE

The importance of disturbance and forest structure to bird abundance in the Black Hills

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Submitted October 24, 2018; Accepted December 18, 2018; Published March 16, 2019

ABSTRACT

Many North American birds associated with forest disturbances such as wildfire and mountain pine beetle (*Dendroctonus ponderosae*) outbreaks are declining in abundance. More information on relationships between avian abundance and forest structure and disturbance is needed to guide conservation and management. Our objective was to determine densities of American Three-toed Woodpecker (*Picoides dorsalis*), Black-backed Woodpecker (*Picoides arcticus*), Red-breasted Nuthatch (*Sitta canadensis*), Brown Creeper (*Certhia americana*), 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 3 point counts from late March to late June 2015 and 2016 at more than 2,300 locations distributed across a gradient of forest structure and disturbance types. We estimated densities using 3-level hierarchical time-removal models that simultaneously estimated abundance, availability, and detection probability. Black-backed Woodpeckers were positively related to percent area in 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. Brown Creepers were strongly linked with spruce 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 needs of a diverse bird community in the Black Hills.

Keywords: bird abundance, Black Hills, disturbance, point counts, time-removal models

Importancia del disturbio y de la estructura del bosque para la abundancia de aves en las Black Hills

RESUMEN

Muchas aves de América del Norte asociadas con los disturbios del bosque, como el fuego silvestre y los brotes del escarabajo del pino de montaña (*Dendroctonus ponderosae*), están disminuyendo su abundancia. Se necesita más información sobre las relaciones entre la abundancia de aves y la estructura y el disturbio del bosque para guiar las acciones de conservación y manejo. Nuestro objetivo fue determinar las densidades de *Picoides dorsalis*, *P. arcticus*, *Certhia americana*, *Sitta canadensis* y *Junco hyemalis aikeni* con relación a las características de la vegetación y los disturbios a nivel puntual y de paisaje en Black Hills y las montañas Bear Lodge de Dakota del Sur y Wyoming. Realizamos conteos en puntos en 1222 y 1128 localizaciones en 2015 y 2016, respectivamente, distribuidos a través de un gradiente de tipos de estructura y disturbio del bosque. Visitamos cada punto tres veces desde fines de marzo hasta fines de junio. Obtuvimos valores de densidad usando modelos de eliminación de tiempo de tres niveles jerárquicos que estimaron simultáneamente abundancia, disponibilidad y probabilidad de detección. *P. arcticus* estuvo positivamente relacionado al porcentaje de área en fuegos silvestre de 1 a 3 años de edad y *C. americana* estuvo positivamente asociado al porcentaje de área en fuegos silvestre de 4 a 5 años de edad; sin embargo, *S. canadensis* estuvo negativamente relacionado al porcentaje de área en fuegos silvestres de 3 a 5 años de edad. Con la excepción de *P. dorsalis*, las especies estuvieron positivamente relacionadas al porcentaje de cobertura de árboles muertos por los escarabajos. *C. americana*, *J. h. aikeni* y *S. canadensis* tuvieron respuestas mixtas al porcentaje de cobertura del dosel. *J. h. aikeni* también tuvo una asociación positiva con el porcentaje de vegetación del suelo a escala puntual y de paisaje, mientras que *C. americana* estuvo fuertemente vinculada con la vegetación tipo abeto. *P. dorsalis*, que se piensa que ocupa bosques de abeto en Black Hills, no mostró una relación fuerte con ninguna co-variable. El mantenimiento de algunas áreas de disturbios naturales junto a la heterogeneidad de las características de la vegetación al interior de los rodales y a la escala de paisaje beneficiará las necesidades de una diversa comunidad de aves en Black Hills.

Palabras clave: abundancia de aves, Black Hills, conteos en puntos, disturbio, modelos de eliminación de tiempo

INTRODUCTION

Natural and anthropogenic disturbance to forests creates habitats that are used by many birds. North American birds that are associated with forest disturbance are declining, on average, more than birds associated with mature or closed-canopy forests (Brawn et al. 2001). Forest landscapes and bird populations of western North America are significantly affected by natural disturbances, such as fire and insect outbreak, and anthropogenic disturbance, such as timber harvest. Historically, fire was a primary recurring disturbance, and variability in fire severity and frequency created heterogeneity and promoted species diversity across the landscape (Peet 2000). However, fire suppression has altered the occurrence of natural fire regime, resulting in denser forests with younger, smaller trees (Fulé et al. 1997, Brown and Cook 2006). Fire suppression, even-aged management, and climate warming have increased tree densities, making forests more susceptible to mountain pine beetle (*Dendroctonus ponderosae*, hereafter MPB) outbreaks (Taylor et al. 2006). MPB populations occur at endemic levels with periodic outbreaks naturally lasting 6–18 yr (Graham et al. 2016), resulting in a widespread loss of trees that alters structure, composition, and function of forests (Raffa et al. 2008). Forest management to mitigate wildfires and MPB reduces their occurrence and economic impacts; however, many species benefit from these disturbances because of the abundance of food resources and standing dead trees (snags). Better knowledge of the effects of natural and anthropogenic forest disturbance on bird populations is needed to inform management decisions that balance tradeoffs among forest health, economic value, and bird populations.

The effects of wildfire and MPB outbreaks on bird communities vary among species and forest type. Several bird species are adapted to, or dependent upon, natural disturbances like fire and MPB outbreaks in all or portions of their range (Saab and Powell 2005). Bock and Lynch (1970) found that 17% of 54 observed species in the Sierra Nevada were in unburned plots only, whereas 35% were unique to burned forest. Fire severity and time since fire also influence bird responses in the Rocky Mountains (Hutto 1995, Smucker et al. 2005). In the Black Hills of South Dakota and Wyoming, most bird species had greater abundances in forests recently burned by wildfire compared to other vegetation types (Beason et al. 2006). Woodpeckers and aerial foragers are generally more abundant in burned forests; foliage-gleaning species favor unburned forests (Kotliar et al. 2002). Cavity nesters generally respond more positively to MPB outbreaks than open-cup nesters, and birds nesting in the shrub layer respond more positively than ground and open-cup canopy nesters (Saab et al. 2014). Relationships between bird abundance and richness with MPB infestations vary for avian foraging guilds in lodgepole pine (*Pinus contorta*)–dominated forests in British Columbia (Drever et al. 2009).

The Black Hills recently experienced one of the largest and most intensive MPB outbreaks in the last 100 yr (Graham et al. 2016). Combined with varying levels of wildfire throughout the forest, these disturbance events provide a unique opportunity to study how species are responding to wildfires and MPB outbreaks. The Black Hills represents a unique bird community with both eastern and western species (Dykstra et al. 1997, Mills et al. 2000). We selected 5 focal species, 3 of conservation concern and 2 more common species that could inform forest management and bird conservation. One species, the Black-backed Woodpecker (*Picoides arcticus*), was recently petitioned, but deemed not warranted, to be listed under the U.S. Endangered Species Act (Hanson et al. 2012). The American Three-toed Woodpecker (*Picoides dorsalis*) is a rare permanent resident of the Black Hills and a species of greatest conservation need in South Dakota (South Dakota Game, Fish and Parks 2014). The White-winged Junco (*Junco hyemalis aikeni*), a subspecies of Dark-eyed Junco, is common in most wooded habitats of the Black Hills (Mills et al. 2000), but a species of greatest conservation need in South Dakota because of its endemism to the Black Hills region (South Dakota Game, Fish and Parks 2014). The Red-breasted Nuthatch (*Sitta canadensis*) is abundant in the Black Hills but requires high snag densities, which could be impacted by forest management practices (Mills et al. 2000). Brown Creepers (*Certhia americana*) are sensitive to a variety of forest management practices, making the species an important indicator of forest health (Wiggins 2004, USDA Forest Service 2005). Our objective was to determine the effects of disturbance, forest structure, and landscape composition on densities of American Three-toed Woodpecker, Black-backed Woodpecker, Red-breasted Nuthatch, Brown Creeper, and White-winged Junco in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming.

