



Research Article

Black-Backed Woodpecker Abundance in the Black Hills

ELIZABETH A. MATSEUR,¹ *School of Natural Resources, University of Missouri, 302 Natural Resources Building, Columbia, MO 65211, USA*
 FRANK R. THOMPSON, III, *U.S. Forest Service Northern Research Station, 202 Natural Resources Building, Columbia, MO 65211, USA*
 BRIAN E. DICKERSON, *U.S. Forest Service Rocky Mountain Research Station, 8221 Mt. Rushmore Road, Rapid City, SD 57702, USA*
 MARK A. RUMBLE, *U.S. Forest Service Rocky Mountain Research Station, 8221 Mt. Rushmore Road, Rapid City, SD 57702, USA*
 JOSHUA J. MILLSPAUGH, *W. A. Franke College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA*

ABSTRACT The Black Hills population of black-backed woodpeckers (*Picoides arcticus*) was petitioned, but deemed not warranted, to be listed as a threatened or endangered species under the Endangered Species Act and more information on their population size in the region is needed. Our objective was to map abundance and provide a population estimate of black-backed woodpeckers in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, USA. We conducted 3,666 and 3,384 5-minute point count surveys from late-March to late-June in 2015 and 2016, respectively. We characterized vegetation around each point using geographic information system-derived landscape variables and fit 3-level hierarchical time-removal models in R package unmarked using gmultmix. The global abundance model received the most support and included year, latitude, and percent area of green trees, beetle-killed trees, dead trees, 1- to 2-year-old wildfire, 3-year-old wildfire, and 4- to 5-year-old wildfire. Points with high percent cover of beetle-killed trees had the greatest density of black-backed woodpeckers, followed by 1- to 2-year-old wildfires. After 4 years, areas burned by wildfire supported lower densities of black-backed woodpeckers than undisturbed forests. Mean density was 0.528 birds/km² in 2015 and 0.626 birds/km² in 2016. There were an estimated 2,920 and 3,439 black-backed woodpeckers in the Black Hills and Bear Lodge Mountains in 2015 and 2016, respectively. We suggest areas with high percent cover of beetle-killed trees may support high densities of black-backed woodpeckers and are important to sustaining populations when the availability of recent (<4 years old) wildfire is declining or scarce. Published 2018. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS abundance, black-backed woodpecker, Black Hills, *Picoides arcticus*, point count, population estimate.

Natural disturbances play an important role in shaping landscapes and bird distributions across western North America (Hejl 1992, 1994). Fire is a natural disturbance in the Black Hills, USA, and has shaped the vegetation community, resulting in decreased understory growth and stand densities (Brown and Cook 2006). For much of the twentieth century, however, fire has largely been suppressed because of potential human conflicts, including efforts to protect marketable timber (Nix 2012). Changes in the occurrence of natural fire regimes have altered the composition and structure of western forests resulting in less early successional post-fire vegetation, thus affecting bird communities (Hejl 1992, 1994). Mountain pine beetle (*Dendroctonus ponderosae*; MPB) infestations are a source of large-scale disturbance in the Black Hills and were abundant during our study (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). The vegetation communities created by these disturbances contain temporary, ephemeral food resources, which are exploited by organisms for a short time following the disturbance.

Black-backed woodpeckers (*Picoides arcticus*) are almost completely restricted to disturbed ephemeral areas because of their diet. As a result, the black-backed woodpecker is a Sensitive Species and Management Indicator Species in Region 2 of the United States Forest Service (USFS 2005). Black-backed woodpeckers are also 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). Furthermore, the Black Hills population of black-backed woodpeckers was petitioned, but deemed not warranted, to be listed as threatened or endangered as a Distinct Population Segment subspecies under the Endangered Species Act (Hanson et al.

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¹E-mail: eamatseur@mail.missouri.edu

2012). 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. Population estimates of black-backed woodpeckers in the Black Hills in the petition were calculated from density estimates of other areas and were below the threshold value for an effective population size to ensure population viability (Hanson et al. 2012). However, re-analysis of a population estimate by Mohren et al. (2014) estimated approximately 50% more breeding pairs than the Hanson et al. (2012) estimate.

Black-backed woodpeckers rely on a patchwork of recently burned, beetle-killed, and undisturbed forests to maintain their population (Hutto 1995, Hoyt and Hannon 2002, Hutto 2008, Rota et al. 2014a). Black-backed woodpeckers nest in burned forest as early as 2 weeks after a fire (Villard and Schieck 1997) and are common to abundant the first 2 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 may be attracted to MPB-killed forests (Rota et al. 2014a). However, black-backed woodpeckers have lower fledging rates, juvenile survival, nesting success, and population growth in forests affected by MPB infestations compared to those affected by wildfire (Rota et al. 2014a). Despite the negative population growth and lower demographic rates black-backed woodpeckers exhibit in MPB infestations, beetle-affected forests likely harbor some value to the species (Rota et al. 2014a).

