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Snag density and use by cavity-nesting birds in managed stands of the Black Hills National Forest

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Abstract

We examined whether *cavity-nesting bird abundance was related to the density of snags in managed ponderosa pine stands* (*Pinus ponderosa* Laws.) on the Black Hills National Forest. We also examined whether *snag variables were related to bird use of snags as nest sites and for foraging*. Study plots ($n = 144$ plots) were established throughout the forest in managed ponderosa pine stands and data on the density, size, and condition of 2886 snags were collected. We searched snags for cavities and signs of foraging, and surveyed plots for cavity-nesting birds ($n = 272$ counts). Nine species of cavity-nesting birds were detected, with red-breasted nuthatch (*Sitta canadensis*), black-capped chickadee (*Poecile atricapillus*), and hairy woodpecker (*Picoides villosus*) occurring most frequently. The mean number of cavity-nesting birds at a plot was independent of snag density or other plot variables. Larger DBH and greater snag height were positively associated with the presence of a cavity, and advanced stages of decay and the presence of a broken top were negatively associated with the presence of a cavity. Snags in larger DBH size classes had more evidence of foraging than expected based on abundance. Combining the data on the presence of a cavity and evidence of foraging, snags with large DBH were used most by cavity-nesting birds. Our study found no relationship between the number of cavity-nesting birds and snag density across the range of snag densities, snag sizes, and snag conditions measured. However, the densities of large snags may have been too low to influence the abundance of cavity-nesting birds, limiting our ability to detect such an effect.

Keywords: Snags; Cavity-nesting birds; Managed forests; Ponderosa pine; *Pinus ponderosa*; Black Hills

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1. Introduction

Snags provide sites for feeding, nesting, roosting, perching, and singing for birds (Davis, 1983). Many species of birds are dependent on snags for nest sites, including 85 species of cavity-nesting birds in North America (Scott et al., 1977), and 31 cavity-nesting birds with ranges that include the Black Hills of South Dakota and Wyoming (South Dakota Ornithologists' Union, 1991). The presence and abundance of cavity-nesting birds in managed ponderosa pine (*Pinus ponderosa* Laws.) stands on the Black Hills National

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Forest (BHNF) is dependent on retention of suitable snags for these species. Therefore, information of how many and what types of snags are required by cavity-nesting bird species is critical for wildlife biologists, silviculturists, and forest managers.

Forest management practices and snag removal affect populations of cavity-nesting birds occurring in managed forests. Cavity-nesting birds declined by 52% when ponderosa pine snags were removed during a timber harvest in Arizona (Scott, 1979). On a large forest clear-cut in Texas, avian species richness, diversity and bird abundance were all significantly higher on plots where hardwood snags were retained, whereas cavity-nesting birds were virtually absent from snagless plots (Dickson et al., 1983). In the BHNF where shelterwood logging occurred, some species of cavity-nesting birds where less abundant in treated areas, whereas others species were more abundant, but none showed significant differences in abundance (Anderson and Crompton, 2002).

In addition to total snag density, characteristics of individual snags are important to cavity-nesting birds for selecting nest trees and foraging sites. Researchers across many forest types have found that cavity-nesting birds utilize snags with large DBH and tall height for nest trees (Scott, 1978; Cunningham et al., 1980; Mannan et al., 1980; Raphael and White, 1984; Reynolds et al., 1985; Zarnowitz and Manuwal, 1985; Schreiber and deCalesta, 1992). Characteristics such as tree species, the state of decay, percent bark cover, and presence of a broken top are also important, but selection for specific characteristics can vary by bird species (McClelland and Frissell, 1975; McClelland et al., 1979; Cunningham et al., 1980; Mannan et al., 1980; Raphael and White, 1984; Zarnowitz and Manuwal, 1985; Schreiber and deCalesta, 1992). Dead trees are selected over live trees as foraging sites by cavity-nesting birds (Raphael and White, 1984; Imbeau and Desrochers, 2000). Snags are colonized by bark beetles and wood boring beetles which provide a critical food resource for some bird species, especially the *Picoides* woodpeckers (Anderson, 2003).

Our study was designed to examine the relationship between cavity-nesting birds and snag density in managed ponderosa pine stands on the BHNF. We hypothesized the abundance of cavity-nesting birds will increase with increased snag density. We also examined if cavity-nesting bird use of snags as nest sites was related to the following snag characteristics: DBH (diameter at breast height), snag height, state of decay, percent bark cover, and the presence of a broken top, and if evidence of foraging on snags was related to the following snag characteristics: tree species, DBH, and state of decay. We hypothesized that the presence of a cavity and evidence of foraging would be more likely in larger snags.