METHODS

Study Area

Our study area included 554,627 ha of the Black Hills National Forest (BHNF) and Custer State Park (CSP) in southwestern South Dakota and the Bear Lodge Mountains in northeastern Wyoming (Figure 1). The southern portion of the area receives less rainfall, contains a grassier understory, and integrates pine forests with native mixed-grass prairies to form a unique landscape. Conversely, the northern Black Hills receives more rainfall and supports a denser understory 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 (*Pinus ponderosa*) 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 composed of western snowberry (*Symphoricarpos occidentalis*), white coralberry (*Symphoricarpos albus*), juniper (*Juniperus communis*), and kinnikinnick (*Arctostaphylos uva-ursi*) (Severson and Thilenius 1976, Hoffman and Alexander 1987), along with a diversity of native and nonnative grasses, sedges, and forbs.

Wildfires in the Black Hills National Forest have ranged in size from 5 ha to 33,795 ha and have burned more than 216,506 ha between 1909 and 2015 (USDA Forest Service 2017). Ten percent or 19,836 ha of those wildfires have occurred in the past 10 yr (USDA Forest Service 2017). The Black Hills is currently emerging from the largest and most intensive MPB epidemic in the last 100 yr (Graham

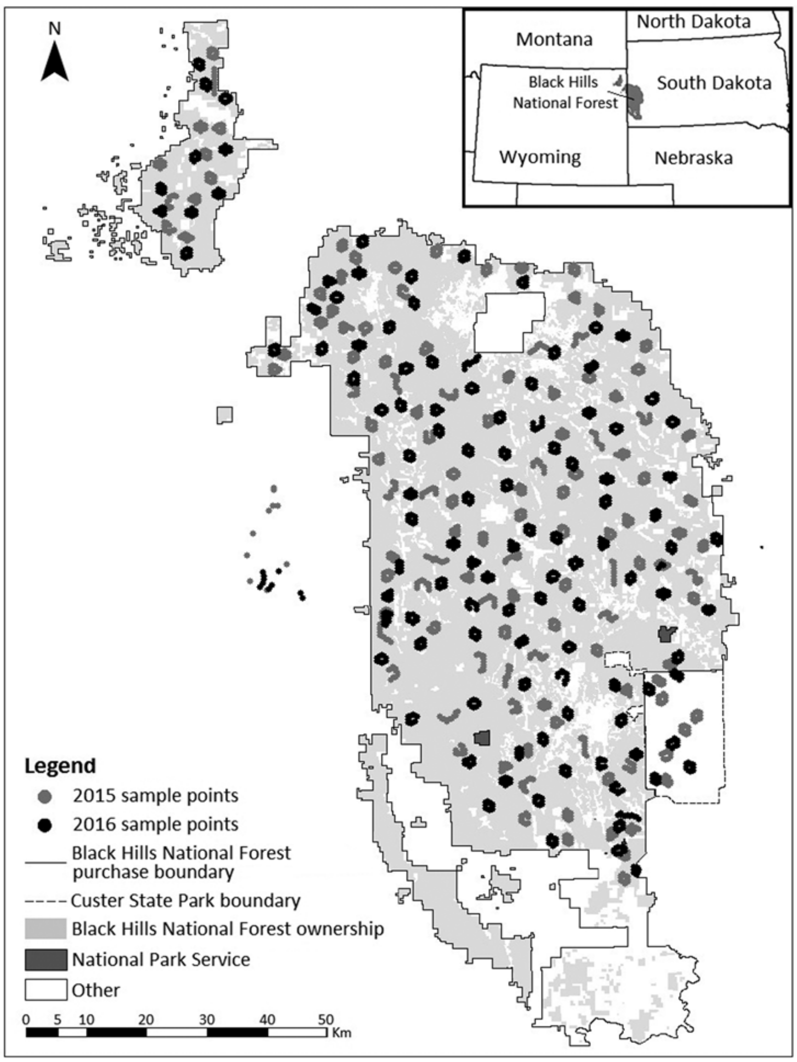

FIGURE 1. Study area and sample point locations (*n* = 2,370) for 2015 (light gray circles) and 2016 (dark gray circles) in the Black Hills National Forest and Custer State Park, South Dakota and Wyoming.

et al. 2016). Approximately one-quarter of the Black Hills (188,583 ha) has been affected since the outbreak began in 1996. The rate of infestation is now declining from a peak in 2012 (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.

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. The center point of each hexagon represented a potential point count site. Each hexagon was 16.28 ha and ~450 m 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 resampled 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 2). 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 1–2, 3, 4–5, and 6–10 yr 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 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

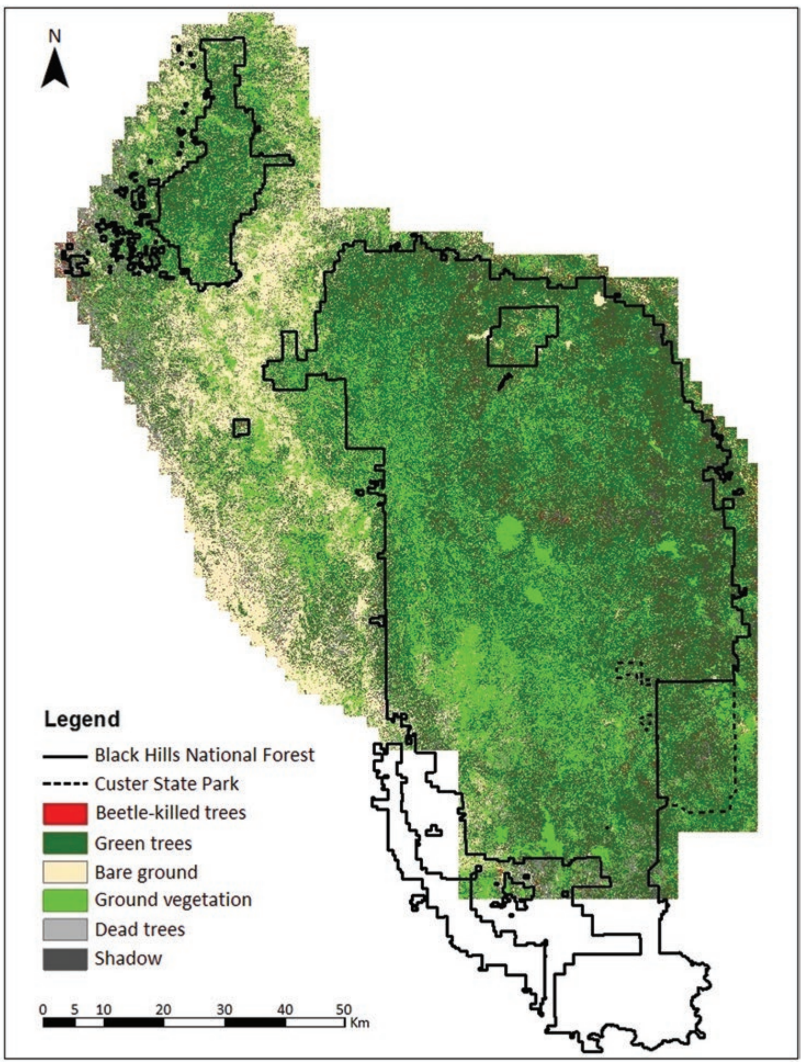

FIGURE 2. We classified 6 categories of forest vegetation on 1-m pixels from aerial photography and measured the percent cover of each category in 16-ha hexagons for use as covariates in bird abundance models in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, 2015–2016.