Since the last population estimate of black-backed woodpeckers in 2000 on Black Hills National Forest, varying levels of disturbance have affected 50–60% of the forest through wildfire and MPB infestation (USFS 2014). The extent of change in forest structure combined with the uncertainty of the population status and trend support the need to develop 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, USA, and provide a population estimate for black-backed woodpeckers in the region.

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 (Fig. 1). The BHNF and CSP were 554,627 ha and consisted of a variety of forests with prairies adjacent to much of the property boundaries. Elevation in the Black Hills and Bear Lodge Mountains ranged from 1,065 m to 2,207 m (Froiland 1990). Climate varied with latitude and elevation, and annual precipitation ranged from 46 cm to 71 cm, with the northern Black Hills tending to receive more than the southern Black Hills (Orr 1959).

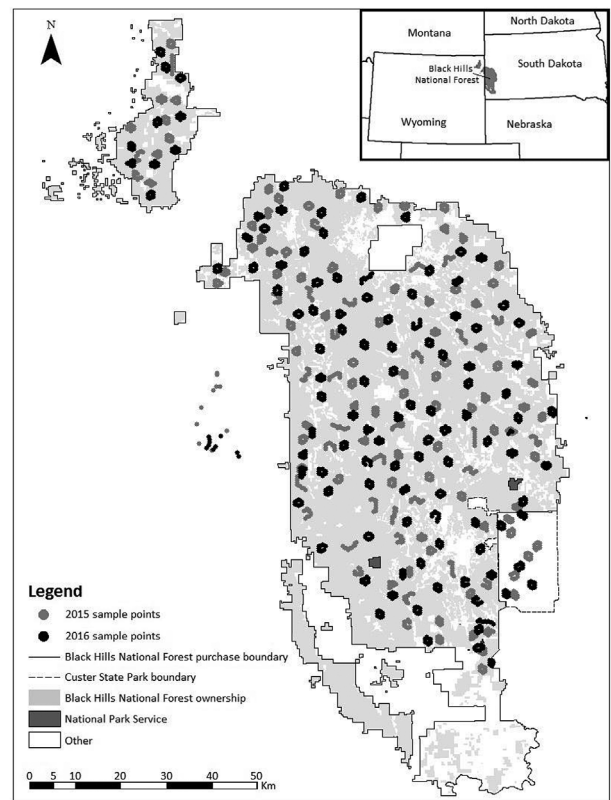


Figure 1. Study area and sample point locations ($n = 2,350$) for 2015 (light gray circles) and 2016 (dark gray circles) in the Black Hills National Forest and Custer State Park, South Dakota and Wyoming, USA.

The region was dominated by Rocky Mountain coniferous forests predominantly comprised of ponderosa pine (*Pinus ponderosa*) with quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*) 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 (*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 non-native grasses, sedges, and forbs. The Black Hills bird community was unique in that both eastern and western species are present (Dykstra et al. 1997, Mills et al. 2000). Dominant woodpecker species not included in our surveys were the hairy woodpecker (*Picoides villosus*), northern flicker (*Colaptes auratus*), and red-naped sapsucker (*Sphyrapicus nuchalis*), but the Black Hills also contained uncommon species like the downy woodpecker (*Picoides pubescens*), Lewis's woodpecker (*Melanerpes lewis*), and American three-toed woodpecker (*Picoides dorsalis*; White and Giroir 2008).

Historically natural disturbances, such as frequent fires and beetle infestations, created a unique vegetation community in the Black Hills and Bear Lodge Mountains. Wildfires burned more than 216,506 ha between 1909 and 2015 in the BHNF. Wildfires were common with several fires often occurring in the same year and ranging in size between 5 ha and 33,795 ha (USFS 2013). Mountain pine beetles were

endemic throughout the Black Hills and there have been many outbreaks during the last century (Allen and Long, 2008). The most recent, largest, and intensive MPB epidemic in the last 100 years started in 1996 and has since affected 188,583 ha or about a quarter of the Black Hills. In the past 4 years (2012–2016), 28,327 ha of the affected area was infested with MPBs; 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 (USFS 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 250 m on a side, 16.28 ha in area, and approximately 450 m from center to center. We *a priori* classified each hexagon as potentially low- or high-density habitat for black-backed woodpeckers; if a hexagon contained disturbance by MPBs or fire, we considered it to be 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), recently dead trees with red needles (beetle-killed trees), and dead trees with no needles (dead trees; Fig. 2). Dead trees could be caused by wildfires, beetles, or other mortality. We also obtained the wildfire history from the Black Hills National Forest and characterized hexagons based on the percent area in each hexagon affected by wildfire. In wildfire areas, we grouped wildfire into 4 categories: 1- to 2-, 3-, 4- to 5-, and 6- to 10-year-old wildfires to account for the declining value to black-backed woodpeckers (Rota et al. 2014b). We then intersected the hexagon grid with the raster to determine the percent of each hexagon represented by the 3 classes of trees and hexagons that burned within the last 10 years.

