JOURNAL OF FIELD ORNITHOLOGY

Published by
Association of Field Ornithologists

VOL. 71, NO. 2 | Spring 2000 | PAGES 187–384

J. Field Ornithol., 71(2):187–206

HABITAT OF BIRDS IN PONDEROSA PINE AND ASPEN/BIRCH FOREST IN THE BLACK HILLS, SOUTH DAKOTA

TODD R. MILLS[1] AND MARK A. RUMBLE

U.S. Department of Agriculture Forest Service
Center for Great Plains Ecosystem Research
Rocky Mountain Research Station
501 East St. Joe, Rapid City, South Dakota 57701 USA

LESTER D. FLAKE

Department of Wildlife and Fisheries Sciences
South Dakota State University
Brookings, South Dakota, 57007 USA

Abstract.—Birds with both eastern and western distributions occur in the Black Hills of western South Dakota. This forest is mostly ponderosa pine (*Pinus ponderosa*) and is managed for timber. Logging alters forest characteristics and the bird community. We studied habitat relations of breeding songbirds at the stand- and site-level scales in ponderosa pine and quaking aspen (*Populus tremuloides*)/paper birch (*Betula papyrifera*) forest. Sixty bird species were observed ≤50 m from count points. Species richness was greater in aspen/birch than in ponderosa pine. Species richness was generally lower in ponderosa pine with >40% overstory canopy cover (OCC) than in ponderosa pine with ≤40% OCC and than aspen/birch of any structural stage. Seven bird species were associated with the ponderosa pine, while four species were associated with aspen/birch. Bird associations at the stand-level were further refined by OCC and diameter-at-breast-height (DBH) structural stage of each forest type. Habitats for most birds in the Black Hills can be managed using current forest inventory descriptions that include OCC and DBH. However, Red-naped Sapsuckers (*Sphyrapicus nuchalis*), Red-breasted Nuthatches (*Sitta canadensis*), White-breasted Nuthatches (*S. carolinensis*), Ovenbirds (*Seiurus aurocapillus*), and Western Tanagers (*Piranga ludoviciana*) were strongly associated with site-level vegetation characteristics. Snag density, snag condition, and deciduous trees beneath the ponderosa pine canopy should be included in forest inventories to better quantify habitats for these birds.

EL HÁBITAT DE LAS AVES EN UN BOSQUE DE *PINUS PONDEROSA* Y *POPULUS TREMULOIDES/BETULA PAPYRIFERA* EN LOS BLACK HILLS DE DAKOTA DEL SUR

Sinopsis.—En los Black Hills del oeste de Dakota del Sur hay aves distribuídas en el este y en el oeste del continente. El bosque es mayormente de *Pinus ponderosa* y se maneja principalmente para madera, alterando las características del bosque y de la comunidad de aves.

[1] *Current address: U.S. Department of Agriculture Forest Service, Black Hills National Forest, RR 2 Box 200, Custer, South Dakota 57730-9504 USA.*

Estudiamos las relaciones de habitat de las aves reproduciéndose en las escalas de setos y del nivel de sitio en bosques de esta especie y de *Populus tremuloides*/*Betula papyrifera*. Se observaron 60 especies de aves a ≤50 m de los puntos de observación. La riqueza de especies fué mayor en *Populus tremuloides*/*Betula papyrifera* que en *Pinus ponderosa*. La riqueza de especies fué generalmente menor en *Pinus ponderosa* con >40% de de cubierta dobredosel (OCC) que en *Pinus ponderosa* de ≤40% OCC y que en sitios con *Populus tremuloides*/*Betula papyrifera* de cualquier etapa estructural. Se asociaron siete especies de aves con *Pinus ponderosa,* mientras que con *Populus tremuloides*/*Betula papyrifera* se asociaron cuatro. Las asociaciones de aves a nuvel de seto se refinaron más aún usando OCC y el diámetro a la altura del pecho (DBH) de las etapas estructurales en cada tipo de bosque. Los hábitats para la mayoría de las aves en los Black Hills se pueden manejar usando las descripciones de inventario actuales de los bosques que incluyen OCC y DBH. Sin embargo, las aves *Sphyrapicus nuchalis, Sitta canadensis, S. carolinensis, Seiurus aurocapillus* y *Piranga olivacea* se asociaron fuertemente con las características de la vegetación a nivel del lugar. La densidad de espeques, la calidad de estos, y los árboles deciduos detrás del dosel de *Pinus ponderosa* debiera incluírse en los inventarios forestales para cuantificar mejor los hábitats para estas aves.

Most of the Black Hills National Forest is managed for timber production (Black Hills National Forest 1996). Logging changes the structure, diversity, composition, and patchiness of vegetation, which affects the distribution and abundance of birds (Franzreb and Ohmart 1978, Szaro and Balda 1979a,b) by altering their patterns of habitat selection, foraging behavior, and reproductive success (James and Wamer 1982, Robinson and Holmes 1984, Hansen et al. 1995). Removal of 17% of the canopy foliage in ponderosa pine (*Pinus ponderosa*) alters the abundance and species composition of both songbirds and cavity-nesting birds (Bull and Meslow 1977, Szaro and Balda 1979a, Cunningham et al. 1980).

Although a large body of literature exists describing how vegetation conditions affect habitat selection by birds, managers need information that corresponds to the scales at which forests are managed. In the Rocky Mountains, studies on songbird habitat relations to specific silviculture practices are rare (Hejl et al. 1995). Some information regarding the effects of forest management on birds is aggregated for regions (Hansen et al. 1995), but terminology and descriptions of forest vegetation vary among regions, which complicates application of knowledge regarding bird responses to altered vegetation. For example, in the southeast and northwest, bird-habitat associations to forest vegetation are described as plantations, from stand age, or tree density (Dickson et al. 1995, Hansen et al. 1995). In the Black Hills, managers describe forest vegetation using the dominant species of growth form, DBH categories, and overstory canopy cover (OCC) categories.

The bird community of the Black Hills is unusual in that birds of both eastern and western distributions occur there. We investigated the habitat relationships of birds at three scales in a ponderosa pine-dominated forest. First, we evaluated avian abundance in ponderosa pine and quaking aspen (*Populus tremuloides*)/paper birch (*Betula papyrifera*) forest vegetation types. Second, we evaluated avian abundance in structural stages of these vegetation types. Structural stages are vegetation descriptions applied by the national forests for long-term resource planning and impact analyses of planned land management actions. Third, we evaluated avian abundance relative to vegetation structure.

STUDY AREA

The Black Hills encompass approximately 15,540 km^2 in west-central South Dakota and east-central Wyoming. Elevation ranges from 1450–1770 m. Our study was conducted in the central Black Hills (44°00′ to 44°22″N, 103°30′ to 103°45′W) of South Dakota from 1992 to 1993.