sufficient detections to fit abundance models of uncommon species, such as 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 100 m off a road. We laid out the remaining 9 points in a transect by choosing the center point of hexagons along a path that maximized sampling efficiency and remained within the same stratum, undisturbed or disturbed, as the starting point. Transects contained a maximum of 10 points because that was the estimated number of points a technician could complete in a morning. Three percent of transects contained <10 points because we were unable to access points once in the field. Adjacent transects were >1,000 m apart. We placed 124 transects (1,232 sampling points) and 115 transects (1,138 sampling points) in 2015 and 2016, respectively (Figure 1).

Avian Surveys

We surveyed abundance of 5 focal species (Table 1) from April 1 through June 28 in 2015 and March 31 through June 23 in 2016. We conducted 5-min point counts at sampling points 3 times each year, approximately 1 mo 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 ~6 hr later. We navigated to each point using a global positioning system (GPS) unit. For each survey we recorded the point number, observer (n = 11), 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 bird. 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, and dominant tree size class in April, overstory canopy cover in May, and understory vegetation in June at each sampling point. 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 4 readings taken with a concave spherical densitometer at the point while facing 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.

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	*Picoides dorsalis*	41
Black-backed Woodpecker	*Picoides arcticus*	362
Red-breasted Nuthatch	*Sitta canadensis*	5,848
Brown Creeper	*Certhia americana*	558
White-winged Junco	*Junco hyemalis aikeni*	2,639

Analytical Methods

We used 3-level hierarchical time-removal models that simultaneously estimated abundance (λ), availability (ϕ), and detection probability (σ). Time-removal models estimate availability, the probability that an individual is present and provides a detectable cue, and detection, the probability of the observer detecting said cue using repeated visits to a single point within a season (Chandler et al. 2011). Simpler models that estimate abundance for unmarked individuals include a geographical populations closure assumption (e.g., 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). Black-backed Woodpeckers and American Three-toed Woodpeckers have large home ranges in the Black Hills and would likely violate this closure assumption across 3 visits to a point (Goggans et al. 1989, Ervin 2011, Rota et al. 2014b). The model that we used 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 5 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-min 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

$$\text{birds ha}^{-1} = \lambda \times \phi \times (\pi \times r^2 \times 10,000^{-1})^{-1}$$

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 acknowledge the potential for spatial autocorrelation among counts, however the R package UNMARKED does not allow spatial or random effects to account for these effects. Furthermore, we evaluated spatial autocorrelation in counts for the most wide-ranging species, the Black-backed Woodpecker, by calculating Moran's I, from which we could not reject the null hypothesis that there was zero spatial autocorrelation ($Z = 1.81$, $P = 0.07$; Proc Variogram, SAS Institute, Cary, North Carolina, USA; Matseur et al. 2018).

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 4 stages: landscape-level wildfire, landscape-level vegetation cover, point-level vegetation, and with and without latitude and year. A priori we constructed 3 landscape-level wildfire, 7 landscape-level vegetation, and 11 point-level vegetation models for all species except the White-winged Junco, which differed slightly by having 6 landscape-level vegetation and 13 point-level vegetation models. Landscape-level wildfire covariates included percent area burned 1–2 yr ago, 3 yr ago, 4–5 yr ago, and 6–10 yr 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 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, except for dominant tree species and size class, which we held at ponderosa pine and sawtimber, 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 5 focal species (Table 1, Appendix Table 4). There was no evidence of lack of fit for the most-supported model of any species based on goodness-of-fit tests ($P > 0.10$). Given that we only had 41 detections of American Three-toed Woodpecker, we caution that we likely had limited power to detect habitat relationships and that supported relationships are conditional on this small sample.

Detection probability for Black-backed Woodpeckers and American Three-toed Woodpeckers was related to day of year, minute, observer, and year (Table 3). 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. 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, whereas Red-breasted Nuthatches were negatively related to percent area of 3- to 5-year-old wildfires (Appendix Table 5). Black-backed Woodpecker densities increased from 0.0027 to 0.0324 birds ha^{-1} and from 0.0027 to 0.0214 birds ha^{-1} across the range of percent area 1- to 2-year-old and 3-year-old wildfires, respectively (Figure 3). Brown Creeper density increased from 0.075 to 0.19 birds ha^{-1} as percent area of 4- to 5-year-old wildfires increased (Figure 3). However, Red-breasted Nuthatch densities decreased from 0.20 to 0.08 birds ha^{-1} and 0.20 to 0.11 birds

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	0.52/0.48		
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	0.04/0.02/0.07/0.82/0.04		
Dominant size class (None/SAPL/POLE/SAWT)	Sc	0.06/0.24/0.14/0.55		
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 Nuthatch	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

ha^{-1} 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 4 of 5 focal species had a strong positive relationship to percent cover of beetle-killed trees (Appendix Table 5). Black-backed Woodpecker densities increased from 0.0027 to 0.0425 birds ha^{-1} across a range of 0–16% cover of beetle-killed trees (Figure 4). Similarly, Brown Creeper (0.075–0.347 birds ha^{-1}), White-winged Junco (0.21–0.53 birds ha^{-1}), and Red-breasted Nuthatch (0.20–0.29 birds ha^{-1}) densities also increased as percent cover of beetle-killed trees increased from 0 to 16% cover (Figure 4). Conversely, percent cover of dead trees had a negative effect on abundances of 2 of our focal species. Red-breasted Nuthatch densities decreased from 0.20 to 0.12 birds ha^{-1} as percent cover of dead trees increased (Figure 5). American Three-toed Woodpeckers also responded negatively to percent cover of dead trees, but confidence intervals overlapped zero. White-winged Junco was 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 to 0.38 birds ha^{-1} and from 0.21 to 0.33 birds ha^{-1} when percent ground vegetation and green trees increased, respectively (Figure 5).

There was weaker support for point-level vegetation covariates and many confidence intervals overlapped zero for all of our focal species. However, Brown Creepers had the highest densities when the dominant tree type was spruce (0.15 birds ha^{-1}) and increased densities from 0.024 to 0.081 birds ha^{-1} when overstory canopy cover ranged from 0 to 80% (Figure 6). White-winged Junco density increased slightly when percent grass/forb cover increased from 0 to 100% (0.19 to 0.23 birds ha^{-1}), but densities decreased as overstory canopy cover increased from 40 to 100% (0.22 to 0.15 birds ha^{-1}) (Figure 6). Last, densities for Red-breasted Nuthatches ranged from 0.15 to 0.19 birds ha^{-1} as percent overstory canopy cover increased from 0 to 80% (Figure 6).