We randomly selected hexagons for starting points for point count transect so 20% occurred in potential low-density habitat (no disturbance by MPBs or fire) and 80% in potential high-density habitat (disturbance by MPBs or fire) for black-backed woodpeckers. Given the expected low detection rates for this species (White and Giroir 2008), this design ensured we would have an adequate number of detections to fit models that would enable us to estimate abundance based on a range of vegetation conditions in each hexagon. We also established point count transects in

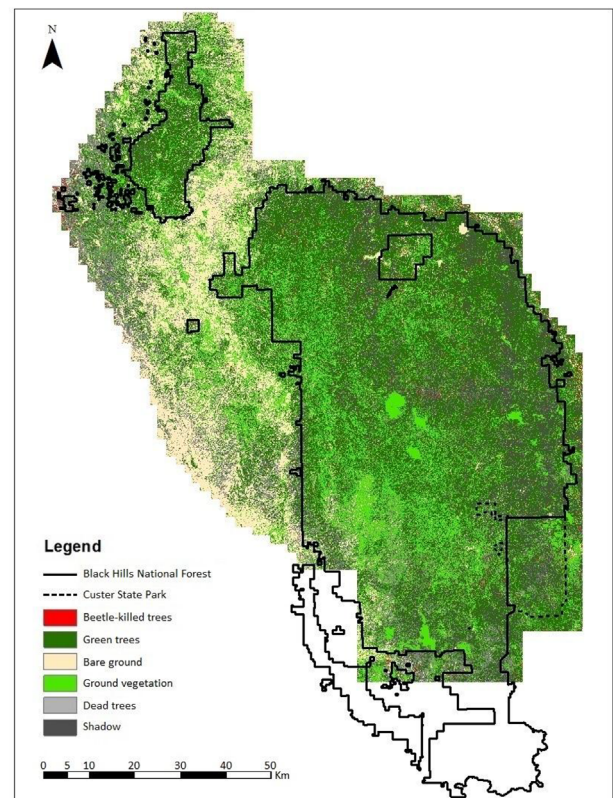


Figure 2. We classified 6 categories of forest vegetation on 1-m pixels from aerial photography so we could classify 16-ha hexagons as potentially low density (hexagons not containing disturbance by mountain pine beetles or fire) and high density (hexagons containing disturbance by mountain pine beetles or fire) 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.

low-density habitat to ensure we sampled all available habitat conditions. Each start point was ≥ 100 m from a road to avoid noise associated with roads. We laid out point transects beginning from the starting points in a geographic information system (ArcGIS; Environmental Systems Research Institute, Redlands, CA, USA) along a path that maximized sampling efficiency and remained within the strata they started in. Each transect contained up to 10 points because that was the estimated number of points a technician could complete in a morning. We located 123 and 114 transects, containing 1,222 and 1,128 sampling points, in 2015 and 2016, respectively, for a sample size of 2,350 points (Fig. 1).

Surveys and Vegetation

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 3 times each year, approximately 1 month apart, resulting in 3,666 and 3,384 point counts in 2015 and 2016, respectively. We conducted surveys on days with minimal to no precipitation and light to moderate wind speeds and started at official sunrise and terminated approximately 6 hours later. We navigated to points with the aid of a global positioning 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 5 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, Lewistown, PA, 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 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). All protocols were part of a study plan approved by the Wyoming Game and Fish Commission, South Dakota Division of Agriculture, Division of Conservation and Forestry, South Dakota Department of Game, Fish, and Parks (State Wildlife Grant T-65-R-1, Study 2476), U.S. Forest Service Rocky Mountain Research Station, and University of Missouri (Project 00046994).

We characterized vegetation variables around each sampling point and all points across the BBNF and CSP using the classification layer mentioned above (green trees, beetle-killed trees, dead trees). We measured vegetation in a 500-m-radius buffer around each point, increasing our area of measurements from the 16.28-ha hexagon to a 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. We acknowledge that the 500-m buffers overlapped for adjacent points (i.e., 1–2 of 2,350 points), but preliminary analyses indicated vegetation summarized in a 500-m radius had more support than those summarized within the hexagon boundaries. Therefore, we thought it was more important to use the most supported scale for these measures than to be concerned about this overlap.