Ponderosa pine is the dominant climax forest vegetation type (84%) with snowberry (*Symphoricarpos albus*), kinnikinnick (*Arctostaphylos uva-ursi*), juniper (*Juniperus communis*), or bur oak (*Quercus macrocarpa*) as co-dominant species (Hoffman and Alexander 1987). Most of the ponderosa pine forest has been logged in the past. Quaking aspen comprises 4% of the Black Hills National Forest as early successional forest in some areas where ponderosa pine is climax or as a climax forest vegetation type with paper birch as a co-dominant (Hoffman and Alexander 1987). White spruce (*Picea glauca*) occurs sporadically in ponderosa pine and aspen/birch vegetation types or as a climax vegetation type (2%), but was not included in this study. Meadows also are recognized vegetation types in the Black Hills (8%), but are not impacted by logging so were not included in this study.

METHODS

Sampling design.—We studied bird-habitat relationships in seven vegetation structural stages of ponderosa pine and four vegetation structural stages of aspen/birch. Vegetation structural stages are descriptions of vegetation types that include categories for DBH and overstory canopy cover (OCC, Buttery and Gillam 1983). When applicable, structural stages are used by the Black Hills National Forest for modeling wildlife responses to vegetation conditions and are typically applied to land units (stands) of 4–32 ha. Vegetation structural stages represent the hypothesized seral processes that generally follow clearcutting and include grass-forb and DBH classes of shrub-seedling (<2.5 cm DBH), sapling-pole (2.5–22.9 cm DBH), mature (>22.9 cm DBH), and old-growth. Sapling-pole and mature forests are further stratified into three OCC categories of 0–40%, 41–70%, and >71%. Clearcutting is not the typical method of logging ponderosa pine in the Black Hills. Thus, the grass-forb and shrub-seedling structural stages of ponderosa pine were not available for study. Clearcutting is the method used for logging aspen/birch. Because aspen/birch sprout from roots following clearcutting, the grass-forb structural stage of aspen/birch lasts only a few months and also was not available for this study. Aspen/birch, often does not attain large enough DBH to meet the criteria of the ''mature'' structural stage in the Black Hills. The structural stage criteria assigned are agency criteria applied throughout the Rocky Mountains and thus, even though these stands are mature, they do not meet the DBH criteria for the structural stage assignments. At the time of this study, the old-growth structural stage of ponderosa pine was determined by subjective assignments of scores to stands >38 cm DBH for the presence of multiple canopy layers and amount and size of forest residue on the ground. Scores exceeding a threshold value were identified as old-growth. Old-growth stands were determined by national forest personnel prior to our study, and we did not modify this characterization. The Black Hills National Forest now determines old-growth stands using definitions from Mehl (1992). Thus, we characterized these stands as multi-storied ponderosa pine. Otherwise, vegetation structural stages were verified in the field prior to establishing sites in stands.

We identified prospective stands from 1989 forest inventory data and aerial photographs. We selected seven stands in each of the 11 structural stages, but one multi-storied ponderosa pine was logged during our study, resulting in six stands in the multi-storied structural stage of ponderosa pine. In aspen/birch, we included four upland stands and three stands that occurred in drainages; both types of aspen/birch are managed similarly by the BHNF. Stands in this study ranged between 5.3 and 59.5 ha and were >0.5 km apart.

Bird counts.—Within each stand, we selected three sites for counting birds using variable circular plots (Reynolds et al. 1980). All sites were >150 m apart to minimize double counting individual birds, and most were 150 m from an edge to avoid counting birds in adjacent habitats (Robbins et al. 1989, Manuwal and Carey 1991); aspen/birch drainages were too narrow to avoid placing sites 150 m from an edge. At each site, we counted breeding birds on two consecutive days during each of two sample sessions between 15 May and 7 July of each year. We began bird counts at sunrise and completed them by 1100 h (Verner and Ritter 1986) during which we recorded all birds seen or heard and their estimated distances during 8-min counts (Verner 1988, Ralph et al. 1993). Birds near the count point that were flushed while approaching were recorded, and the distance estimate was made relative to the count point. We discontinued bird counts if wind speed exceeded 10 km/h, temperatures were <7 C or >24 C, or during periods of moderate to heavy rain (Manuwal and Carey 1991). We used three observers to count birds. The order of counts on consecutive days at a site was reversed to spread counts equitably throughout the morning, decrease bias, and maximize the number of species detected (Gotfryd and Hansell 1985, Verner and Milne 1989). Additionally, each observer counted birds at different sites during each sample session. Observers were experienced and trained for estimating distances, visual, and audio identification of birds that occur in the Black Hills (Verner and Milne 1989).

Habitat characteristics.—At each site we established five, 0.04-ha circular plots. One plot was centered over the bird count point, and four plots were located 30 m away in the cardinal directions. This design was modified for sites in aspen/birch drainages because these were too narrow to support plots 30 m perpendicular to the drainage. In aspen/birch drainages, we used three, 0.04-ha circular plots. One plot was located at the bird count point, the others were located 30 m above and below the drainage. Within each plot, we recorded DBH of trees >2.5 cm by species, estimated canopy height (height above ground to first live branches) using a clinometer, crown height of each tree using a clinometer, and the width of the canopy. These data were used to calculate tree density, tree basal area, and canopy volume. Tree basal area is standard forestry terminology that represents the cumulative cross-sectional area of trees per unit area (Spurr 1952). We calculated canopy volume using formulae for a cone for white spruce and half-ellipsoid for aspen/birch (Sturman 1968); for ponderosa pine, canopy volume was calculated as a combination of the cone and half-ellipsoid (Aney 1984). We calculated foliage-height diversity (MacArthur and MacArthur 1961) from stratified canopy volume in 1-m intervals. We counted snags in a 0.28-ha circular plot centered over the bird count point and recorded DBH, height, percent of bark cover, and condition for each snag (Cunningham et al. 1980). Density of ponderosa pine and aspen/birch snags was calculated for snags >15 cm DBH.

We estimated percent cover of total vegetation, grasses, forbs, shrubs, shrub species, bare ground, litter, and rocks (>7.5 cm diameter) in 20, 0.10-m^2 quadrats (Daubenmire 1959) at 2-m intervals along four, 10-m transects radiating from the center of each 0.04 ha plot. We counted the shrub stems in 0.5-m^2 circular hoops at the plot center and the 5- and 10-m intervals along four, 10-m transects in each plot. Overstory canopy cover was estimated at the center of each plot and at the 15- and 30-m intervals of each 30-m transect using a spherical densiometer (Griffing 1985). Percent slope was estimated at the center of each plot using a clinometer and aspect was recorded as the down-hill compass bearing at the bird count point.