Abundance of Black-backed Woodpeckers and Red-breasted Nuthatches were related to latitude. Black-backed Woodpecker density decreased from 0.0048 to 0.0013 birds ha^{-1}, whereas Red-breasted Nuthatch density increased from 0.14 to 0.31 birds ha^{-1}, as latitude ranged from 43.51° to 44.76° (Figure 7). Year was included in all of the

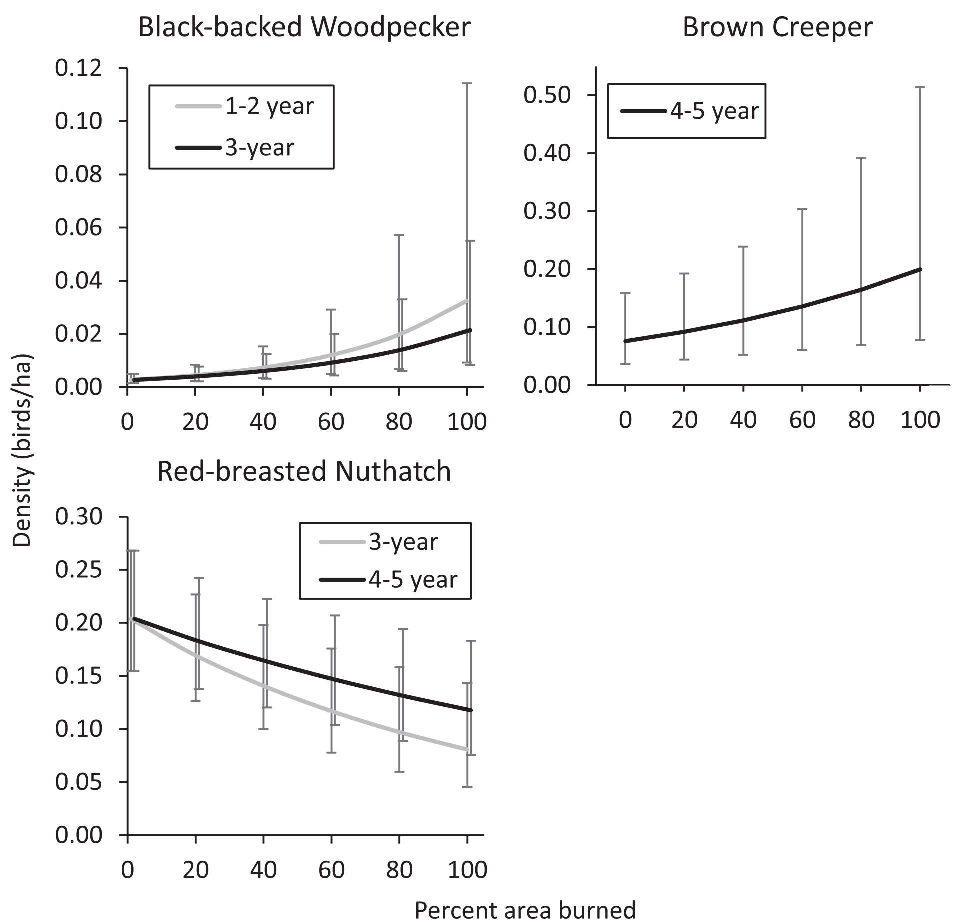

FIGURE 3. Predicted densities and SE of bird species across ranges of percent area burned and time since fire.

top models for Black-backed Woodpecker, Red-breasted Nuthatch, and White-winged Junco, but confidence intervals overlapped zero for Black-backed Woodpecker and White-winged Junco.

DISCUSSION

We found mixed relationships between bird abundance and natural disturbances and forest structure. Abundances of Black-backed Woodpeckers and Brown Creepers were positively related, and Red-breasted Nuthatches negatively related, to the presence of wildfire. With the exception of American Three-toed Woodpeckers, species were positively related to percent cover of beetle-killed trees. More species showed stronger relationships with landscape-level vegetation measurements than point-level variables, but species responses to vegetation measurements varied.

Wildfires can significantly alter forest structure, creating unique habitat that attracts many plant and animal species. Black-backed Woodpeckers are known to be strongly associated with burned habitats (Hutto 2008). Rota et al. (2014a) found that Black-backed Woodpeckers had higher fledging rates, juvenile survival, nesting success, and positive population growth in wildfire habitat as compared to MPB infestations and prescribed burns. Black-backed Woodpeckers likely had a stronger positive response to percent cover of 1- to 2-year-old wildfires than 3-year-old wildfires, and no effect of 4- to 5-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). Despite their strong association with mature, old-growth forests (Sallabanks et al. 2006), Brown Creepers are more abundant in burned than unburned forests (Morissette et al. 2002). Others have shown Brown Creeper detections to be 2 times greater in 4- to 5-year-old wildfires than more recently burned forests (Panjabi 2005, Hutton et al. 2006). Brown Creepers need large, loose pieces of bark to nest, which is more common on trees as time 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 (Bock and Lynch 1970, Raphael and White 1984). The majority of wildfires we surveyed were high-intensity fires, which greatly reduces forest canopy cover and is likely why abundance of Red-breasted Nuthatch was negatively related to wildfire.

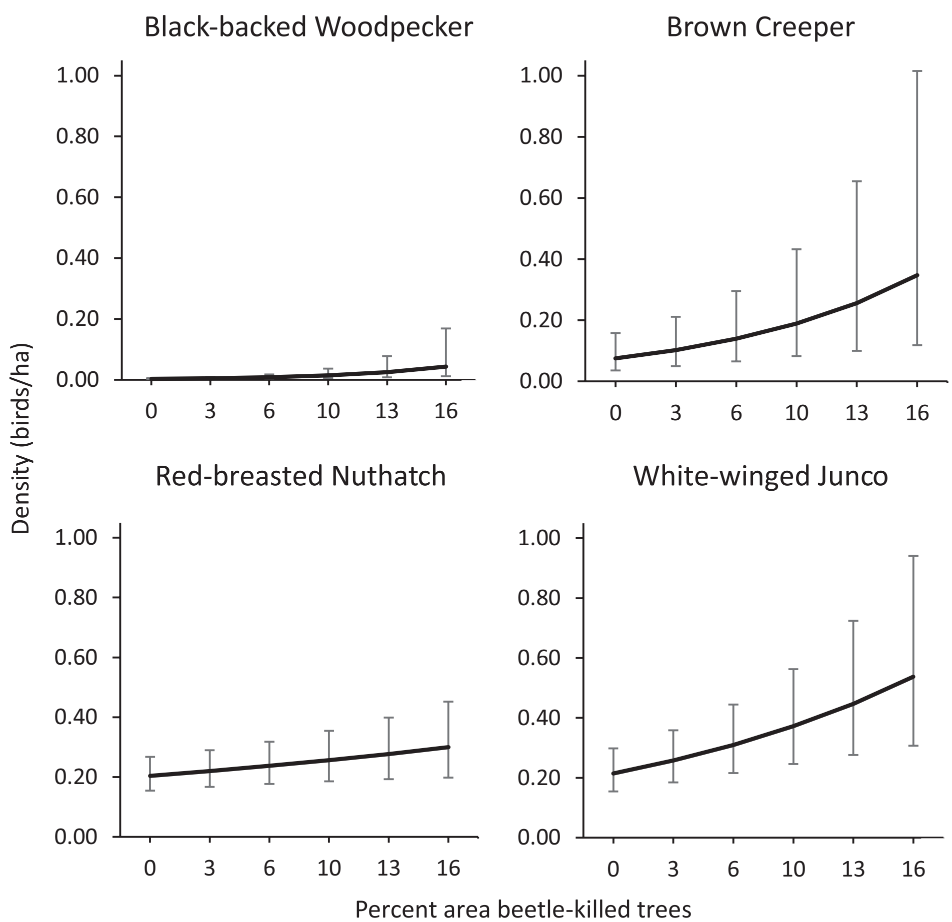

FIGURE 4. Predicted densities and SE of bird species across a gradient of percent area of beetle-killed pine trees.