Analytical Methods

We used 3-level hierarchical time-removal models that simultaneously estimated global abundance (λ), availability (ϕ), and detection probability (σ). This model allows for repeated visits to a single point within a season and estimates availability, the probability that an individual is within the detection radius and available for detection by providing a detectable cue, and detection, the probability an individual is present and the observer detects the cue (Chandler et al. 2011). The global abundance is the number of individuals using the point at any time during our study. 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 large home ranges because they are more mobile and likely to leave the sampling plot during surveys (Chandler et al. 2011). The availability parameter addresses the concern that an individual can be at a different location than the sampling point or at another sampling point during the survey because of its large home range. We used a model that allowed temporary emigration because black-backed woodpecker home ranges are 20–1,248 ha in the Black Hills (Rota et al. 2014b) and would likely violate an assumption of closure over the 3 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 abundance of interest was the average abundance at a point in time (e.g., during any 1 visit) and estimated as $\lambda \times \phi$ (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 evaluated 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, farther distances had a greater potential for errors in distance estimation, and it was consistent with recommendations to remove the top 5–10% of detection distances in distance sampling (Buckland et al. 2001). Therefore, we estimated abundance for a 200-m-radius plot with estimated density (birds/km²) = $(\lambda \times \phi / \pi \times 200^2) \times 1,000,000$. We included only black-backed woodpecker detections from the 5-minute passive count and assigned detections into 5 1-minute intervals. We used only 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). Our models treated the number of points surveyed (2,350) as the sample size. We acknowledge the potential for spatial correlation among counts; however, the R package `unmarked` does not allow spatial or random effects to account for these. Furthermore, we evaluated spatial autocorrelation in counts for the black-backed woodpecker by calculating Moran's I (Moran 1950) and could not reject the null hypothesis that there was 0 spatial autocorrelation ($Z = 1.81$, $P = 0.07$; Proc Variogram, SAS Institute, Cary, NC, USA); thus, our approach is reasonable.

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, minutes since sunrise, observer, visit, and year) with Poisson and negative binomial distributions, resulting in 20 models (Table 1). We selected

Table 1. Number of parameters (K), Akaike's Information Criterion (AIC), difference in AIC (Δ AIC), Akaike weight (w_i), and cumulative Akaike weight ($\sum w_i$) for models evaluating detection (σ) covariates for black-backed woodpeckers in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, USA, 2015–2016 ($n = 2,350$).

Model ^{a,b}	K	AIC	Δ AIC	w_i	$\sum w_i$
NB, $\sigma(\text{min}+\text{doy}+\text{obs}+\text{year})$	17	3,359.96	0.00	0.540	0.54
NB, $\sigma(\text{min}+\text{doy}+\text{obs})$	16	3,360.32	0.36	0.460	1.00
NB, $\sigma(\text{doy}+\text{obs})$	15	3,373.21	13.25	0.001	1.00
NB, $\sigma(\text{min}+\text{visit}+\text{obs}+\text{year})$	18	3,381.13	21.17	0.000	1.00
NB, $\sigma(\text{obs})$	14	3,421.34	61.37	0.000	1.00
NB, $\sigma(\text{doy})$	5	3,430.67	70.71	0.000	1.00
NB, $\sigma(\text{min})$	5	3,437.83	77.87	0.000	1.00
NB, $\sigma(\text{year})$	5	3,445.16	85.20	0.000	1.00
NB, $\sigma(\text{visit})$	6	3,447.42	87.45	0.000	1.00
NB, $\sigma(.)$	4	3,449.65	89.68	0.000	1.00
P, $\sigma(\text{min}+\text{doy}+\text{obs}+\text{year})$	16	3,450.17	90.21	0.000	1.00
P, $\sigma(\text{min}+\text{doy}+\text{obs})$	15	3,450.80	90.84	0.000	1.00
P, $\sigma(\text{doy}+\text{obs})$	14	3,467.77	107.80	0.000	1.00
P, $\sigma(\text{min}+\text{visit}+\text{obs}+\text{year})$	17	3,476.00	116.04	0.000	1.00
P, $\sigma(\text{obs})$	13	3,524.24	164.28	0.000	1.00
P, $\sigma(\text{doy})$	4	3,535.38	175.42	0.000	1.00
P, $\sigma(\text{min})$	4	3,543.64	183.68	0.000	1.00
P, $\sigma(\text{year})$	4	3,554.16	194.19	0.000	1.00
P, $\sigma(\text{visit})$	5	3,558.35	198.39	0.000	1.00
P, $\sigma(.)$	3	3,561.85	201.88	0.000	1.00

^a Distributions: NB = negative binomial and P = Poisson.

^b doyear = day of year, min = minutes since sunrise, obs = observer.

the top-ranked model (Δ AIC < 2) for use with abundance covariates.

We evaluated abundance covariates in 3 stages: landscape-level wildfire, landscape-level vegetation, and latitude and year. We first fit the top detection models with 3 different additive combinations of our wildfire covariates: percent cover 1- to 2-, 3-, 4- to 5-, and 6- to 10-year-old wildfires. We separately fit models with all additive combinations of the landscape-level vegetation covariates: percent cover green trees, beetle-killed trees, and dead trees, resulting in 6 models. We then created a model consisting of the top landscape-level fire and landscape-level vegetation models and considered it 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 plotted predicted black-backed woodpecker abundances and 95% confidence intervals for approximately 6 values across the ranges of supported density covariates while holding landscape-level vegetation covariates at zero and latitude at its mean.