Analyses.—Data characterizing vegetation at each site were averaged within stands. We eliminated from the analyses understory vegetation variables that comprised <1% canopy cover or whose frequency in stands was <5%, because minor or trivial variables can produce spurious results (Everitt 1977). We also eliminated one of a pair of vegetation variables that had linear correlation coefficients (r) ≥0.70 or variables that represented a more parsimonious characterization of the forest. For example, DBH and tree density were omitted from analyses because (1) they were moderately correlated, (2) are included in computations for basal area, (3) DBH is one of the criteria used to describe structural stage categories, and (4) the Black Hills National Forest characterizes stands using basal area, not tree density.

We averaged counts of birds within 50 m of the count point that occurred in the prescribed vegetation structural stage across count-days, sample sessions, sites, and years to estimate abundance for each stand. Bird species richness was the number of species observed in stands during the study. Homogeneous variances in our data were uncommon; so where possible we selected statistical tests that did not require this assumption. We tested hypotheses that bird abundances and species richness did not differ between vegetation types using Mann-Whitney U-tests. Hypotheses that bird abundances did not differ among vegetation structural stages were tested using a Kruskal-Wallis test with a Tukey-type multiple comparison (Hochberg and Tamhane 1987). For birds that were associated primarily with ponderosa pine or aspen, we made tests of bird abundance for structural stages of these vegetation types separately. We did this to keep the number of treatments (k) considered to a minimum ($k = 7$ for ponderosa pine and $k = 4$ for aspen/birch). Structural stage comparisons for birds that were cosmopolitan in the selection of vegetation types were made with $k = 11$ structural stages. Because stand structural stage descriptions did not include potential habitat characteristics for cavity nesting birds, we used rank-order correlations to evaluate relations of abundance of these birds to density of ponderosa pine and aspen/birch snags and condition of these snags. We considered significance at $\alpha \leq 0.1$ and all multiple comparison tests preserve the experiment-wise error rate. We report actual P values for tests of bird abundance between vegetation types unless the value was ≤ 0.01; statistical significance of bird abundance among structural stages was determined from established critical values determined from tables (Hochberg and Tamhane 1987), so exact P values were not available.

RESULTS

Birds in relation to vegetation type.—Sixty bird species were observed within 50 m of the count points and within the vegetation types sampled, and 22 species were common enough for further analyses. Seven species were more abundant in ponderosa pine than aspen/birch (Table 1). Eight bird species were more abundant in aspen/birch than ponderosa pine, and disparity in abundance between forest types suggested that four of these species could be considered aspen/birch associates.

Birds in relation to structural stages and microhabitat.—For the most part, understory vegetation in ponderosa pine declined with increased overstory canopy cover in both sapling-pole and mature structural stages (Table 2). In mature structural stages, understory vegetation tended to be slightly greater than the sapling-pole structural stages. The multi-storied structural stage had high OCC and moderately high understory vegetation. Basal area of ponderosa pine increased with both overstory cover categories and from sapling-pole to mature structural stages. Most stands were homogeneous regarding the dominant species of vegetation as other tree species comprised a very small portion of the basal area. Canopy volume followed similar trends, as did basal area in ponderosa pine structural stages. Density of snags in ponderosa pine varied with structural stage, but most occurred in sapling-pole <40% OCC and multi-storied stands. Understory vegetation was relatively high in all structural stages of aspen/birch. OCC, basal area, and canopy volume increased in aspen/birch structural stages. Measured OCC showed that most stands were classified appropriately from forest inventory data.

Differences in species richness among vegetation structural stages resulted from fewer species in sapling-pole ponderosa pine 41–70% and

TABLE 1. Average birds per count (± SE) and species richness in ponderosa pine and aspen/birch stands in the Black Hills, South Dakota, 1992–1993.

Species		Ponderosa pine $\bar{x}$	± SE	Aspen/birch $\bar{x}$	± SE	P[a]
Red-naped Sapsucker	*Sphyrapicus nuchalis*	0.02	0.01	0.13	0.03	<0.01
Downy Woodpecker	*Picoides pubescens*	0.03	0.01	0.03	0.01	0.35
Hairy Woodpecker	*Picoides villosus*	0.11	0.02	0.07	0.02	0.11
Northern Flicker	*Colaptes auratus*	0.02	0.01	0.04	0.01	<0.01
Dusky Flycatcher	*Empidonax oberholseri*	<0.01	<0.01	0.40	0.05	<0.01
Warbling Vireo	*Vireo gilvus*	0.07	0.02	0.88	0.07	<0.01
Gray Jay	*Perisoreus canadensis*	0.08	0.02	<0.01	<0.01	<0.01
Black-capped Chickadee	*Poecile atricapillus*	0.47	0.03	0.47	0.04	0.92
Red-breasted Nuthatch	*Sitta canadensis*	0.46	0.03	0.18	0.03	<0.01
White-breasted Nuthatch	*Sitta carolinensis*	0.14	0.02	0.07	0.02	<0.01
Brown Creeper	*Certhia americana*	0.02	<0.01	0.00	0.00	0.04
Mountain Bluebird	*Sialia currucoides*	0.05	0.02	0.06	0.02	0.29
Townsend's Solitaire	*Myadestes townsendi*	0.23	0.02	0.04	0.01	<0.01
Swainson's Thrush	*Catharus ustulatus*	0.03	0.01	0.05	0.01	0.20
American Robin	*Turdus miratorius*	0.09	0.02	0.23	0.05	<0.01
Yellow-rumped Warbler	*Dendroica coronata*	0.59	0.03	0.16	0.03	<0.01
Ovenbird	*Seiurus aurocapillus*	0.14	0.04	0.31	0.07	<0.01
MacGillivray's Warbler	*Oporornis tolmiei*	<0.01	<0.01	0.06	0.02	<0.01
Western Tanager	*Piranga ludoviciana*	0.15	0.02	0.05	0.01	<0.01
Chipping Sparrow	*Spizella passerina*	0.15	0.03	0.28	0.05	0.01
Dark-eyed Junco	*Junco hyemalis*	0.62	0.06	0.76	0.07	0.08
Brown-headed Cowbird	*Molothrus ater*	0.03	0.01	0.04	0.01	0.82
Species Richness		14.79	0.46	18.07	0.50	<0.01

[a] Probability that average ranked abundance differed between ponderosa pine and aspen/birch vegetation types from Mann-Whitney *U*-test.

TABLE 2. Average (± SE) vegetation characteristics in stands of ponderosa pine and aspen/birch in the Black Hills, South Dakota, 1992–1993.