MPB outbreaks 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 had the greatest 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 bird 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 White-winged Junco abundance and MPB outbreaks (Saab et al. 2014). Brown Creepers also responded positively to beetle-killed trees, but past research shows a mixed response by this species to MPB outbreaks in ponderosa or lodgepole pine dominant forests (Saab et al. 2014). Red-breasted 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 Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine beetle-infested forests (Norris and Martin 2008). Black-backed Woodpeckers 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 burned forest (Rota et al. 2014a). Research in lodgepole pine forests has shown an increase in woodpecker abundances in areas of MPB outbreak, but no change in fecundity (Edworthy et al. 2011). Although these areas may look attractive due to the increased resource availability, the breeding benefits of MPB infestations is unclear.

White-winged Junco, the only ground-nesting species that we surveyed, was associated with greater percent cover by ground vegetation and green trees at the landscape-level scale. 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. White-winged 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.

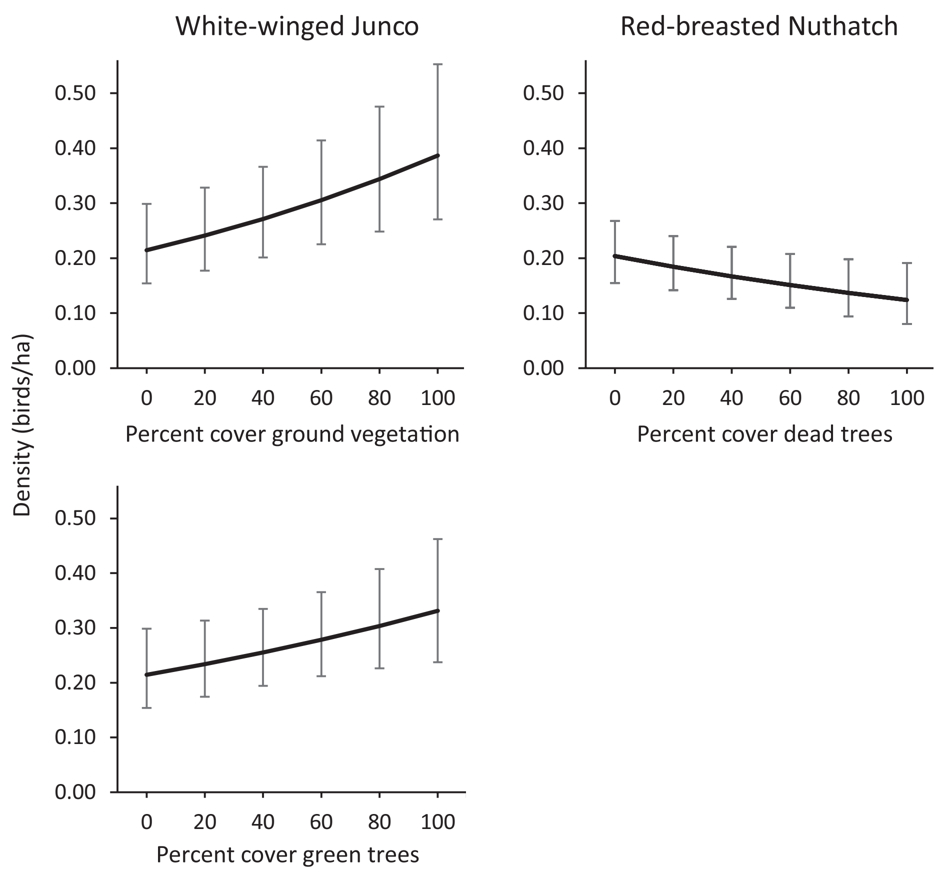

FIGURE 5. Predicted densities and SE of bird species across a gradient of landscape-level percent cover measurements.

The White-winged Junco is primarily a forest and forest edge species that is 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 White-winged Junco abundances as overstory canopy cover increases above 40% (Mills et al. 2000).

Only 3 of 5 focal species had strong associations with point-level vegetation characteristics. Brown Creeper densities peaked at 80% point-level canopy cover. Brown Creepers prefer dense, mature stands of ponderosa pine and reach high densities when canopy cover is >70% (Mills et al. 2000, Anderson and Crompton 2002). They showed a strong relationship with spruce trees in our study, which is consistent with previous research that showed highest densities in spruce (Panjabi 2003). Although only 4% of our sampling points were in spruce forests, this forest type is not usually managed for timber. Spruce forest had large-diameter old-growth trees that are conducive to Brown Creeper foraging and nesting (Weikel and Hayes 1999, Poulin et al. 2008). At the point level, Red-breasted Nuthatch density was highest at 60–80% overstory canopy cover. Mills et al. (2000) repeatedly observed nuthatches selecting mature and multi-storied ponderosa pine stands with moderate to high canopy cover. Other studies in the Black Hills also show nuthatch densities are highest in late-successional pine habitat (Beason et al. 2006). Although our woodpecker species included point-level covariates in their top models, all confidence intervals overlapped zero. The Black-backed Woodpecker and American Three-toed Woodpeckers' 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 that encompass vegetation characteristics at a broader scale. Our point-level measurements only encompassed a small area around each point, which may not be representative of the entire area within the detection radius.

Black-backed Woodpeckers and Red-breasted Nuthatches had strong but opposite relationships to latitude. Black-backed Woodpecker density decreased as latitude increased in the Black Hills. The majority of burned habitat existed in the southern hills, which may be why we saw higher densities in lower latitudes. Higher latitudes in our study included the Bear Lodge Mountains of Wyoming, which were isolated from the main body of the forest and had less natural disturbance than the main portion of the BHNF and CSP (Graham et al. 2016, USDA Forest Service

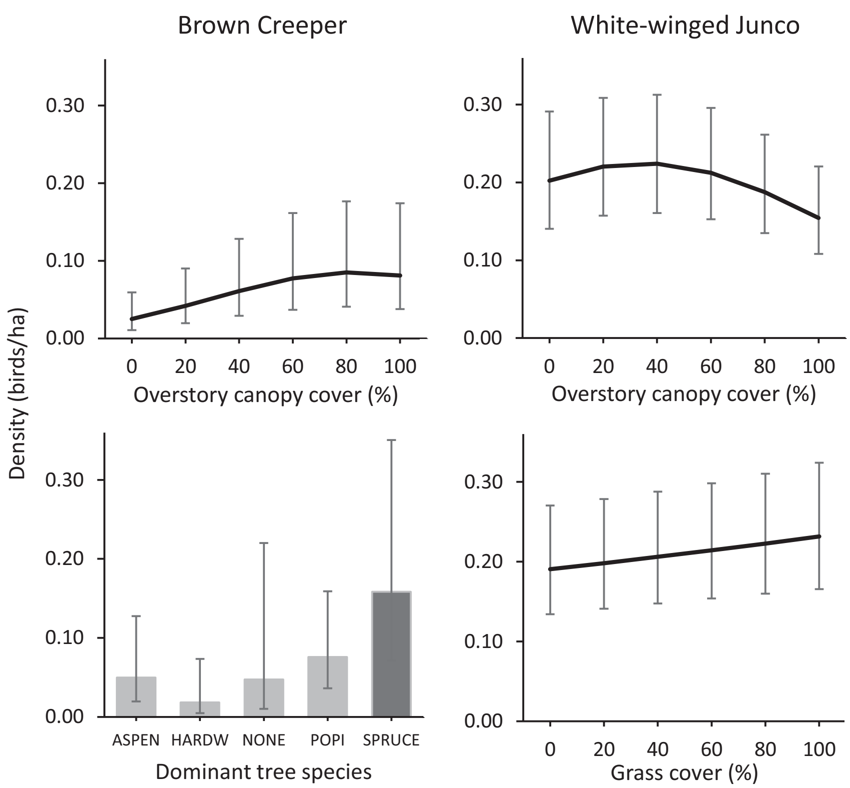

FIGURE 6. Predicted densities and SE of bird species across a gradient of point-level vegetation measurements.