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 3,666 point counts during 3 visits to 1,222 points and detected 300 black-backed woodpeckers in 2015 and 3,384 point counts during 3 visits to 1,128 points and detected 310 black-backed woodpeckers in 2016. We obtained 362 detections from the passive count and an additional 248 from the playback counts. We measured vegetation at 1,222 and 1,128 points in 2015 and 2016, respectively. Vegetation measurements for surveyed sampling points were comparable to vegetation characteristics across all potential sampling points in the BHNF (Table 2), ranging from open areas in 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 ($\beta = 0.249 \pm 0.402$ [SE]) than 2015. Black-backed woodpecker detections varied by observers and were negatively correlated with day of year ($\beta = -0.536 \pm 0.102$) and minute ($\beta = -0.379 \pm 0.114$). The estimate of availability was 0.0376 ± 0.011 .

The global abundance model with year, 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 0.41 to 77.59 birds/km² over a range of 0–16% cover of beetle-killed trees (Fig. 3). Black-backed woodpecker densities ranged from 0.41–19.11, 0.41–6.10, and 0.41–1.46 birds/km² across a range of 0–100% cover of 1- to 2-, 3-, and 4- to 5-year-old wildfires, respectively (Fig. 3).

Table 2. Descriptive statistics for landscape vegetation characteristics at sampling point locations ($n = 2,350$) and all points in Black Hills National Forest used to predict the population of black-backed woodpeckers across the Black Hills and Bear Lodge Mountains in South Dakota and Wyoming, USA, 2015 and 2016 with a 78.5-ha buffer.

Sample, covariate	$\bar{x}$	Min.	Max.	SD
Sample points				
Green trees (%)	38.48	0.00	88.52	14.21
Beetle-killed trees (%)	0.93	0.00	17.43	1.03
Dead trees (%)	11.94	0.00	76.62	10.71
1- to 2-year-old wildfire (%)	0.29	0.00	100.00	4.54
3-year-old wildfire (%)	2.02	0.00	100.00	13.57
4- to 5-year-old wildfire (%)	2.05	0.00	100.00	13.75
6- to 10-year-old wildfire (%)	0.34	0.00	100.00	4.20
Latitude	44.06	43.51	44.75	0.29
Black Hills National Forest				
Green trees (%)	35.59	0.00	88.52	16.23
Beetle-killed trees (%)	0.92	0.00	17.43	1.02
Dead trees (%)	11.70	0.00	76.62	10.71
1- to 2-year-old wildfire (%)	0.02	0.00	89.78	0.99
3-year-old wildfire (%)	0.45	0.00	100.00	6.12
4- to 5-year-old wildfire (%)	0.47	0.00	100.00	6.31
6- to 10-year-old wildfire (%)	0.48	0.00	100.00	6.05
Latitude	44.06	43.51	44.79	0.28

Table 3. Number of parameters (K), Akaike's Information Criterion (AIC), difference in AIC (Δ AIC), Akaike weight (w_i), and cumulative Akaike weight ($\sum w_i$) for final model combinations estimating black-backed woodpecker abundance (λ) in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, USA, 2015 and 2016 ($n = 2,350$). We did not use covariates to model availability, and detection covariates included minutes since sunrise, day of year, observer, and year in all abundance models.

Model ^a	K	AIC	Δ AIC	w_i	$\sum w_i$
$\lambda(\text{latitude} + \text{green} + \text{beetle} + \text{dead} + \text{burn12} + \text{burn3} + \text{burn45} + \text{year})$	25	3,226.10	0.00	0.98	0.98
$\lambda(\text{green} + \text{beetle} + \text{dead} + \text{burn12} + \text{burn3} + \text{burn45})$	23	3,233.86	7.76	0.02	1.00
$\lambda(\text{burn12} + \text{burn3} + \text{burn45})$	20	3,258.92	32.82	0.00	1.00
$\lambda(\text{burn12} + \text{burn3} + \text{burn45} + \text{burn610})$	21	3,259.58	33.48	0.00	1.00
$\lambda(\text{burn12} + \text{burn3})$	19	3,266.65	40.56	0.00	1.00
$\lambda(\text{latitude} + \text{green} + \text{beetle} + \text{dead})$	21	3,278.22	52.12	0.00	1.00
$\lambda(\text{green} + \text{beetle} + \text{dead})$	20	3,279.10	53.00	0.00	1.00
$\lambda(\text{beetle} + \text{dead})$	19	3,281.40	55.30	0.00	1.00
$\lambda(\text{dead})$	18	3,296.47	70.37	0.00	1.00
$\lambda(\text{green} + \text{beetle})$	19	3,312.13	86.04	0.00	1.00
$\lambda(\text{latitude})$	18	3,316.12	90.03	0.00	1.00
$\lambda(\text{green})$	18	3,322.47	96.37	0.00	1.00
$\lambda(\text{beetle})$	18	3,349.68	123.59	0.00	1.00

^a green = green trees, beetle = beetle-killed trees, dead = dead trees, burn12 = 1- to 2-year-old wildfire, burn3 = 3-year-old wildfire, burn45 = 4- to 5-year-old wildfire, burn 610 = 6- to 10-year-old wildfire.