Vegetation characteristic[b]	Ponderosa pine[a]											
	Sapling/pole						Mature					
	<40% OCC		41–70% OCC		>70% OCC		<40% OCC		41–70% OCC		>70% OCC	
	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE
Canopy cover in understory												
Total cover	33.0	3.1	31.9	3.8	17.8	2.1	49.2	0.2	31.3	2.7	31.4	4.5
Grass cover	12.6	1.4	14.3	2.5	3.5	0.6	15.1	2.1	13.4	2.3	9.6	2.6
Forb cover	7.8	1.0	9.0	1.4	2.9	0.5	9.1	1.1	6.7	0.8	5.5	1.4
Shrub cover	15.6	2.2	14.6	2.3	12.9	1.5	28.9	2.7	14.0	2.2	20.2	2.7
Shrub density	11.6	1.6	5.5	0.8	4.8	1.1	8.0	1.4	15.8	4.5	7.5	0.9
Overstory canopy cover	25.5	1.1	52.0	0.9	70.3	1.5	23.8	1.6	54.3	1.4	72.3	0.9
Ponderosa pine basal area	5.5	0.7	4.9	0.5	14.4	1.3	8.3	0.9	14.0	0.9	18.5	1.7
Aspen/birch basal area	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Canopy volume	4.7	0.4	4.2	0.4	7.9	1.0	5.3	0.9	10.8	1.4	8.9	0.9
Foliage-height diversity	2.5	0.1	2.2	0.1	2.2	<0.1	2.5	0.1	2.7	0.1	2.6	0.1
Ponderosa pine snags	16.4	1.9	8.1	0.8	13.0	2.4	9.0	1.7	15.4	0.9	15.1	2.3
Aspen/birch snags	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.9	0.0	0.0	0.0	0.0
Bark cover on snags	73.3	2.3	78.4	3.1	75.3	2.4	34.0	8.6	78.1	4.0	71.7	3.9

[a] DBH and overstory canopy cover (OCC) structural stage categories taken from Buttery and Gillam (1983).
[b] Units of measure for understory canopy cover variables are %, shrub density is m^2/ha, BA are m^3/ha, canopy volume is $m^3 \times 100$, composition are %, snags are no./ha, and bark cover is %.

TABLE 2. Continued, Extended.

Vegetation characteristic[b]	Ponderosa pine[a]		Aspen/birch[a]							
	Multi-storied		Shrub		Sapling/pole					
					<40% OCC		41–70% OCC		>70% OCC	
	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE
Canopy cover in understory										
Total cover	37.2	4.2	76.2	1.2	85.4	1.0	70.8	3.1	74.9	1.8
Grass cover	13.0	2.6	27.2	1.9	39.3	3.2	22.8	2.9	28.4	3.1
Forb cover	6.3	1.1	28.1	1.9	39.3	3.2	22.8	2.9	28.4	3.1
Shrub cover	20.9	2.8	25.3	2.0	25.8	2.2	20.3	2.2	23.6	2.2
Shrub density	12.7	1.6	21.2	1.0	18.2	1.3	18.1	1.4	21.6	3.6
Overstory canopy cover	74.7	1.4	14.0	2.7	20.0	1.9	57.0	1.9	69.8	2.0
Ponderosa pine basal area	16.3	1.6	0.1	0.1	0.3	0.1	2.4	0.7	2.7	0.5
Aspen/birch basal area	<0.1	<0.1	1.0	0.2	1.6	0.2	6.8	0.9	9.9	0.6
Canopy volume	9.6	1.4	1.7	0.3	3.1	0.5	12.8	1.1	12.0	1.4
Foliage-height diversity	2.7	<0.1	1.9	0.1	2.2	0.1	2.5	0.1	2.3	<0.1
Ponderosa pine snags	16.1	2.6	4.8	0.7	2.9	0.8	2.9	0.9	2.9	1.1
Aspen/birch snags	5.7	0.9	6.5	2.0	2.9	0.9	15.8	3.6	11.6	3.2
Bark cover on snags	81.8	2.3	35.6	5.1	59.1	8.8	85.5	1.5	80.9	1.5

>70% OCC and sapling-pole aspen / birch 41–70% OCC than in sapling-pole aspen / birch 41–70% and >70% OCC (Table 3). We also conducted tests to determine if species richness differed among structural stages within ponderosa pine and aspen / birch separately, but these tests did not identify any differences.

Northern Flickers (*Colaptes auratus*), Downy Woodpeckers (*Picoides pubescens*), and Hairy Woodpeckers (*P. villosus*) were uncommon, but these species tended to be more abundant in stands with ≤70% OCC in ponderosa pine and aspen / birch (Table 3). Black-capped Chickadees (*Poecile atricapillus*) were abundant in all structural stages but were most abundant in multi-storied ponderosa pine and sapling-pole aspen / birch >70% OCC. Structural stages with forest canopy cover ≤40% OCC had more Mountain Bluebirds (*Sialia currucoides*) than forest structural stages with >70% OCC. None of these cavity nesting birds exhibited significant correlations with density or condition of snags.

Although Swainson's Thrushes (*Catharus ustulatus*) occurred in several vegetation structural stages, they were abundant only in multi-storied ponderosa pine and sapling-pole aspen / birch >70% OCC. Nevertheless, abundance of Swainson's Thrushes in sapling-pole aspen / birch >70% OCC was 50% lower than abundance in the multi-storied ponderosa pine stands. American Robins (*Turdus migratorius*) were most abundant in sapling-pole aspen / birch ≤70% OCC. Chipping Sparrows (*Spizella passerina*) were abundant in ponderosa pine ≤40% OCC and sapling-pole aspen / birch ≤70% OCC. Dark-eyed Junco (*Junco hyemalis*) abundance declined in both ponderosa pine and aspen / birch stands with greater OCC. Brown-headed Cowbirds (*Molothrus ater*) were uncommon in our study and equally abundant among structural stages of ponderosa pine, and aspen / birch. Abundance of Brown-headed Cowbirds was correlated with bird species richness $r = 0.3$, $P < 0.01$), but not with abundance of non-cavity nesting birds ($r = 0.1$, $P = 0.28$).

Gray Jays (*Perisoreus canadensis*) were more abundant in mature ponderosa pine than sapling-pole ponderosa pine. Within mature pine, Gray Jays were most abundant in stands >40% OCC (Table 4). White-breasted Nuthatches (*Sitta carolinensis*) were common in all pine stands, but tended to select stands 40–70% OCC. Abundance of White-breasted Nuthatches was similar among other structural stages of ponderosa pine, except that the sapling-pole 0–40% OCC had the fewest. White-breasted Nuthatches exhibited a moderate positive correlation ($r = 0.2$, $P = 0.09$) with density of ponderosa pine snags >15 cm DBH. Red-breasted Nuthatches (*S. canadensis*) were common in all structural stages of ponderosa pine but tended toward greater abundance in sapling / pole ponderosa pine stands >70% OCC, mature ponderosa pine >40% OCC, and multistoried stands of pine. Red-breasted Nuthatches exhibited strong correlations with density of ponderosa pine snags >15 cm DBH ($r = 0.5$, $P < 0.01$) and % bark on snags ($r = 0.5$, $P < 0.01$). Although no differences were evident in abundance of Brown Creepers among vegetation structural stages, they only occurred in the mature and multi-storied stages.