2. Methods

2.1. Study area

The BHNF is located in southwestern South Dakota and northeastern Wyoming (43°16′13″–44°47′49″N, 103°19′15″–104°43′3″W) and encompasses 504,072 h (Fig. 1). The Black Hills rise out of grasslands, and topography varies from rolling forested hills to steep and rugged rock outcroppings. Major tree species in the BHNF include ponderosa pine, white spruce (*Picea glauca* (Moench) Voss), aspen (*Populus tremuloides* Michx.), and bur oak (*Quercus macrocarpa* Michx.), with lodgepole pine (*Pinus contorta* Dougl.), paper birch (*Betula papyrifera* Marsh.), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), and limber pine (*Pinus flexilis* James) also occurring (Hoffman and Alexander, 1987). Ponderosa pine is the dominant tree species covering nearly 95% of forested area and occurs at all elevations and on all soil types (Shepperd and Battaglia, 2002).

The forests of the Black Hills were heavily cut and intensively managed since early settlement in late 1800s (Ball and Schaefer, 2000) and have undergone considerable change (Parrish et al., 1996). Currently, most ponderosa pine stands are managed under a shelterwood silvicultural system (USDA Forest Service, 1997). Forest Service standards in the BHNF propose retaining four snags on north and east slopes and two snags on south and west slopes of at least 25.4 cm (10 in.) DBH with 25% being greater than 50.8 cm (20 inches) DBH (USDA Forest Service, 2001).

The sampling frame for our study was managed ponderosa pine stands. We restricted our sampling to the habitat structural stages of sapling-pole stands (stage 3) and mature forest stands (stage 4) for USDA Forest Service Region 2. Habitat structural stages

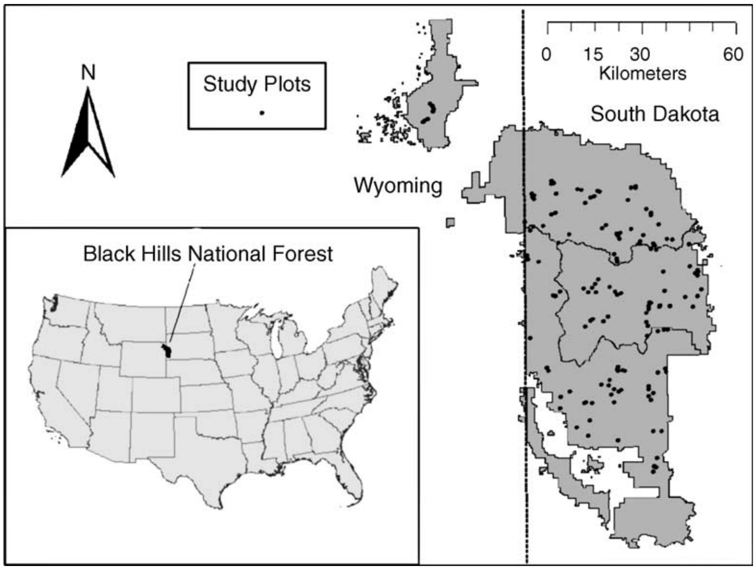

Fig. 1. Black Hills National Forest showing locations of 144 study plots and four ranger districts (RD).

represent a five stage sequence of forest succession (grass-forb (stage 1), shrub-seedling (stage 2), sapling-pole (stage 3), mature (stage 4), old-growth forest (stage 5)), and stages 3 and 4 are further divided into 3a/4a, 3b/4b, and 3c/4c for 11–40%, 41–70%, and 71–100% crown cover, respectively (Buttery and Gillam, 1987). Stands with recorded fires (1939–2001) and active timber sales were not included.

2.2. Data collection

Study plots were 0.4 ha circular plots and were selected from a pool of 500 randomly placed points within the sampling frame. Plots were established after a visual estimate of snag density in the field at the random points to ensure a balanced distribution across a wide range of snag densities. Habitat structural stage was verified and recorded and the presence of ponderosa pine forest cover was confirmed in the field. Live tree basal area was measured by a variable point sample using a 10 BAF (English) prism, and the location of plot center was taken with a GPS unit.

We defined a snag as a dead standing tree, with no green needles or leaves, $\geq$8.0 cm DBH and $\geq$2.0 m in height. Tree species, DBH to the nearest mm, snag height to the nearest 0.1 m (using a clinometer), and decay class were measured for each snag. Decay class was based on snag condition and ranged from 1, a recently dead tree, to 5, a rotting stump, following Thomas et al. (1979) with modifications by Lentile et al. (2000). We estimated the amount of bark remaining on each snag to the nearest 10%, and recorded the presence or absence of a broken top. We noted the presence of cavities in snags, and defined cavities as excavations created by a bird for the purpose of nesting. Evidence of bird foraging including chipped bark, drill holes, and foraging excavations and was also recorded.

All species of cavity-nesting birds seen or heard were recorded during point counts conducted at the center of plots from 20 May to 1 July 2003, which was during the breeding season for these birds in the BHNF. Point counts followed the variable circular-plot method (Reynolds et al., 1980), with adjustments for distance sampling analysis (Buckland et al., 2001). Surveys began at sunrise and ended no more than 4 h later (Mills et al., 2000b), and were not conducted if weather conditions could affect bird activity or detectability. Counts were 5 min in length and began 1 min after reaching plot center. Plots were either visited once or twice during the sampling period.