Woodpecker density was negatively related to latitude and percent cover of green trees and dead trees (Table 4). Black-backed woodpecker density decreased from 0.63–0.20 birds/km² and 0.63–0.30 birds/km² over a range of 0–100% cover of green trees and dead trees, respectively (Fig. 4), but their confidence intervals overlapped zero (Table 4). Black-backed woodpecker density decreased from 1.06 to 0.21 birds/km² as latitude increased from 43.51 to 44.78 (Fig. 4). Black-backed woodpeckers had higher densities in 2016 than 2015, but the confidence interval for the year effect overlapped zero (Table 4).

After accounting for detection probability and availability, we estimated there were 98.4 and 104.7 black-backed woodpeckers across all survey points in 2015 and 2016, respectively. Mean density across all survey points and both years was 0.69 birds/km² (range = 0.15–32.16). We predicted abundance across all hexagons in the BHNF and CSP ranged from 0.027 to 1.820 birds/hexagon in 2015 and from 0.031 to 5.371 birds/hexagon in 2016 (Fig. 5). We estimated there were 2,920 (95% lower CL [LCL] = 1,449; 95% upper CL [UCL] = 5,917) and 3,439 (LCL = 1,739; UCL = 6,908) black-backed woodpeckers in the Black Hills and Bear Lodge Mountains in 2015 and 2016, respectively. The

estimated mean density for black-backed woodpeckers in the study area was 0.528 birds/km² (LCL = 0.262; UCL = 1.069) in 2015 and 0.626 birds/km² (LCL = 0.315; UCL = 1.285) in 2016.

DISCUSSION

Given status and conservation concerns for black-backed woodpeckers, our primary objective was to estimate and map abundance of black-backed woodpeckers in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming. Our population estimate was more than triple the abundance estimate in the petition to list black-backed woodpeckers; however, their estimate was not based on a large-scale survey effort like our study. Our abundance estimate was more than double the most recent survey-based estimate by Mohren et al. (2014) but needs to be placed within the broader context of habitat disturbance that existed on the landscape. Average density across both years of our study for all points in the BHNF and CSP was 0.577 birds/km². Mohren et al. (2014) reported an average 0.06 birds/km² (0.12 pairs/km²) in the Black Hills; however, their estimate was likely conservative because they eliminated individuals from their estimate that were <1,500 m apart, which was related to their sampling and design. Their surveys also occurred before the current beetle epidemic and only 2,307 ha of the forest had been subjected to wildfire in the previous 4 years (Mohren et al. 2016). Abundance during our study was likely a result of the high levels of disturbance just prior to our study. More than 8,813 ha of the BHNF and CSP burned in the 4 years before our study and the peak of the most recent MPB infestation was reached around 2012 (Graham et al. 2016). This variation in density demonstrates that black-backed woodpecker population size can fluctuate coinciding with different amounts of disturbance on the landscape. The inherent value of these disturbances for black-backed woodpeckers indicates that they will be important for conservation of this species in the Black Hills.

Black-backed woodpecker densities at points infested by MPBs in our study were higher than all other vegetation

Table 4. Coefficients (Coeff), standard errors (SE), and 95% lower and upper 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, USA, 2015–2016 ($n = 2,350$).

Covariate	Coeff	SE	LCL	UCL
Intercept	0.331	0.324	−0.304	0.967
Latitude	−0.262	0.099	−0.456	0.068
Green trees	−0.100	0.095	−0.285	0.086
Beetle-killed trees	0.286	0.056	0.177	0.396
Dead trees	−0.032	0.094	−0.215	0.151
1- to 2-year-old wildfire	0.155	0.031	0.094	0.216
3-year-old wildfire	0.307	0.047	0.215	0.400
4- to 5-year-old wildfire	0.115	0.050	0.017	0.213
2016	0.443	0.230	−0.009	0.894