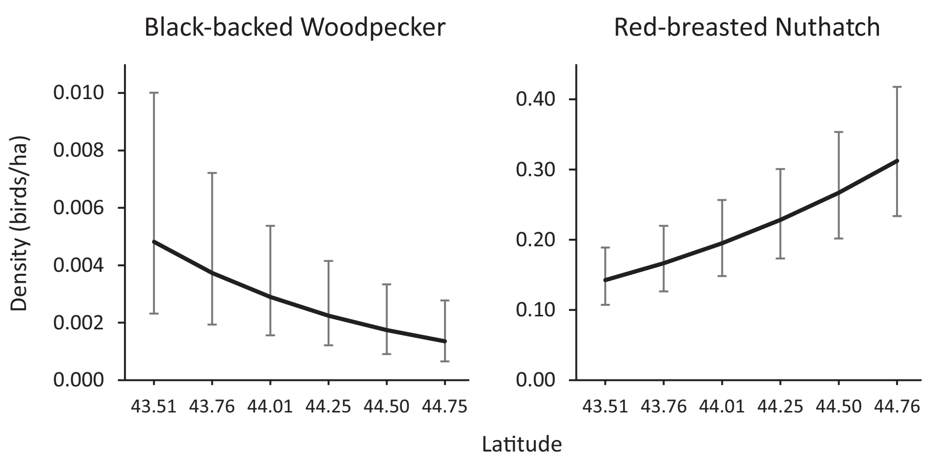

FIGURE 7. Predicted densities and SE of bird species by latitude.

2017). We observed the highest densities for Red-breasted Nuthatches 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 contained 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 the Black Hills, latitude is also correlated with elevation and precipitation (Orr 1959), which could affect abundances of these species.

Abundance of American Three-toed Woodpeckers was not strongly related to any vegetation variables in our study. Other studies have found them to be most abundant or even exclusively found in spruce forests (Panjabi 2003, Ervin 2011). Alternatively, Mohren et al. (2016) observed them in aspen and ponderosa pine stands in the Black Hills. Dominant tree species was included in the top model for American Three-toed Woodpecker, but we did not see a strong association with any specific tree species. We were likely not able to detect habitat relationships for American Three-toed Woodpeckers because of our low number of detections. They exploit burns in other parts of their range (Hoffman 1997, Murphy and Lehnhausen 1998, Hoyt and Hannon 2002), but recent surveys did not record any American Three-toed Woodpeckers in burned habitats of the Black Hills (Panjabi 2003, Ervin 2011). Although we had low detections of American Three-toed Woodpeckers, we did observe them in burned ponderosa pine stands. Spruce forests typically occur in moist areas, so the majority of burned forest in the Black Hills is ponderosa pine. We may have observed American Three-toed Woodpeckers in burned ponderosa pine stands close to spruce stands.

CONCLUSIONS

Our large-scale survey efforts enabled us to predict avian density over a variety of vegetation conditions across the BHNF and CSP. Many of our focal species are considered sensitive to forest management practices. Because habitat relationships varied among our focal species, there is potential for management and natural disturbance to adversely affect abundance of some species while promoting habitat 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 yr will supply Black-backed Woodpeckers with newly burned habitat (<3 yr), providing opportunity for population growth, and also give Brown Creepers the 4- to 5-year-old wildfires they prefer. Also, retaining a mixture of canopy cover between 40% and 80% will allow for increased grass/shrub cover for ground-nesters such as White-winged Juncos, while providing closed-canopy conditions favored by Red-breasted Nuthatches. Due to the small sample size of American Three-toed Woodpeckers we could not confidently link the species to any vegetation variables in our study; however, past research has shown American Three-toed Woodpeckers prefer spruce forests in the Black Hills (Ervin 2011). Conserving spruce forests also provides large-diameter old-growth trees for Brown Creepers. Spruce forests are largely untouched by timber harvest, creating a unique habitat for species in a highly managed forest. However, information on species diversity and habitat use of these spruce forests is needed to understand the potential benefits this habitat provides.

AKNOWLEDGMENTS

We thank J. Guenther, J. Wilson, C. Yeager, T. Jacobs, L. McCullough, S. Freeman, Z. McDonald, and N. Meadows for their help with fieldwork.

Funding statement: Major funding for this project was provided by U.S. Forest Service Rocky Mountain Research Station agreement 14-JV-11221632-104, Black Hills National Forest agreement ISA_0203-14-009, South Dakota Division of Agriculture, Division of Conservation and Forestry agreement 14-CO-11221532-090, South Dakota Department of Game, Fish and Parks, Division of Wildlife agreement 14-CO-11221632-151, and Wyoming Game and Fish Commission agreement 14-CO-11221632-144. This study was funded in part by federal funding through State Wildlife Grant T-65-R-1, Study 2476, administered through the U.S. Fish and Wildlife Service and provided by the South Dakota Department of Game, Fish and Parks. None of these funding agencies had input into the content of this manuscript or required approval of the manuscript before submission or publication.

Ethics statement: The University of Missouri Standard of Conduct was followed throughout this study and university employees completed the required training "Building a Foundation: Discrimination Prevention and Title IX." No animal subjects were handled in this research.

# These authors contributed equally to the paper.

Author contributions: E.A.M, J.J.M., F.R.T., and M.A.R. formulated the questions; E.A.M. and B.E.D. collected data and supervised research; E.A.M., F.R.T., and J.J.M. analyzed the data; and E.A.M. wrote the paper.

Data deposits: Data is deposited with the USDA Forest Service Rocky Mountain Research Station, and can be accessed at https://www.fs.fed.us/rmrs/search/data?f%5B0%5D = type%3Adatasets.

LITERATURE CITED

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

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

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, USA.

Bock, C. E., and J. F. Lynch (1970). Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. The Condor 72:182–189.

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 259:220–228.

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.

Brawn, J. D., S. K. Robinson, and F. R. Thompson III (2001). The role of disturbance in the ecology and conservation of birds. Annual Review of Ecology and Systematics 32:251–276.

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 92:1429–1435.

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 112:2064–2073.

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: 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. U.S. Department of Interior Geological Survey Open file report 00-329. Denver, CO, USA.

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. In First Biennial North American Forest Ecology Workshop, June 24–26, 1997, North Carolina State University, Raleigh (J. E. Cook and B. P. Oswald, Compilers). pp. 16–26. 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 Management 261:203–210.

Ervin, A. M. (2011). Habitat selection, nesting success, and genetic structure of the American Three-toed Woodpecker (*Picoides dorsalis*) in the Black Hills of South Dakota. Ph.D. dissertation, University of South Dakota, Vermillion, SD, 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

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

Ghalambor, C. K., and T. E. Martin (1999). Red-breasted Nuthatch (*Sitta canadensis*). In The Birds of North America 459 (F. B. Gill and A. Poole, Editors). Academy of Natural Sciences, Philadelphia, PA, USA, and American Ornithologists' Union, Washington, DC, 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. USDA Forest Service, General Technical Report RMRS-353, Rocky Mountain Research Station, Fort Collins, CO, USA.