2.3. Statistical analysis

Program DISTANCE (Version 4.1 Release 2; Thomas et al., 2003) was used to analyze the point count data and calculate density estimates for the cavity-nesting bird species detected. Distance sampling (Buckland et al., 2001) provides an estimate of bird density while avoiding the assumption of constant probability of detection despite differences in observers' ability, environmental and vegetation differences at the time and location of surveys, and differing physical and behavioral attributes of bird species (Rosenstock et al., 2002). We modeled the probability of detection as a function of radial distance from plot center using models suggested by Buckland et al. (2001) for each bird species separately. Akaike's information criteria (AIC) was used to select the best model. We examined χ^2 goodness-of-fit values to assure models adequately fit the data ($P > 0.05$).

Regression analysis with generalized linear models (McCullagh and Nelder, 1989) was used to examine the relationship between the mean number of cavity-nesting birds recorded at a plot and plot variables including: snag density, density of snags $\geq$25.4 cm DBH, live tree basal area, habitat structural stage, and latitude of plot center. Due to few plots in habitat structural stage 3c, stages 3b and 3c were combined for analysis. Latitude was included as a parameter to account for a north/south moisture gradient that occurs in the Black Hills. Simple and multiple regression models with the plot variables in all possible combinations, including a fully parameterized global model, were examined. Diagnostic plots and residual values were examined to assure assumptions of normality and homogeneity of variance were met and to check the data for outliers.

An information-theoretic approach was used to analyze the relationship between the presence of a cavity in a snag and characteristics of that snag and to select the "best" model to describe the data and rank the remaining models (Burnham and Anderson, 2002). Snag characteristics included DBH, snag height, decay class (classes 1 and 2 were combined as early stages of decay and classes 3–5 were grouped as advanced stages of decay), percent bark cover, and the presence of a broken top. An a priori candidate set of logistic regression models was developed, based on published literature and existing knowledge of cavity-nesting bird ecology, to evaluate the probability of the presence of a cavity in a snag. Characteristics such as DBH, tree height and the process of decay differ between tree species; therefore, tree species were analyzed separately using the same candidate set of logistic regression models. These sets of models included a fully parameterized global model, and the Hosmer–Lemeshow goodness-of-fit test (Hosmer and Lemeshow, 2000) was used to determine whether the global models adequately fit the data ($P > 0.05$). The overdispersion parameter ($\hat{c}$) was calculated for the global models to assess whether a correction for overdispersed data was necessary. These models were ranked using Akaike's information criteria with an adjustment for small sample size ($\mathrm{AIC_c}$) and $\Delta\mathrm{AIC_c}$ values and model weights (w_i) were calculated. To evaluate model parameters individually, sets of models containing all possible combinations of parameters were analyzed and model averaged parameter estimates along with confidence intervals and parameter weights were calculated for all parameters. Burnham and Anderson (2002) provide a thorough review of the application of AIC with relevant references. We used PROC LOGISTIC to compute Hosmer and Lemeshow goodness-of-fit tests, overdispersion parameters, and log likelihood values (SAS version 8.2; SAS, 2001).

The presence of chipped bark, drill holes, or foraging excavations were combined to classify snags as either utilized by foraging birds or not utilized. Evidence of foraging on snags was analyzed using Pearson's χ^2 goodness-of-fit tests to examine if evidence of foraging differed by DBH size class (8.0–23.0, 23.1–38.0, 38.1–48.0, >48.0 cm), decay class (classes 1–5, each class analyzed separately), or tree species (Zar, 1999). The proportion of snags with evidence of foraging in each DBH size class, decay class, or tree species was compared to the proportion of all snags in the same DBH size class, decay class, or tree species. We compared P-values to 0.05 alpha value and used SAS version 8.2 (SAS, 2001) for analysis.

3. Results

3.1. Snag population

Data on 2886 snags from 144 plots were collected. The median snag density was 32 snags/ha and snag

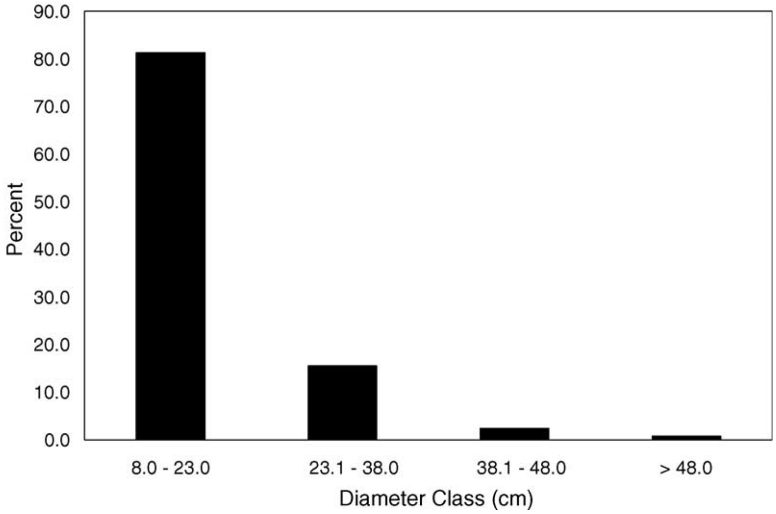

Fig. 2. Percent of 2886 snags by diameter class in managed stands of ponderosa pine across the Black Hills National Forest (8.0–23.0 cm = 2346 snags, 23.1–38.0 cm = 448 snags, 38.1–48.0 cm = 70 snags, >48.0 = 22 snags). Snags in the smallest diameter class dominated the sampled snag population, and large diameter snags are rare.

densities ranged from 0 to 304 snags/ha. Snags were identified from the following four tree species: aspen, paper birch, ponderosa pine, and white spruce. Ponderosa pine was the most abundant species, with 2546 snags (88.2%), followed by aspen with 235 snags (8.1%), paper birch with 54 snags (1.9%), white spruce with 37 snags (1.3%), and 14 snags were classified as unknown.