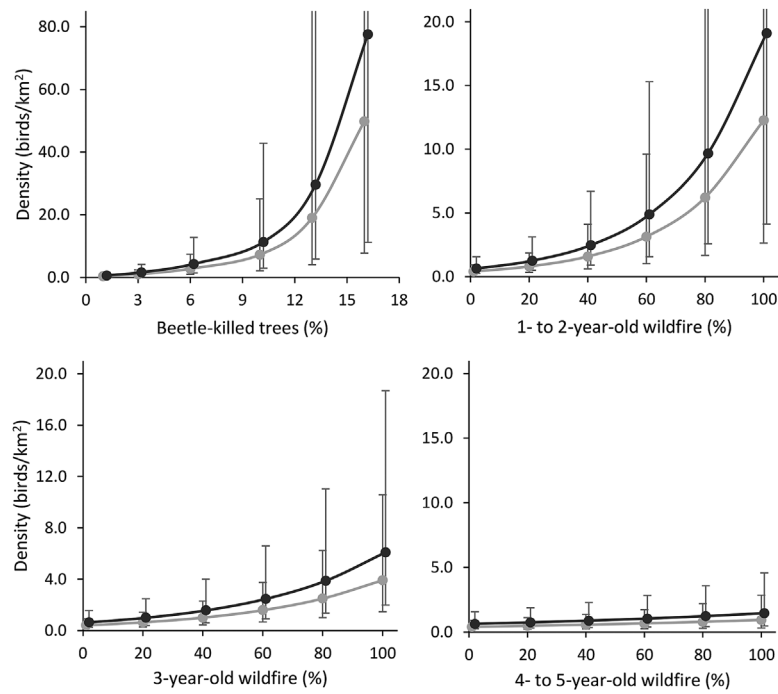


Figure 3. Predicted density and standard errors of black-backed woodpeckers across percentages of beetle-killed trees, 1- to 2-year-old wildfires, 3-year-old wildfires, and 4- to 5-year-old wildfires in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, USA, March–June 2015 (light gray) and 2016 (dark gray). Error bars not capped with a horizontal line extended beyond the range of the y-axis.

types surveyed. Black-backed woodpeckers respond to outbreaks of bark beetles and have shown increased densities in infested stands (Drever and Martin 2007, Bonnot et al. 2009, Rota et al. 2014a). However, beetle infested areas may

be sink habitats because woodpeckers experienced lower nesting success, juvenile and adult survival, and negative population growth in areas affected by MPBs compared to wildfire areas, which may be source habitats (Rota et al.

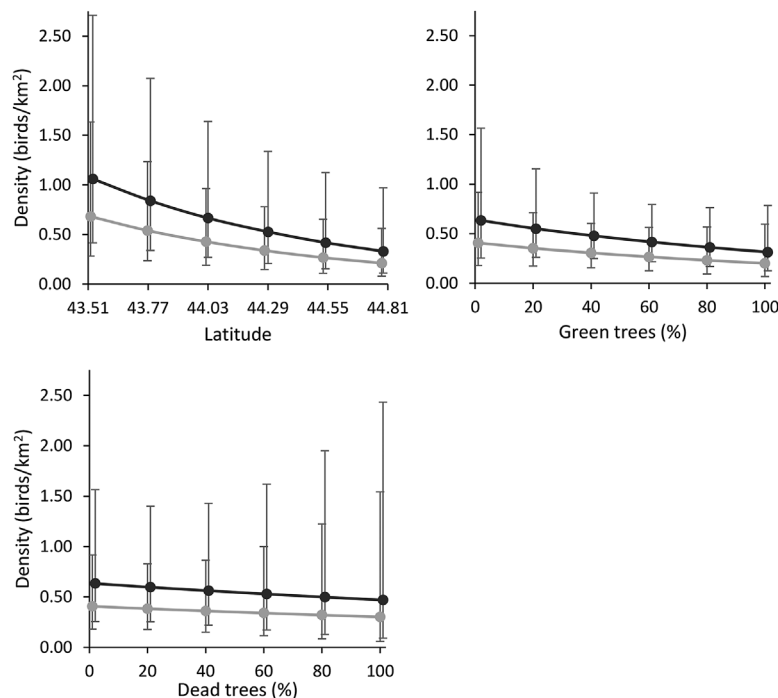


Figure 4. Predicted density and standard errors of black-backed woodpeckers across a gradient of latitude and percentages of green trees and dead trees in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, USA, March–June 2015 (light gray) and 2016 (dark gray).

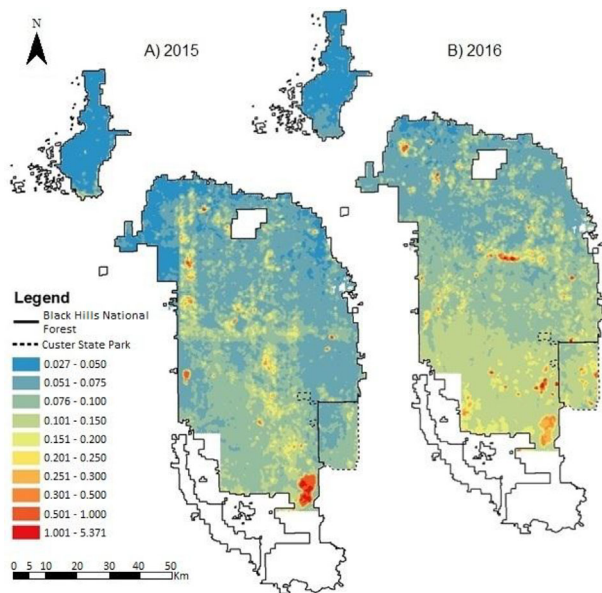


Figure 5. Abundance of black-backed woodpeckers (birds/hexagon) across all hexagons (16.28 ha) in the Black Hills National Forest and Custer State Park in South Dakota and Wyoming, USA, 2015 (A) and 2016 (B).