Townsend's Solitaires (*Myadestes townsendii*) and Yellow-rumped Warblers (*Dendroica coronata*) did not differ in abundance among structural stages of ponderosa pine. Western Tanagers were most abundant in multi-storied ponderosa pine.

Red-naped Sapsuckers (*Sphyrapicus nuchalis*), Dusky Flycatchers (*Empidonax oberholseri*), and Warbling Vireos (*Vireo gilvus*) were equally abundant among structural stages of aspen/birch (Table 5). Red-naped Sapsuckers exhibited a strong positive correlation ($r = 0.7$, $P < 0.01$) with density of aspen/birch snags >15 cm DBH. Ovenbirds (*Seirus aurocapillus*) were most abundant in structural stages of aspen/birch with >40% OCC. However, Ovenbirds also were common in multi-storied ponderosa pine. MacGillivray's Warblers (*Oporornis tolmiei*) were most abundant in shrub-seedling and sapling-pole aspen/birch with less than 70% OCC.

DISCUSSION

Aspen/birch birds.—In the Black Hills, aspen/birch that occurs in drainages exhibits characteristics similar to riparian habitats; some had surface water during the spring. Riparian zones tend to be centers of biological diversity in conifer forests (Knopf et al. 1988). Upland stands of aspen/birch are more mesic than the ponderosa pine. Greater bird species richness in the aspen/birch than ponderosa pine probably occurs because deciduous forests have greater invertebrate food resources (Schimpf and MacMahon 1985).

Although aspen/birch is not intensively managed for forest products in the central Black Hills, it provides important habitat for the bird community. Logging in the aspen/birch vegetation types is done to ensure that it does not succeed to ponderosa pine or white spruce. Five bird species were primarily associated with aspen/birch. Of these, Dusky Flycatchers, Warbling Vireos, and MacGillivray's Warblers could be considered aspen/birch obligates in the central Black Hills. Ovenbirds could be considered aspen/birch associates. These species are considered aspen associates or obligates throughout the Rocky Mountain region (Holthausen 1984, Finch and Reynolds 1987, Scott and Crouch 1988). MacGillivray's Warblers and Dusky Flycatchers prefer open canopied aspen/birch stands (Ralph et al. 1991) or low to intermediate density forests with a shrub understory (DeGraaf et al. 1991). In addition to aspen/birch, Ovenbirds also occurred in multi-storied ponderosa pine that included about 3% deciduous trees, such as bur oak or aspen/birch, as understory trees. In the northern Black Hills, Ovenbirds used stands of mature ponderosa pine >70% OCC and multi-storied ponderosa pine with deciduous trees below the pine canopy. (Dykstra et al., in press). We also considered Red-naped Sapsuckers aspen/birch obligates in the Black Hills. Structural stages with high abundance of Red-naped Sapsuckers averaged >11 snags/ha that were >15 cm DBH. The strong association of Red-naped Sapsuckers to snags in aspen/birch suggests that monitoring habitat suitability for this species should include data quantifying snag abundance. Current policy on the Black Hills National Forest allows cut-

TABLE 3. Average birds/count (± SE) of generalist birds and species richness ≤50 m from count points in the Black Hills, South Dakota, 1992–1993.[a]

Bird species	Ponderosa pine[b]											
	Sapling/pole						Mature					
	<40% OCC		41–70% OCC		>70% OCC		<40% OCC		41–70% OCC		>70% OCC	
	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE
Downy Woodpecker	0.04	0.02A	0.04	0.03A	0.05	0.02A	0.03	0.02A	0.03	0.01A	0.01	0.01A
Hairy Woodpecker	0.17	0.07A	0.12	0.05A	0.05	0.03A	0.12	0.03A	0.10	0.03A	0.07	0.03A
Northern Flicker	0.02	0.01AC	0.00	0.00A	0.01	0.01AC	0.05	0.03CD	0.01	0.01AC	0.01	0.01AC
Black-capped Chickadee	0.34	0.05A	0.51	0.10A	0.45	0.07A	0.44	0.06A	0.55	0.07A	0.42	0.08A
Mountain Bluebird	0.18	0.07D	0.00	0.00A	0.01	0.01AC	0.11	0.05C	0.01	0.01AC	0.01	0.01AC
Swainson's Thrush	0.00	0.00A	0.02	0.01AB	0.00	0.00A	0.00	0.00A	0.01	0.01AB	0.04	0.02AB
American Robin	0.10	0.06A	0.14	0.04AC	0.09	0.06A	0.13	0.05AC	0.07	0.02A	0.05	0.03A
Chipping Sparrow	0.39	0.16D	0.13	0.04AB	0.08	0.03BC	0.21	0.05BCD	0.10	0.03AB	0.03	0.02A
Dark-eyed Junco	1.04	0.16DE	0.63	0.11B	0.17	0.04A	0.98	0.20CDE	0.56	0.08BC	0.45	0.10B
Brown-headed Cowbird	0.03	0.02A	0.03	0.01A	0.02	0.01A	0.05	0.03A	0.05	0.02A	0.01	0.01A
Bird Species Richness	15.86	1.10BCD	13.00	0.79A	12.71	1.23A	16.71	1.27BCD	15.29	0.89ABC	14.29	0.87AB

[a] Averages followed by the same letter are not different among structural stages ($P \leq 0.1$), Tukey-type multiple comparison among ranks following Kruskal-Wallis test.

[b] DBH and overstory canopy cover (OCC) structural stage categories taken from Buttery and Gillam (1983).

TABLE 3. Continued, Extended.

	Ponderosa pine[b]		Aspen/birch[b]							
	Multi-storied		Shrub		Sapling/pole					
					<40% OCC		41–70% OCC		>70% OCC	
Bird species	$\bar{x} \pm$ SE		$\bar{x} \pm$ SE		$\bar{x} \pm$ SE		$\bar{x} \pm$ SE		$\bar{x} \pm$ SE	
Downy Woodpecker	0.01	0.01A	0.01	0.01A	0.01	0.01A	0.07	0.04A	0.02	0.01A
Hairy Woodpecker	0.12	0.06A	0.06	0.04A	0.04	0.02A	0.08	0.03A	0.11	0.06A
Northern Flicker	0.01	0.01AC	0.05	0.02D	0.04	0.02BC	0.05	0.01BC	0.03	0.02AC
Black-capped Chickadee	0.58	0.10B	0.44	0.09A	0.41	0.08A	0.57	0.10B	0.48	0.08A
Mountain Bluebird	0.00	0.00A	0.10	0.04D	0.10	0.07BC	0.05	0.03BC	0.00	0.00A
Swainson's Thrush	0.18	0.06B	0.04	0.03AB	0.06	0.04AB	0.02	0.02AB	0.07	0.03B
American Robin	0.05	0.0A	0.08	0.04A	0.22	0.05CD	0.45	0.13D	0.17	0.07BC
Chipping Sparrow	0.11	0.04BC	0.34	0.06D	0.39	0.17CD	0.27	0.09CD	0.10	0.02AB
Dark-eyed Junco	0.41	0.10B	1.07	0.08E	0.79	0.17BCD	0.62	0.12BC	0.57	0.13BC
Brown-headed Cowbird	0.02	0.01A	0.09	0.04A	0.01	0.01A	0.01	0.01A	0.03	0.01A
Bird Species Richness	15.83	1.91BCD	18.43	1.13D	17.29	0.99CD	18.57	0.65D	18.00	1.28CD

TABLE 4. Average birds/count (± SE) ≤50 m of count points associated with ponderosa pine in the Black Hills, South Dakota, 1992–1993[a].