The DBH of snags ranged from 8.0 to 63.0 cm, with small diameter snags greatly outnumbering larger diameter snags (Fig. 2). The smallest diameter class, 8.0–23.0 cm, made up 81.3% of the snags, while there were only 22 snags >48.0 cm diameter, comprising 0.8% of the sampled snag population. Heights of snags sampled ranged from 2.0 to 27.8 m with a mean height of 5.8 m (S.D. = 3.6). Snags in the early stages of decay dominated the sampled population, with 82.3% of snags in either decay class 1 or 2. This lack of decay is also evident by the high mean bark cover of 85.2% (S.D. = 30.8). There were 75.2% of the snags with broken tops.

3.2. Cavity-nesting birds

Nine species of cavity-nesting birds were recorded during 272 point counts (Table 1). Red-breasted nuthatch, black-capped chickadee, and hairy woodpecker were the most common species detected and had sufficient sample sizes to estimate densities.

We detected little relationship between the mean number of cavity-nesting birds and plot variables. The mean number of cavity-nesting birds detected at a plot was independent of snag density ($R^2 = 0.0029$, $P > 0.05$). The fully parameterized global model, including snag density, density of snags $\geq$25.4 cm DBH, live tree basal area, habitat structural stage, and latitude of plot center, was significant ($P = 0.0132$), but had little explanatory power ($R^2 = 0.1203$). Examination of the residuals and diagnostic plots did not reveal violations of normality or homogeneity of variance assumptions and no outliers were found.

3.3. Snags with cavities

A total of 153 snags contained one or more cavities. Of these snags with cavities, 133 were ponderosa pine, 17 were aspen, 2 were paper birch and 1 was a white spruce. Ponderosa pine and aspen snags were analyzed separately whereas the other two species were not analyzed due to small sample sizes.

The Hosmer and Lemshow goodness-of-fit test for the fully parameterized global model predicting the probability of the presence of a cavity in a ponderosa pine snag indicated the model adequately fit the data

Table 1
Cavity-nesting bird species detected during 272 counts in 2003 on 144 plots in managed ponderosa pine stands on the Black Hills National Forest

Species	*N*	Density (birds/ha)	CV (%)	No. of plots
Hairy woodpecker (*Picoides villosus*)	50	0.08	19.3	38
Black-backed Woodpecker (*Picoides arcticus*)	1			1
Northern flicker (*Colaptes auratus*)	17			14
Red-naped sapsucker (*Sphyrapicus nuchalis*)	20			17
Black-capped chickadee (*Poecile atricapillus*)	66	0.11	15.8	51
White-breasted nuthatch (*Sitta carolinensis*)	10			9
Red-breasted nuthatch (*Sitta canadensis*)	81	0.09	12.4	62
Brown creeper (*Certhia americana*)	2			2
House wren (*Troglodytes aedon*)	1			1
Total detections	248			

N is the number of detections per species; density and the coefficient of variation (CV) were calculated using program DISTANCE (Thomas et al., 2003) by truncating detections at 99 m and modeled with the Hazard-rate key function. Species without density estimates did not have an adequate number of detections to estimate density. The no. of plots is the total number of plots where each species was detected.

($\chi^2 = 6.23$, d.f. = 8, $P = 0.622$) and a correction for overdispersed data was not necessary since the overdispersion parameter was close to one. The candidate set of a priori logistic regression models were ranked using AIC$_c$ (Table 2). The top two models are the only models supported by the data ($\Delta_i < 2$ and larger w_i values; Burnham and Anderson, 2002) and differ only by the inclusion of the percent bark cover in the second model. The parameters were evaluated individually (Table 3) and DBH, presence of a broken top, height, and decay class all had high parameter weights indicating their importance. Since the percent bark cover had a much lower weight, the first model in Table 2 was supported as the single ‘‘best’’ model. DBH and height had positive parameter estimates and confidence intervals that did not include zero (Table 3) indicating larger DBH and greater height were positively associated with the probability of a cavity in a ponderosa pine snag. Decay class and the presence of a broken top had negative parameter estimates and confidence intervals that did not include zero (Table 3). Therefore, advanced stages of decay (decay classes 3–5) and a broken top were negatively associated with the probability of a cavity in a ponderosa pine snag. Percent bark cover had a positive parameter estimate, but the confidence interval included zero (Table 3) so the direction of an effect is ambiguous.