2014a). Densities were highest in 1- to 2-year-old wildfires compared to 3- to 5-year-old wildfires, which is consistent with previous black-backed woodpecker research (Murphy and Lehnhausen 1998, 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. 2002), making them more accessible and possibly a more profitable food resource to woodpeckers when they are experiencing increased population sizes during beetle epidemics. Although habitat created by beetle infestations may not be equal to burned forests in terms of population growth, beetle outbreaks are likely an attractive food source and provide habitat when recently burned areas are unavailable.

We suspect the high density of black-backed woodpeckers associated with MPB infestation was partly due to the recent disturbance history in the region. The majority of our sampling points in burned areas were in 3- to 4-year-old wildfires, which means there was an abundance of 1- to 2-year-old wildfires prior to our surveys. The increased availability of recently burned areas likely provided habitat that 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-killed forest, which could be why there were higher black-backed woodpecker densities in beetle outbreaks than in older burned forests. Areas affected by MPBs are also likely important to population persistence

because large numbers of birds can reside there and they may prevent the population from catastrophic declines when suitable burned habitat is unavailable (Rota et al. 2014a). Overall, black-backed woodpeckers preferred these disturbed areas; average densities were 13–45 times greater in 1- to 2-year-old wildfires and MPB outbreaks compared to undisturbed forests.

Our density estimates for black-backed woodpeckers in the Black Hills are comparable to density estimates for black-backed woodpeckers in other parts of their range. Our mean density was slightly greater than density estimates for black-backed woodpeckers in Oregon. Bate (1995) observed 0.16 birds/40 ha or 0.4 birds/km² in a moderately harvested ponderosa pine stand and Dixon (1995) reported 0.15 birds/40 ha or 0.375 birds/km² in old-growth ponderosa pine (Tremblay et al. 2016). These forests had isolated outbreaks of MPBs and only 1 small wildfire available, whereas the Black Hills was going through a MPB epidemic. Arnett et al. (1997a,b) observed densities in lodgepole pine (*Pinus contorta*) stands killed by MPBs of 1.99–5.3 birds/40 ha or 4.97–13.25 birds/km², whereas our mean densities were slightly greater at points affected by MPBs (17.13 birds/km²). We estimated densities of 0.82 and 5.21 birds/km² at points with 100% coverage of 4- to 5- and 1- to 2-year-old wildfires. Model densities for black-backed woodpeckers ranged from 0.0068 to 0.0013 pairs/ha or 0.34–0.065 birds/km² 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 this could be why our density estimates are higher. Densities in Quebec, Canada were greater and were 12 pairs/100 ha (24 birds/km²) 1 year post-wildfire and 1 pair/100 ha (2 birds/km²) 3 years 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. 2004), 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 (Settingington et al. 2000, Huot and Ibarzabal 2006, Tremblay et al. 2009, Fogg et al. 2014, Mohren et al. 2014). We observed black-backed woodpeckers in undisturbed forest throughout the Black Hills and Mohren et al. (2016) reported black-backed woodpeckers occurred in association with small patches of MPB-killed trees within the forest. 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 and perhaps elevation and precipitation in the Black Hills. The majority of burned forest existed in the southern Black 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 are isolated from the main body of the BHNF and had low levels of disturbance.

Our survey design was a compromise between maximizing the number of points that could be sampled in a morning (and therefore minimizing distance between points) and maintaining independence among points. This tradeoff occurs in most point-count surveys, but it is particularly challenging for birds with large home ranges, such as black-backed woodpeckers. We used a detection radius that did not overlap on adjacent points, a model that allowed for temporary emigration from a point, and did not detect significant spatial autocorrelation in counts. Nevertheless, we acknowledge the potential for an individual black-backed woodpecker to be detected at different times at more than one point, and that multiple points occurred in the same disturbance patches, which creates the potential for lack of independence among points. This could result in a negative bias for standard errors of our abundance estimates but not of the estimate itself. We do not believe this was a major issue given the observed lack of significant spatial autocorrelation in counts.

MANAGEMENT IMPLICATIONS

Areas with high percent cover of beetle-killed trees may support high densities of black-backed woodpeckers and may be important to sustaining populations when the area affected by recent wildfire (<4 years) is declining or scarce. Retention of beetle-killed trees could benefit black-backed woodpeckers; however, retaining beetle-killed trees may increase the spread of MPB infestations. Thus, managers can assess these relative trade-offs in light of management goals. A better understanding of habitat requirements of black-backed woodpeckers in undisturbed forests in the Black Hills, and how populations fluctuate with changing levels of disturbance, may be important for conserving this species because of the unpredictable nature of disturbance in forests. Future viability analyses would be particularly informative for management if they considered multiple disturbance scenarios.

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