Bird species	Ponderosa pine[b] Sapling/pole <40% OCC $\bar{x}$	± SE	41–70% OCC $\bar{x}$	± SE	>70% OCC $\bar{x}$	± SE
Gray Jay	0.01	0.01A	0.03	0.02AB	0.04	0.02AB
White-breasted Nuthatch	0.06	0.03A	0.24	0.08C	0.16	0.04BC
Red-breasted Nuthatch	0.29	0.06AB	0.38	0.04BC	0.58	0.05DE
Brown Creeper	0.00	0.00A	0.00	0.00A	0.00	0.00A
Townsend's Solitaire	0.29	0.05CD	0.28	0.06CD	0.34	0.06D
Yellow-rumped Warbler	0.43	0.09A	0.72	0.05E	0.66	0.07CDE
Western Tanager	0.08	0.03AB	0.19	0.07C	0.06	0.02A

[a] Averages followed by the same letter are not different among structural stages ($P \leq 0.1$), Tukey-type multiple comparison among ranks following Kurskal-Wallis test.
[b] DBH and overstory cover (OCC) structural stage categories taken from Buttery and Gillam (1983).

ting of snags for firewood and because many drainages have roads in them, this important habitat component to Red-naped Sapsuckers is vulnerable.

Ponderosa pine birds.—Within the ponderosa pine vegetation type, there may have been a trend toward greater richness in vegetation structural stages in stands with low OCC ($P = 0.19$). Understory vegetation (Uresk and Severson 1989) and invertebrate biomass (Rumble and Anderson 1996) are inversely related to basal area and OCC in ponderosa pine. Thus, open pine stands would probably provide greater food resources for ground foraging birds. Many of the species contributing to the species richness in open pine are common generalist species in conifer forests. For these species, selective logging that opens the forest canopy will increase their populations. If logging removes the vertical structure, species richness will then decline (e.g., Bender et al. 1998) such as occurs in the southwest following clearcutting ponderosa pine (Szaro and Balda 1979a).

Mature and old multi-storied stands contain the highest value timber for harvesting. Intensive overstory harvest of these stands of ponderosa pine would, based on our data, reduce abundance of Gray Jays, Red-breasted Nuthatches, Brown Creepers, Swainson's Thrushes, and Western Tanagers in the Black Hills. These species selected mature and multi-storied ponderosa pine with moderate to high canopy cover. Red-breasted Nuthatches are associated with mature and old-growth conifer stands in Montana (Aney 1984), but are also associated with open canopy forests in the west (Hansen et al. 1995). In addition to their preference for dense and mature ponderosa pine, we found Red-breasted Nuthatches strongly associated with snag density in ponderosa pine and the % of bark on snags. These characteristics of snags in ponderosa pine stands were cor-

TABLE 4. Extended.

Ponderosa pine[b]							
Mature						Multi-storied	
<40% OCC		41–70% OCC		>70% OCC			
$\bar{x}$ ± SE		$\bar{x}$ ± SE		$\bar{x}$ ± SE		$\bar{x}$ ± SE	
0.07	0.03B	0.19	0.04C	0.19	0.06C	0.03	0.02AB
0.12	0.02B	0.19	0.03C	0.12	0.05AB	0.06	0.01A
0.23	0.05A	0.57	0.10DE	0.52	0.09CD	0.71	0.07E
0.02	0.02A	0.04	0.03A	0.04	0.03A	0.01	0.02A
0.21	0.04BC	0.23	0.05BC	0.17	0.04B	0.08	0.04A
0.48	0.06AB	0.68	0.12DE	0.62	0.11BCD	0.52	0.04ABC
0.16	0.03C	0.13	0.03BC	0.07	0.03A	0.44	0.07D

related both linearly (r = 0.44) and nonlinearly (r = 0.71). Thus, we were not able to determine which characteristic of snags was most important to Red-breasted Nuthatches. Although, Swainson's Thrushes also occurred in sapling-pole aspen/birch >70% OCC, their low abundance in these aspen stands suggests they were not preferred habitat. Habitat for Swainson's Thrushes includes moderate to high density managed, unlogged, or old-growth conifer forest (Brawn and Balda 1988, Tobalske et al. 1991, Hansen et al. 1995). Similar to the multi-storied stands in our study, deciduous trees or shrub >3-m tall occurred in these conifer forests with high abundance of Swainson's Thrushes (Brawn and Balda 1988, Tobalske et al. 1991).

Brown Creepers require dense and mature stands of ponderosa pine in the Black Hills. In the northern Black Hills, Brown Creepers occurred only in mature stands >70% OCC and old-growth stands of ponderosa pine (Dykstra et al., in press). These stands had high densities of ponderosa pine >38 cm DBH (unpubl. data, Rocky Mtn. Research Stn., Rapid City). Mature structural stages of ponderosa pine >40% OCC and large DBH multi-storied ponderosa pine are necessary to ensure habitat for Brown Creepers.

In the northern Black Hills, which are more mesic than our study area, Western Tanagers are common in ponderosa pine >40% OCC. Conifer stands with moderate tree densities had the greatest abundances of western tanagers in other western forests (Hansen et al. 1995). However, deciduous trees or tall shrubs also occurred in these moderate density conifer stands (Szaro and Balda 1986, Brawn and Balda 1988, Tobalske et al. 1991). The preference for multi-storied ponderosa pine by Western Tanagers in the central Black Hills may be partially explained by bur oak and aspen/birch beneath these stands.

Generalist birds.—Brown-headed Cowbirds were cosmopolitan in their association with vegetation structural stages. Although no statistical patterns were evident among structural stages, their abundance was positively

TABLE 5. Average birds/count (± SE)(≤50 m of count points associated with aspen/birch in the Black Hills, South Dakota, 1992–1993[a].