Table 2
Model selection results for predicting the probability of the presence of a cavity in a ponderosa pine snag

Model	K	log(L)	AIC$_c$	Δ_i	w_i
DBH, ht, decay, bktop	5	−414.06	838.15	0.00	0.707
DBH, ht, decay, bark%, bktop	6	−413.94	839.91	1.76	0.293
DBH, ht, decay	4	−432.07	872.15	34.00	2.92E−08
DBH, decay	3	−433.81	873.63	35.48	1.40E−08
DBH	2	−437.95	879.89	41.74	6.09E−10
DBH, ht	3	−437.75	881.51	43.36	2.72E−10
decay	2	−485.97	975.94	137.79	8.48E−31

The top two models are the only models supported by the data. $N = 2546$ snags, DBH is the snag diameter at breast height, ht is the snag height, decay is either early stages (decay classes 1 and 2) or advanced stages (decay classes 3–5), bktop is the presence of a broken top, bark% is the percent bark cover, K is the number of parameters in the model including an intercept, log(L) is the log likelihood value for each model, AIC$_c$ is the Akaike's information criteria with an adjustment for small sample size, Δ_i is the difference between the AIC$_c$ value for each model and the model with the lowest AIC$_c$, w_i is the weight of evidence for each model.

The Hosmer and Lemshow goodness-of-fit test for the fully parameterized global model predicting the probability of the presence of a cavity in an aspen snag indicated the model adequately fit the data ($\chi^2 = 4.46$, d.f. = 8, $P = 0.813$) and a correction for overdispersed data was not necessary since the overdispersion parameter was close to one. The candidate set of a priori logistic regression models were ranked using AIC$_c$ (Table 4). The top four models are equally competitive models ($\Delta_i < 2$ and similar w_i values; Burnham and Anderson, 2002). DBH and decay class had high parameter weights and are the only parameters whose confidence intervals do not include zero (Table 5). This adds support to the first model containing only these two parameters in Table 4. The

Table 3
Ponderosa pine snag parameter weights, estimates, standard errors, and confidence intervals

Parameter	Parameter weight	Parameter estimate	Standard error	95% lower CI	95% upper CI
DBH (+)	1	7.278	0.089	7.096	7.461
bktop (−)	1	−2.571	0.004	−2.579	−2.563
ht (+)	0.999	16.906	0.126	16.648	17.164
decay (−)	0.987	−0.961	0.063	−1.090	−0.833
bark%	0.302	0.053	0.095	−0.141	0.248

The parameters DBH, bktop, ht, and decay are important in determining the presence of a cavity in a ponderosa pine snag with the direction of the effect indicated in parenthesis; $N = 2546$ snags, DBH is the snag diameter at breast height, ht is the snag height, decay is either early stages (decay classes 1 and 2) or advanced stages (decay classes 3–5), bktop is the presence of a broken top, bark% is the percent bark cover (+/−) after the parameter name indicates the confidence interval did not include zero and the direction of the parameter effect on the probability of the presence of a cavity.

Table 4
Model selection results for predicting the probability of the presence of a cavity in an aspen snag

Model	K	$\log(L)$	$\mathrm{AIC_c}$	Δ_i	w_i
DBH, decay	3	−46.15	98.3	0.00	0.342
DBH, ht, decay, bktop	5	−44.24	98.51	0.21	0.309
DBH, ht, decay	4	−45.75	99.51	1.21	0.187
DBH, ht, decay, bark%, bktop	6	−43.91	99.86	1.56	0.157
DBH, ht	3	−50.89	107.78	9.48	0.003
DBH	2	−53.66	111.33	13.03	5.08E−04
decay	2	−55.87	115.74	17.44	5.59E−05

The top four models are equally competitive models supported by the data; $N = 235$ snags, DBH is the snag diameter at breast height, ht is the snag height, decay is either early stages (decay classes 1 and 2) or advanced stages (decay classes 3–5), bktop is the presence of a broken top, bark% is the percent bark cover, K is the number of parameters in the model including an intercept, $\log(L)$ is the log likelihood value for each model, $\mathrm{AIC_c}$ is Akaike's information criteria with an adjustment for small sample size, Δ_i is the difference between the $\mathrm{AIC_c}$ value for each model and the model with the lowest $\mathrm{AIC_c}$, w_i is the weight of evidence for each model.

positive parameter estimate for DBH indicates that larger DBH is positively associated with the probability of a cavity in an aspen snag, and the negative parameter estimate for decay class indicates that advanced stages of decay (decay classes 3–5) are negatively associated with the probability of a cavity in an aspen snag.

3.4. *Snags with foraging evidence*

There were 1589 snags (55.1% of 2886 snags) that had evidence of foraging. Of these snags there were 1476 ponderosa pine, 73 aspen, 24 paper birch, 15 white spruce, and 1 unknown species. The goodness-of-fit of test was significant ($\chi^2 = 28.36$, d.f. = 1, $P < 0.001$), indicating that ponderosa pine snags were foraged on more than expected and aspen snags less than expected. Due to the small numbers of most species, only ponderosa pine and aspen snags were compared in this analysis.