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. Master's thesis, Montana State University, Bozeman, MT, USA.

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. USDA Forest Service Research Paper RM-276, Fort Collins, CO, USA.

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 100:377–394.

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 32:1881–1888.

Hutto, R. L. (1995). Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) coniferous forests. Conservation Biology 9:1041–1058.

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

Hutton, K., J. Beason, G. Giroir, A. Panjabi, R. Sparks, and D. Hanni (2006). Monitoring the birds of the Black Hills: 2006 field season report. Technical Report MMBBH06-01, Rocky Mountain Bird Observatory, Brighton, CO, USA.

Kotliar, N. B., S. J. Hejl, R. L. Hutto, V. A. Saab, C. P. Melcher, and M. McFadzen (2002). Effects of fire and post-fire salvage logging on avian communities in conifer-dominated forests of western United States. In Effects of Habitat Fragmentation on Birds in Western Landscapes: Contrasts with Paradigms from the Eastern U.S. (T. L. George and D. S. Dobkin, Editors). Studies in Avian Biology 25:49–64.

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 7:10–24.

Matseur, E. A., F. R. Thompson III, B. E. Dickerson, M. A. Rumble, and J. J. Millspaugh (2018). Black-backed Woodpecker abundance in the Black Hills. Journal of Wildlife Management 82:1039–1048.

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 71:187–206.

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. 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 32:2169–2183.

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

Norris, A. R., and K. Martin (2008). Mountain pine beetle presence affects nest patch choice of Red-breasted Nuthatches. Journal of Wildlife Management 72:733–737.

Orr, H. K. (1959). Precipitation and streamflow in the Black Hills. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Station Paper No. 44, Fort Collins, Colorado, USA.

Ostfeld, R. S., and F. Keesing (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology & 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, USA.

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, USA.

Peet, R. K. (2000). Forests and meadows of the Rocky Mountains. In North American Terrestrial Vegetation (M. G. Barbour and W. D. Billings, Editors). Cambridge University Press, Cambridge, UK. pp. 76–121.

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*). In The Birds of North America (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.669

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.

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.

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: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 27:375–386.

Saab, V. A., and H. D. W. Powell (2005). Fire and avian ecology in North America: Process influencing pattern. In Fire and Avian Ecology in North America (V. A. Saab and H. D. W. Powell, Editors). Studies in Avian Biology 30:1–13.

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 60:539–559.

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. USDA Forest Service Research Paper RM-166, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, USA.

Sharpe, G. W., C. W. Hendee, and S. W. Allen (1976). Introduction to Forestry. McGraw-Hill Books, New York, NY, USA.

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-97, Rocky Mountain Research Station, Fort Collins, CO, USA.

Smucker, K. M., R. L. Hutto, and B. M. Steele (2005). Changes in bird abundance after wildfire: Importance of fire severity and time since fire. Ecological Applications 15:1535–1549.

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

Taylor, S. W., A. L. Carroll, R. I. Alfaro, and L. Safranyik (2006). Forest, climate and mountain pine beetle outbreak dynamics in western Canada. In The Mountain Pine Beetle: A Synthesis of Biology, Management, and Impacts on Lodgepole Pine (L. Safranyik and B. Wilson, Editors). Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Canada. pp. 67–94.

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, USA. http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsm9_011678.pdf

USDA Forest Service (2017). Black Hills National Forest large fire history map 1910–2017. https://www.fs.usda.gov/Internet/FSE_MEDIA/fseprd546822.jpg

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. USDA Forest Service Resource Bulletin NRS-83, Northern Research Station, Newtown Square, PA, USA.

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. The 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, USA.

Wiggins, D. (2004). American Three-toed Woodpecker (*Picoides dorsalis*): A technical conservation assessment. USDA Forest Service, Rocky Mountain Region. https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5182071.pdf

APPENDIX

APPENDIX TABLE 4. Number of parameters (*k*), AIC, ΔAIC, Akaike weight (w_i) 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	w_i	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
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	3,314.36	0.00	1.00	1.00
λ(lat+F12+F3+F45+RT+DS+dt)φ(.)σ(min+doy+obs+year)	28	3,331.80	17.45	0.00	1.00
λ(F12+F3+F45+RT+DS+dt)φ(.)σ(min+doy+obs+year)	27	3,341.21	26.86	0.00	1.00
λ(F12+F3+F45)φ(.)σ(min+doy+obs+year)	21	3,362.51	48.16	0.00	1.00
λ(F12+F3+F45+F610)φ(.)σ(min+doy+obs+year)	22	3,362.79	48.43	0.00	1.00
λ(RT+DS)φ(.)σ(min+doy+obs+year)	20	3,375.41	61.06	0.00	1.00
λ(F12+F3)φ(.)σ(min+doy+obs+year)	20	3,375.71	61.35	0.00	1.00
λ(RT+DS+HT)φ(.)σ(min+doy+obs+year)	21	3,377.40	63.05	0.00	1.00
λ(DS)φ(.)σ(min+doy+obs+year)	19	3,382.06	67.71	0.00	1.00
λ(RT+HT)φ(.)σ(min+doy+obs+year)	20	3,439.71	125.35	0.00	1.00
λ(HT)φ(.)σ(min+doy+obs+year)	19	3,443.46	129.11	0.00	1.00
λ(dt)φ(.)σ(min+doy+obs+year)	22	3,447.50	133.15	0.00	1.00
λ(ba+dt+sc)φ(.)σ(min+doy+obs+year)	26	3,452.69	138.33	0.00	1.00
λ(dt+sc)φ(.)σ(min+doy+obs+year)	25	3,453.29	138.93	0.00	1.00
λ(cc+dt+sc)φ(.)σ(min+doy+obs+year)	26	3,454.32	139.96	0.00	1.00
λ(ba+cc+dt+sc)φ(.)σ(min+doy+obs+year)	27	3,454.67	140.32	0.00	1.00
λ(RT)φ(.)σ(min+doy+obs+year)	19	3,456.12	141.76	0.00	1.00
λ(sc)φ(.)σ(min+doy+obs+year)	21	3,457.50	143.14	0.00	1.00
λ(ba+sc)φ(.)σ(min+doy+obs+year)	22	3,458.13	143.77	0.00	1.00
λ(.)φ(.)σ(min+doy+obs+year)	18	3,461.76	147.41	0.00	1.00
λ(cc)φ(.)σ(min+doy+obs+year)	19	3,463.13	148.78	0.00	1.00
λ(ba)φ(.)σ(min+doy+obs+year)	19	3,463.68	149.32	0.00	1.00
λ(cc2)φ(.)σ(min+doy+obs+year)	20	3,465.00	150.64	0.00	1.00
Brown Creeper					
λ(F12+F3+F45+RT+cc2+dt+sc)φ(.)σ(min+doy)	20	5,058.40	0.00	0.49	0.49
λ(yr+F12+F3+F45+RT+cc2+dt+sc)φ(.)σ(min+doy)	21	5,059.00	0.61	0.36	0.86
λ(lat+yr+F12+F3+F45+RT+cc2+dt+sc)φ(.)σ(min+doy)	22	5,060.91	2.51	0.14	1.00
λ(cc2+dt+sc)φ(.)σ(min+doy)	15	5,068.80	10.40	0.00	1.00
λ(ba+cc2+dt+sc)φ(.)σ(min+doy)	16	5,069.86	11.46	0.00	1.00
λ(cc2)φ(.)σ(min+doy)	8	5,082.93	24.54	0.00	1.00
λ(cc)φ(.)σ(min+doy)	7	5,088.40	30.00	0.00	1.00
λ(ba+dt+sc)φ(.)σ(min+doy)	14	5,092.50	34.10	0.00	1.00
λ(dt)φ(.)σ(min+doy)	10	5,096.22	37.83	0.00	1.00
λ(dt+sc)φ(.)σ(min+doy)	13	5,101.43	43.03	0.00	1.00
λ(ba)φ(.)σ(min+doy)	7	5,102.13	43.73	0.00	1.00
λ(RT)φ(.)σ(min+doy)	7	5,104.22	45.83	0.00	1.00
λ(RT+GT)φ(.)σ(min+doy)	8	5,105.65	47.25	0.00	1.00
λ(RT+DS+GT)φ(.)σ(min+doy)	9	5,107.62	49.22	0.00	1.00
λ(F12+F3+F45)φ(.)σ(min+doy)	9	5,107.89	49.49	0.00	1.00
λ(ba+sc)φ(.)σ(min+doy)	10	5,107.93	49.54	0.00	1.00
λ(F12+F3+F45+F610)φ(.)σ(min+doy)	10	5,108.33	49.93	0.00	1.00
λ(F12+F3)φ(.)σ(min+doy)	8	5,110.21	51.81	0.00	1.00