	Aspen/birch[b]							
	Shrub/seedling		Sapling pole					
			<40% OCC		41–70% OCC		>70% OCC	
Bird species	$\bar{x}$ ± SE		$\bar{x}$ ± SE		$\bar{x}$ ± SE		$\bar{x}$ ± SE	
Red-naped Sapsucker	0.08	0.02A	0.05	0.02A	0.24	0.11A	0.13	0.03A
Dusky Flycatcher	0.46	0.10A	0.38	0.09A	0.41	0.10A	0.34	0.10A
Warbling Vireo	0.76	0.10A	0.92	0.14A	0.82	0.11A	1.00	0.19A
Ovenbird	0.08	0.03A	0.08	0.04A	0.38	0.11B	0.69	0.18C
MacGillvray's Warbler	0.05	0.02B	0.12	0.03C	0.08	0.04AB	0.01	0.01A

[a] Averages followed by the same letter are not different among structural stages ($P \leq 0.1$), Tukey-type multiple comparison among ranks following Kruskal-Wallis test.

[b] DBH and overstory canopy cover (OCC) structural stage categories taken from Buttery and Gillam (1983).

correlated with species richness. If correlation is cause and effect, the 0–40% OCC in ponderosa pine and shrub-seedling structural stages of aspen/birch should benefit cowbirds. We found, as did others, that Dark-eyed Juncos (Szaro and Balda 1986, Tobalske et al. 1991), American Robins, and Chipping Sparrows (Ralph et al. 1991) also would benefit from logging that reduces, but maintains some forest canopy.

We found cavity-nesting species under different forest size and stand conditions than previously reported. We did not collect snag use data, but the average DBH of snags in our study was notably smaller than those used by cavity-nesters in other conifer forests (Zarnowitz and Manuwal 1985, Cunningham et al. 1980). Scott (1978) reported that cavity-nesting species in ponderosa pine forests prefer snags ≥15 cm DBH. Cavity-nesters were well represented in the bird community, comprising 30% of the breeding bird richness in our study. The density of snags >15 cm DBH reported here meet snag density recommendations (Mannan et al. 1980) from conifer forests elsewhere. Snag inventories are usually included during timber sales in the BHNF. However, snag abundance data should be stratified by vegetation structural stages to ensure adequate snag density in high OCC stands such as preferred by Red-breasted Nuthatches. Managers should retain the largest snags during timber harvest because they are preferred by birds, survive longer, and provide better winter thermal cover (Cunningham et al. 1980). However, snags <15 cm DBH are also important because they are used as feeding sites by cavity nesting species (Baker 1973).

Conclusions.—Harvesting of the forest will alter habitat for a suite of species. Managers concerned with maintaining regional bird diversity should start by maintaining within and between stand diversity of the forest. To provide habitats across the landscape, the habitat needs of birds must be addressed in management plans (Hansen et al. 1995) at the stand level first. Ensuring habitat for most song birds in the Black Hills can be adequately assessed at the stand level using the vegetation descriptions of forest types and structural stages currently used by the Black Hills National Forest. However, for some species, within stand forest characteristics such as snag size, snag density, snag condition, shrub density, and subdominant trees provide important habitat components and are not currently included in forest inventories. Densities of snags should be estimated and reported by vegetation structural stages in forest inventories. Forest inventories should include subdominant tree species that may be necessary for ovenbirds or western tanagers. With current GIS capabilities, these attributes can be associated with structural stage descriptions of stands. Barring collection of these data for stands, we reiterate the recommendations of McClelland and Frissell (1975) and Tobalske et al. (1991) to leave snags, non-merchantable timber, and deciduous trees within cutting units.

ACKNOWLEDGMENTS

Financial support for this research was provided by the Rocky Mountain Research Station (28-CR4-786), BHNF, and South Dakota State University. We thank T. Hayes, R. McCartney,

T. Pella, and K. Thorstenson for field assistance and R. M. King for statistical advice. Dr. M. Morrison, Dr. M. G. Raphael, and Dr. D. Runde, J. B. Parrish, Dr. R. C. Szaro, and one anonymous reviewer provided comments that greatly enhanced this manuscript.

LITERATURE CITED

ANEY, W. C. 1984. The effects of patch size on bird communities of remnant old-growth pine stands in Western Montana. M.S. thesis, Univ. Montana, Missoula, Montana.

BAKER, W. W. 1973. Longevity of lightning struck trees and notes on wildlife use. Tall Timbers Fire Ecology Conf. 13:497–504.

BENDER, D. J., T. A. CONTRERAS, AND L. FAHRIG. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79:517–529.

BLACK HILLS NATIONAL FOREST. 1996. Land and resource management plan. U.S. Dept. Agric., Black Hills National Forest, Custer, South Dakota.

BRAWN, J. D., AND R. P. BALDA. 1988. The influence of silvicultural activity on ponderosa pine bird communities in the southwestern United States. Pp. 3–21, *in* J. A. Jackson, ed. Bird conservation. Univ. Wisconsin Press, Madison, Wisconsin.

BULL, E. L., AND E. C. MESLOW. 1977. Habitat requirements of the pileated woodpecker in northeastern Oregon. J. For. 75:335–337.

BUTTERY, R. F., AND B. C. GILLAM. 1983. Ecosystem descriptions. Pp. 42–71, *in* R. L. Hoover and D. L. Wills, eds. Managing forested lands for wildlife. Colo. Div. Wildl. in coop. with U.S. Dept. Agric., For. Serv., Rocky Mtn. Reg., Denver, Colorado.

CUNNINGHAM, J. B., R. P. BALDA, AND W. S. GAUD. 1980. Selection and use of snags by secondary cavity-nesting birds of the ponderosa pine forest. U.S. Dept. Agric., For. Serv., Res. Pap. RM-222.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetation analysis. Northwest Sci. 33: 43–64.

DEGRAAF, R. M., V. E. SCOTT, R. H. HAMRE, L. ERNST AND S. H. ANDERSON. 1991. Forest and rangeland birds of the United States: natural history and habitat use. U.S. Dept. Agric., For. Serv., Agric. Handb. AH-688.

DICKSON, J. G., F. R. THOMPSON, III, R. N. CONNER, AND K. E. FRANZREB. 1995. Silviculture in central and southeastern oak-pine forests. Pp. 245–266, *in* T. E. Martin and D. M. Finch, eds. Ecology and management of neotropical migratory birds: a synthesis and review of critical issues. Oxford Univ. Press, New York, New York.

DYKSTRA, B. S., M. A. RUMBLE, AND L. D. FLAKE. *In press*. Effects of harvesting ponderosa pine on birds in the Black Hills of South Dakota and Wyoming. Biannual. North Amer. For. Ecology Workshop.

EVERITT, B. S. 1977. Cluster analysis. Pp. 63–83, *in* C. A. O'Muircheartaigh and C. Payne, eds. The analysis of survey data: exploring data structures. Vol. 1. John Wiley & Sons, New York, New York.

FINCH, D. M., AND R. T. REYNOLDS. 1987. Bird response to understory variation and conifer succession in aspen forests. Pp. 87–96, *in* J. Emmerick et al., eds. Proceedings of issues and technology in the management of impacted wildlife. Thorne Ecological Inst., Colorado Springs, Colorado.