All tree species were pooled to analyze the variables of DBH and decay class. The DBH size classes used for analysis are the same as Fig. 2. There

Table 5
Aspen snag parameter weights, estimates, standard errors, and confidence intervals

Parameter	Parameter weight	Parameter estimate	Standard error	95% lower CI	95% upper CI
DBH (+)	0.998	26.803	1.373	23.999	29.607
decay (−)	0.965	−1.936	0.207	−2.358	−1.514
bktop	0.653	−0.884	0.613	−2.135	0.367
ht	0.347	1.414	4.317	−7.402	10.229
bark%	0.340	−0.295	0.390	−1.091	0.501

The parameters DBH and decay are important in determining the presence of a cavity in an aspen snag with the direction of the effect indicated in parenthesis. $N = 235$ snags, DBH is the snag diameter at breast height, ht is the snag height, decay is either early stages (decay classes 1 and 2) or advanced stages (decay classes 3–5), bktop is the presence of a broken top, bark% is the percent bark cover (+/−) after the parameter name indicates the confidence interval did not include zero and the direction of the parameter effect on the probability of the presence of a cavity.

was an increasing proportion of snags with evidence of foraging from smaller to larger DBH size classes, from 51% in the 8.0–23.0 cm size class to 86% in the >48.0 cm size class. The goodness-of-fit test showed a significant difference between the size class distribution of snags with evidence of foraging and the size class distribution of all snags ($\chi^2 = 46.95$, d.f. = 3, $P < 0.001$). The increasing percent of snags with evidence of foraging in greater DBH size classes indicate that larger snags are foraged on more than would be expected. There was no trend in percent of snags with evidence of foraging by decay class and the goodness-of-fit test was not significant ($\chi^2 = 8.40$, d.f. = 4, $P > 0.05$). Forage use was higher on larger diameter snags, but independent of decay class.

4. Discussion

4.1. Snag population

Snags are a common component of managed ponderosa pine stands on the BHNF. This is apparent from the total number of snags sampled and the high snag densities on some plots. However, most of the plots sampled were at the low end of snag densities, creating a skewed distribution. The snag population was relatively homogenous in terms of snag characteristics. The majority of snags sampled would best be described as *small diameter ponderosa pine snags in the early stages of decay with broken tops*. The most important, and challenging, aspect of this snag population for management of cavity-nesting birds is the dominance of snags in small DBH size classes (Fig. 2). Snags were common, but large snags were rare, and this may limit the quality of habitat for cavity-nesting birds in managed ponderosa pine stands.

In a report to the Secretary of Interior in 1899, Henry R. Graves provided an early description of the forests of the Black Hills, as well as the first estimate of snag densities and sizes. Historic snag densities averaged 273 snags per 100 acres (6.7 snags/ha), with diameters ranging from 9 to 19 in. (22.9–48.3 cm; Graves, 1899). Graves also reports that much of the Black Hills was covered by stands of trees with an average diameter of 20 in. (50.8 cm) and reaching a maximum diameter of 3 ft (91.4 cm). Currently, most snags in managed stands on the BHNF are smaller than the average size of both dead and live trees described by Graves a century earlier.

In ponderosa pine forests with evidence of past logging on two National Forests in northern Arizona, Ganey (1999) reported similar results that snag populations were dominated by small diameter snags, with relatively few snags in the largest DBH size classes, and that guidelines for snag retention were rarely met. Our data confirm that on the BHNF the number of large diameter snags is well below the proposed USDA Forest Service standards for the retention of snags (USDA Forest Service, 2001). Ganey (1999) also reported that snags in advanced stages of decay (stages 4 and 5) dominated the population, whereas we found snags in the earlier stages of decay (stages 1 and 2) were most abundant in the BHNF. This difference is likely due to a large recruitment of snags into the population following a snow and ice storm in April 2000 which damaged and killed many trees.

4.2. Cavity-nesting birds

Nine species of cavity-nesting birds were detected during point counts on our study plots. Only three species had sufficient detections to calculate a density estimate (Table 1). Density estimates for these three species are similar to the estimates from the Rocky Mountain Bird Observatory's monitoring reports for ponderosa pine forests in the Black Hills (Panjabi, 2001, 2003, 2004). There are no density estimates provided in other recent research in the Black Hills (Mills et al., 2000a; Anderson and Crompton, 2002), but the average number of birds per count in ponderosa pine stands reported in these studies were comparable to our data.

There are no quantitative estimates of cavity-nesting bird densities in the Black Hills that pre-date logging and forest management. However, it is interesting to make comparisons with historic qualitative accounts of bird abundance. In 1874, General George Armstrong Custer led a military scouting expedition into the Black Hills and William Ludlow documented birds and wildlife encountered. The species list is incomplete and most accounts are brief, but Ludlow reported on the red-headed woodpecker (*Melanerpes erythrocephalus*),

> "All through Dakota, wherever there was timber, I saw the red-headed woodpecker, and in the Black Hills it was especially abundant. It seemed to me the most common species there and its harsh cries resounded through the forest from morning till night." (Ludlow, 1875).