APPENDIX TABLE 4. CONTINUED

Species, model	*k*	AIC	ΔAIC	w_i	cumltvwt
λ(.)φ(.)σ(min+doy)	6	5,113.02	54.62	0.00	1.00
λ(DS)φ(.)σ(min+doy)	7	5,114.75	56.36	0.00	1.00
λ(GT)φ(.)σ(min+doy)	7	5,114.89	56.49	0.00	1.00
λ(sc)φ(.)σ(min+doy)	9	5,117.79	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	28,564.13	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	28,647.31	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	28,752.89	188.76	0.00	1.00
λ(RT+DS+GT)φ(.)σ(min+visit+obs+year)	21	28,823.03	258.9	0.00	1.00
λ(RT+GT)φ(.)σ(min+visit+obs+year)	20	28,866.61	302.49	0.00	1.00
λ(GT)φ(.)σ(min+visit+obs+year)	19	28,870.70	306.57	0.00	1.00
λ(DS)φ(.)σ(min+visit+obs+year)	19	28,952.88	388.75	0.00	1.00
λ(DS+GT)φ(.)σ(min+visit+obs+year)	20	28,954.83	390.71	0.00	1.00
λ(F12+F3+F45+F610)φ(.)σ(min+visit+obs+year)	22	28,965.92	401.79	0.00	1.00
λ(F12+F3+F45)φ(.)σ(min+visit+obs+year)	21	28,968.70	404.58	0.00	1.00
λ(ba+cc2+dt+sc)φ(.)σ(min+visit+obs+year)	28	28,991.72	427.59	0.00	1.00
λ(cc2+dt+sc)φ(.)σ(min+visit+obs+year)	27	28,992.80	428.67	0.00	1.00
λ(F12+F3)φ(.)σ(min+visit+obs+year)	20	29,006.67	442.55	0.00	1.00
λ(cc2)φ(.)σ(min+visit+obs+year)	20	29,014.08	449.95	0.00	1.00
λ(cc)φ(.)σ(min+visit+obs+year)	19	29,017.47	453.34	0.00	1.00
λ(ba+dt+sc)φ(.)σ(min+visit+obs+year)	26	29,025.70	461.57	0.00	1.00
λ(dt+sc)φ(.)σ(min+visit+obs+year)	25	29,026.85	462.72	0.00	1.00
λ(dt)φ(.)σ(min+visit+obs+year)	22	29,036.92	472.79	0.00	1.00
λ(ba+sc)φ(.)σ(min+visit+obs+year)	22	29,048.49	484.37	0.00	1.00
λ(sc)φ(.)σ(min+visit+obs+year)	21	29,052.19	488.06	0.00	1.00
λ(ba)φ(.)σ(min+visit+obs+year)	19	29,073.37	509.24	0.00	1.00
λ(.)φ(.)σ(min+visit+obs+year)	18	29,090.70	526.57	0.00	1.00
λ(RT)φ(.)σ(min+visit+obs+year)	19	29,092.12	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	16,778.88	0.00	0.68	0.68
λ(lat+yr+RT+GV+GT+ba+cc2+dt+gr)φ(.)σ(min+visit+obs+year)	32	16,780.39	1.52	0.32	1.00
λ(RT+GV+GT+ba+cc2+dt+gr)φ(.)σ(min+visit+obs+year)	30	16,810.17	31.29	0.00	1.00
λ(ba+cc2+dt+gr)φ(.)σ(min+visit+obs+year)	27	16,834.00	55.13	0.00	1.00
λ(ba+cc2+dt+gr+wo)φ(.)σ(min+visit+obs+year)	28	16,834.70	55.83	0.00	1.00
λ(cc2+gr+wo)φ(.)σ(min+visit+obs+year)	23	16,839.56	60.68	0.00	1.00
λ(ba)φ(.)σ(min+visit+obs+year)	20	16,842.59	63.71	0.00	1.00
λ(cc2)σ(min+visit+obs+year)	21	16,842.74	63.86	0.00	1.00
λ(ba+dt+wo)φ(.)σ(min+visit+obs+year)	25	16,844.17	65.29	0.00	1.00
λ(cc)φ(.)σ(min+visit+obs+year)	20	16,852.23	73.36	0.00	1.00
λ(RT+GV+GT)φ(.)σ(min+visit+obs+year)	22	16,853.28	74.40	0.00	1.00
λ(GV+GT)φ(.)σ(min+visit+obs+year)	21	16,857.70	78.82	0.00	1.00
λ(gr+wo)φ(.)σ(min+visit+obs+year)	21	16,865.19	86.31	0.00	1.00
λ(gr)φ(.)σ(min+visit+obs+year)	20	16,865.79	86.91	0.00	1.00
λ(GV)φ(.)σ(min+visit+obs+year)	20	16,871.68	92.81	0.00	1.00
λ(RT)φ(.)σ(min+visit+obs+year)	20	16,871.95	93.08	0.00	1.00
λ(GT)φ(.)σ(min+visit+obs+year)	20	16,874.57	95.70	0.00	1.00
λ(sc)φ(.)σ(min+visit+obs+year)	22	16,876.73	97.86	0.00	1.00
λ(.)φ(.)σ(min+visit+obs+year)	19	16,877.44	98.57	0.00	1.00
λ(F12+F3)φ(.)σ(min+visit+obs+year)	21	16,877.51	98.63	0.00	1.00
λ(wo)φ(.)σ(min+visit+obs+year)	20	16,879.15	100.27	0.00	1.00
λ(F12+F3+F45)φ(.)σ(min+visit+obs+year)	22	16,879.47	100.60	0.00	1.00
λ(F12+F3+F45+F610)φ(.)σ(min+visit+obs+year)	23	16,880.98	102.10	0.00	1.00
λ(dt)φ(.)σ(min+visit+obs+year)	23	16,883.20	104.33	0.00	1.00

APPENDIX TABLE 5. 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
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
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

APPENDIX TABLE 5. CONTINUED

Species, covariate	Coeff	SE	LCL	UCL
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