FRANZREB, K. E., AND R. D. OHMART. 1978. The effects of timber harvesting on breeding birds in a mixed-coniferous forest. Condor 80:431–441.

GOTFRYD, A., AND R. I. C. HANSELL. 1985. The impact of observer bias on multivariate analysis of vegetation structure. Oikos 45:223–234.

GRIFFING, J. P. 1985. The spherical densiometer revisited. Southwest Habitater. Vol. 6, No. 2. U.S. Dept. Agric. For. Serv., Reg. 3, Albuquerque, New Mexico.

HANSEN, A. J., W. C. MCCOMB, R. VEGA, M. G. RAPHAEL, AND M. HUNTER. 1995. Bird habitat relationships in natural and managed forests in the west cascades of Oregon. Ecol. Appl. 5:555–569.

HEJL, S. J., R. L. HUTTO, C. R. PRESTON, AND D. M. FINCH. 1995. Effects of silvicultural treatments in the Rocky Mountains. Pp. 220–244, *in* T. E. Martin and D. M. Finch, eds. Ecology and management of neotropical migratory birds: a synthesis and review of critical issues. Oxford Univ. Press, New York, New York.

HOCHBERG, Y., AND A. C. TAMHANE. 1987. Multiple comparison procedures. John Wiley and Sons, New York, New York.

HOFFMAN, G. R., AND R. R. ALEXANDER. 1987. Forest vegetation of the Black Hills National Forest of South Dakota and Wyoming: a habitat type classification. U.S. Dept. Agric., For. Serv., Res. Pap. RM-276.

HOLTHAUSEN, R. 1984. Coordinated aspen-wildlife management. Pp. 35–37, *in* J. Capp and L. Gadt, eds. Proceedings of aspen symposium. U.S. Dept. Agric., For. Serv. Rocky Mtn. Reg., Colorado Springs, Colorado.

JAMES, F. C., AND N. O. WAMER. 1982. Relationships between temperate forest bird communities and vegetation structure. Ecology 63:159–171.

KNOPF, F. L., R. R. JOHNSON, T. RICH, F. B. SAMSON, AND R. C. SZARO. 1988. Conservation of riparian ecosystems in the United States. Wilson Bull. 100:272–284.

MACARTHUR, R. H., AND J. W. MACARTHUR. 1961. On bird species diversity. Ecology 42:594–598.

MANNAN, R. W., E. C. MESLOW, AND H. M. WIGHT. 1980. Use of snags by birds in douglas-fir forests, Western Oregon. J. Wild. Manage. 44:787–797.

MANUWAL, D. A., AND A. B. CAREY. 1991. Methods for measuring populations of small diurnal forest birds. U.S. Dept. Agric., For. Serv., Gen. Tech. Rep. PNW-278.

MCCLELLAND, B. R., AND S. S. FRISSELL. 1975. Identifying forest snags useful for hole-nesting birds. J. For. 73:414–417.

MEHL, M. S. 1992. Old-growth descriptions for the major forest cover types in the Rocky Mountain Region. Pp. 106–120, *in* M. R. Kaufman, W. H. Moir, and R. L. Bassett, technical coordinators. Old-growth forests in the Southwest and Rocky Mountain Regions, proceedings of a workshop. U.S. Dept., Agric. For. Serv., Gen. Tech. Rep. RM-213.

RALPH, C. J., P. W. C. PATON, AND C. A. TAYLOR. 1991. Habitat association patterns of breeding birds and small mammals in Douglas-fir / hardwood stands in northwestern California and southwestern Oregon. U.S. Dept. Agric., For. Serv., Gen. Tech. Rep. PNW-285.

———, G. R. GEUPEL, P. PYLE, T. E. MARTIN, AND D. F. DESANTE. 1993. Field methods for monitoring landbirds. U.S. Dept. Agric., For. Serv., Gen. Tech. Rep. PSW-GTR-144.

REYNOLDS, R. T., J. M. SCOTT, AND R. A. NUSSBAUM. 1980. A variable circular-plot method for estimating bird numbers. Condor 82:309–313.

ROBBINS, C. S., D. K. DAWSON, AND B. A. DOWELL. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildl. Monogr. 103.

ROBINSON, S. K., AND R. T. HOLMES. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. Auk 101:672–684.

RUMBLE, M. A., AND S. H. ANDERSON. 1996. Feeding ecology of Merriam's turkeys (*Meleagris gallopavo merriami*) in the Black Hills, South Dakota. Am. Mid. Nat. 136:157–171.

SCHIMPF, D. J., AND J. A. MACMAHON. 1985. Insect communities and faunas of a Rocky Mountain subalpine sere. Great Basin Nat. 45:37–60.

SCOTT, V. E. 1978. Characteristics of ponderosa pine snags used by cavity-nesting birds in Arizona. J. For. 76:26–28.

———, AND G. L. CROUCH. 1988. Breeding birds in uncut aspen and 6- to 10-year old clearcuts in Southwestern Colorado. U.S. Dept. Agric., For. Serv., Res. Note RM-485.

SPURR, S. H. 1952. Forest inventory. Ronald Press Co. New York, New York.

STURMAN, W. A. 1968. Description and analysis of breeding habits of the chickadees, *Parus atricapillus* and *P. rufescens*. Ecology 49:418–431.

SZARO, R. C., AND R. P. BALDA. 1979a. Effects of harvesting ponderosa pine on nongame bird populations. U.S. Dept. Agric., For. Serv., Res. Pap. RM-212.

———, AND ———. 1979b. Bird community dynamics in a ponderosa pine forest. Studies in Avian Biol. No. 3.

———, AND ———. 1986. Relationships among weather, habitat structure, and ponderosa pine forest birds. J. Wildl. Manage. 50:253–260.

TOBALSKE, B. W., R. C. SHEARER, AND R. L. HUTTO. 1991. Bird populations in logged and unlogged western larch / douglas-fir forest in northwestern Montana. U.S. Dept. Agric., For. Serv., Res. Pap. INT-442.

URESK, D. W., AND K. E. SEVERSON. 1989. Understory-overstory relationships in ponderosa pine forests, Black Hills, South Dakota. J. Range Manage. 42:203–208.

VERNER, J. 1988. Optimizing the duration of point counts for monitoring trends in bird populations. U.S. Dept. Agric., For. Serv., Res. Note PSW-395.
———, AND K. A. MILNE. 1989. Coping with sources of variability when monitoring population trends. Annals Zool. Fenn. 26:191–199.
———, AND L. V. RITTER. 1986. Hourly variation in morning point counts of birds. Auk 103: 117–124.
ZARNOWITZ, J. E., AND D. A. MANUWAL. 1985. The effects of forest management on cavity-nesting birds in northwestern Washington. J. Wildl. Manage. 49:255–263.

Received 22 Jul. 1998; accepted 23 Mar. 1999.