Another historic account of the red-headed woodpecker describes the species as, "The most abundant woodpecker in the hills" (Cary, 1901). In contrast, we saw and heard no red-headed woodpeckers at any time in managed ponderosa pine stands during our 2-year study.

There are almost no areas in the BHNF that have not been logged and could be used to compare baseline cavity-nesting bird densities in unmanaged ponderosa pine forests to managed stands. However, comparisons with unmanaged stands elsewhere in the west suggest that densities are relatively low in managed ponderosa pine stands on the BHNF. Balda (1975) reported densities, drawn from several sources and calculated using the spot-map method, of secondary cavity-nesting birds in three unmanaged ponderosa pine forests in Arizona. Densities for white-breasted nuthatches (*Sitta carolinensis*) ranged from 7 to 11 breeding pairs per 100 acres (0.35–0.54 birds/ha) and for house wrens (*Troglodytes aedon*) from 0 to 10 breeding pairs per 100 acres (0.0–0.49 birds/ha; Balda, 1975). We did not have sufficient detections to estimate densities for these two species since we only observed 10 white-breasted nuthatches and 1 house wren during 272 point counts. The pygmy nuthatch (*Sitta pygmaea*) and mountain chickadee (*Poecile gambeli*) are not common in the Black Hills (South Dakota Ornithologists' Union, 1991), but densities in Arizona were as high as 43 breeding pairs (2.13 birds/ha) and 20 breeding pairs per 100 acres (0.99 birds/ha) for the pygmy nuthatch and mountain chickadee, respectively (Balda, 1975). These densities are considerably higher than the closely related red-breasted nuthatch and black-capped chickadee (Table 1) that we detected during the breeding season in managed ponderosa pine stands on the BHNF.

Overall, the plot variables we measured provided little predictive power in determining the mean number of cavity-nesting birds detected on a plot. There are two possible reasons for this result. First, we may not have measured a variable that influenced the presence of cavity-nesting birds in managed stands. There could be several such variables (e.g. food availability, presence of predators, surrounding landscape matrix) that were not measured since the focus of our study was on examining the relationship of cavity-nesting birds with snag density. Second, one or more of the variables we measured may have been important in predicting cavity-nesting bird abundance, but the values measured on the plots were not within a range where the variable was influential. For example, the snag density was high on some of the plots, but the density of large snags was low on all of the plots. If cavity-nesting birds respond to the density of large snags, the densities of large snags on our plots may have been too low to affect the abundance of cavity-nesting birds or our ability to detect such an effect.

Increased abundance of cavity-nesting birds in areas with higher snag densities has been reported in western coniferous forests (Balda, 1975; Raphael and White, 1984; Zarnowitz and Manuwal, 1985; Schreiber and deCalesta, 1992). In the Black Hills, study results have been mixed. Abundances of some species of cavity-nesting birds (northern flicker (*Colaptes auratus*), downy woodpecker (*Picoides pubescens*), hairy woodpecker, black-capped chickadee, mountain bluebird (*Sialia currucoides*)) were not significantly correlated with snag densities, while other species (white-breasted nuthatch, red-breasted nuthatch, red-naped sapsucker (*Sphyrapicus nuchalis*)) exhibited weak to strong correlations with the density of snags >15 cm DBH (Mills et al., 2000a). Another study in the northern Black Hills found no association with the habitat used by woodpeckers during the breeding season and with snag variables of that habitat such as snag density, snag DBH, and basal area of snags (Anderson and Crompton, 2002). Black-backed woodpeckers (*Picoides arcticus*) and three-toed woodpeckers (*Picoides tridactylus*) were observed in stands with high densities of trees and snags in the BHNF (Mohren, 2002). A possible reason why cavity-nesting bird abundance was not related to snag density in our study is that the great majority of snags are small in managed ponderosa pine stands on the BHNF.

4.3. Snags with cavities

The model selection results for the a priori logistic regression models (Table 2) and the results when the parameters are examined individually (Table 3) support the model which includes DBH, height, decay class, and the presence of a broken top as the ''best'' model for predicting the probability of a cavity in a ponderosa pine snag. These results show that cavities are more common in ponderosa pine snags with larger DBH and greater height, and less common in snags in the advanced stages of decay and with broken tops. Percent bark cover has little influence on the presence of a cavity. Therefore, larger and taller snags that are not heavily decayed are the most likely locations for cavity-nesting birds to excavate cavities.

The association of larger DBH and greater height of snags with cavities is consistent with other studies (Scott, 1978; Cunningham et al., 1980; Mannan et al., 1980; Raphael and White, 1984; Reynolds et al., 1985; Zarnowitz and Manuwal, 1985; Schreiber and deCalesta, 1992). In unmanaged stands on the BHNF, Lentile et al. (2000) reported that cavity use was correlated with snag DBH ($R^2 = 0.95$). The results for decay class are less straightforward since different species of cavity-nesting birds utilize snags in varying stages of decay (Raphael and White, 1984) and, therefore, we expect all decay classes to be utilized. The negative association of the probability of a cavity in a ponderosa pine snag with advanced stages of decay could be explained by our conservative identification of a nest cavity. A cavity was only recorded if it could clearly be identified as a nesting cavity, whereas cavities in snags in more advanced stages of decay could have been too rotten and decayed to be positively classified as a cavity. The negative association of the presence of a cavity in snags with broken tops is contrary to other research (McClelland and Frissell, 1975; McClelland et al., 1979; Cunningham et al., 1980; Mannan et al., 1980; Raphael and White, 1984; Zarnowitz and Manuwal, 1985). This may be because cavity-nesting birds utilize large snags more frequently, but the tops of small snags are more likely to break due to wind, snow, or ice damage. The lack of percent bark cover influencing the probability of a cavity was not surprising since selection for bark coverage varies by bird species (Raphael and White, 1984; Schreiber and deCalesta, 1992), and like decay class we would expect snags across all percentages of bark cover to be used.

The results for aspen snags are similar to those for ponderosa pine, but slightly less conclusive. The model selection results for the logistic regression models predicting the probability of a cavity in an aspen snag (Table 4) do not clearly support one model. Instead, the top four models are competitive, none of which carried a large percent of the weight. However, when parameters were examined individually (Table 5), both DBH and decay class had high weights lending support to the model which included only these two parameters. These results show that larger DBH was positively associated with the probability of the presence of a cavity in an aspen snag and advanced stages of decay were negatively associated with the presence of a cavity.

Combining the results for both ponderosa pine and aspen snags demonstrates that snags of large DBH and early stages of decay were most likely to have a cavity and, therefore, provide nest sites for cavity-nesting birds. Snags in the early stages of decay were abundant (82.3% of 2886 snags) in managed ponderosa pine stands, but snags with large DBH were uncommon (Fig. 2). This lack of large snags for use as nest sites may be the main reason for the low densities of cavity-nesting birds found in managed stands on the BHNF.

4.4. Snags with foraging evidence

Over half of the snags sampled had evidence of foraging and 85.1% of a sub-sample of ponderosa pine snags showed signs of activity by bark beetles or wood boring insects (Spiering, 2004). This suggests that snags are an important resource for cavity-nesting birds. Cavity-nesting birds that forage by bark-gleening, such as chickadees and nuthatches, search furrows in the bark for invertebrates, but do not have the bill morphology for extensive excavation into the bole of a tree or snag. Due to the types of foraging evidence collected (chipped bark, drill holes, and foraging excavations), we focus our discussion on the foraging of woodpecker species, particularly the *Picoides* woodpeckers.

The increased proportion of snags with evidence of foraging as DBH size class increased and the significant goodness-of-fit test indicate that large snags are the most important for foraging. From evidence of foraging and observational data, Mannan et al. (1980) reported that woodpeckers foraged on large snags most frequently, and Raphael and White (1984) found that snags with feeding sign were larger in diameter than snags with no sign of feeding. Imbeau and Desrochers (2000) observed three-toed woodpeckers foraging on snags with greater DBH than paired nearest available snags. In the BHNF, Lentile et al. (2000), found an increased proportion of snags with evidence of foraging from small to medium size classes, but then a leveling off of the proportion of snags with evidence of foraging in the largest size classes. In our study, over 50% of snags in all size classes, even the smallest size class of 8.0–23.0 cm, had evidence of foraging. Thus, large snags are foraged more frequently, but smaller snags are still utilized and should be maintained increase habitat quality for cavity-nesting birds.

The lack of a significant difference in evidence of foraging in relation to decay class was expected. As a snag progresses in the decay process, it is often colonized first by bark beetles (Scolytidae), followed by wood boring insects (Cerambycidae, Buprestidae, Siricidae), and then by carpenter ants (Formicidae; D. Leatherman, personal communication). All of these insects are eaten by different woodpecker species, and therefore snags provide a changing, but persistent food base as they decay.

5. Conclusion

Snags were common in managed ponderosa pine stands on the BHNF, but snags in the larger DBH size classes were rare in these stands. Snags with large DBH were more likely to have cavities created by and used for nesting by cavity-nesting birds. Evidence of foraging by cavity-nesting birds was greater than expected on snags in larger DBH size classes, but did occur on snags in all DBH size classes. Based on these results, and other published studies, large snags, particularly larger in DBH, are an important habitat component for cavity-nesting birds.

Cavity-nesting birds were detected infrequently in managed ponderosa pine stands and abundances of these birds in our study appear to be lower than historic accounts indicate or have been reported to occur in unmanaged ponderosa pine forests in the western United States. The low numbers of cavity-nesting birds in managed ponderosa pine stands on the BHNF is probably because nearly all snags in these stands are too small to be used as nest trees.

We suggest future studies compare cavity-nesting bird populations in managed and unmanaged stands of similar forest type. Researchers should also measure demographic characteristics of cavity-nesting birds, such as survival and nest success, using snags across a range of DBH size classes from small to large. In the meantime, it appears that managing for large snags, possibly through increased snag retention, longer rotation cycles, or killing large live trees to create snags, is the best way to improve habitat for cavity-nesting birds in managed ponderosa pine stands.

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