

WOODPECKER HABITAT USE IN THE FORESTS OF SOUTHEAST WYOMING

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Abstract.—Woodpeckers were studied in the Medicine Bow National Forest of southcentral Wyoming during 1991 and 1992 to identify habitats used for foraging and nesting. A key component of this study was to evaluate the snag-retention policy of the forest. Thirty of the 33 nests of woodpeckers were in aspen trees. Woodpeckers nested in aspen trees with an average dbh of 26.7 cm (range 18–45 cm). This diameter was larger than the mean dbh of available aspen, 11.8 cm, or snags, 9.0 cm. The majority of the aspen stands used for nesting were comprised of large trees (>20 cm dbh). Woodpeckers were observed foraging in all forest types, but spruce-fir forest was used for foraging more frequently than it occurred in the study sites. Snags were seldom used for nesting or foraging because they were often smaller than 18 cm dbh and in open clear cuts. Larger snags at the edge of clear cuts or in the forest would in all likelihood enhance woodpecker nesting and foraging sites.

UTILIZACIÓN DE HABITAT POR PARTE DE PÁJAROS CARPINTEROS EN EL SURESTE DE WYOMING

Sinopsis.—De 1991 a 1992 fueron estudiados pájaros carpinteros en el Bosque Nacional Medicine Bow localizado al sureste de Wyoming, para identificar los habitats utilizados por éstos para forrajear y anidar. Uno de los componentes claves de este estudio fue evaluar la política de retención de ganchos y tocones por parte de los manejadores. De los 33 nidos, 30 fueron encontrados en árboles de álamo. Los carpinteros utilizaron para anidar árboles de álamo con un DBH promedio de 26.7 cm (alcance 18–45 cm). Este diámetro resultó ser mayor que el DBH promedio de los árboles disponibles (11.8 cm) o de los tocones (9.0 cm). La mayoría de los rodales de álamo utilizados para anidar estaban constituidos por árboles grandes (>20 cm de DBH). Las aves forrajearon en todos los tipos de bosques estudiados. No obstante, el bosque de picea-abeto fue utilizado con mayor frecuencia. Los tocones y ramas casi nunca fueron utilizados para anidar o forrajear debido a que por lo general tenían un DBH menor a los 18 cm, y se encontraban en áreas cosechadas abiertas. Los tocones y ramas de mayor tamaño ya sea en los bordes de áreas en donde la vegetación fue totalmente removida, o en los bosques, deben mejorar los lugares de forrajeo y anidaje de los pájaros carpinteros.

Forest snags provide an important habitat component for many birds. Snag removal has been proven to reduce populations of cavity-nesting birds, including woodpeckers, in a variety of habitats. Scott (1979), in an Arizona ponderosa pine (*Pinus ponderosa*) forest, found cavity-nesting bird densities declined 52% on a timber-and-conifer-snag-harvested plot, whereas these densities increased 23% on an adjacent plot with timber harvest and snag retention. Beaver (1972) recorded a 77% decrease in densities of cavity-nesting birds, including woodpeckers, after snag removal in Sierra Nevada forests, whereas other bird species declined only 6%.

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Snags are important foraging habitat. Mannan et al. (1980) discovered that foraging activity by woodpeckers increased with stand age to 110 yr, and that foraging on snags increased as snag size increased. They found that large snags supported more insects and larvae, which was especially important after snowfall, when down and dead material no longer provided adequate forage.

Snags are also an important nesting substrate for woodpeckers. Once a snag becomes suitable, it remains useful for years and is used by several species (Bull 1983). Raphael and White (1984) found 96% of woodpeckers' nests in snags or dead portions of live trees, whereas only 7% of the available trees were snags. They discovered that nest trees had a larger dbh than other available trees. Similarly, Scott (1978) recorded almost all woodpecker nests in snags. Nests were significantly more abundant in larger dbh snags (≥ 38 cm) and these larger snags contained more cavities per snag.

Clearly, snag availability is a primary factor in maintaining woodpecker populations and diversity. Woodpeckers, in turn, benefit other species in the forest environment. Woodpecker holes are used by secondary cavity nesters, including birds, mammals and amphibians, for reproduction, roosting, shelter or hibernation. The abundance and distribution of some bird and mammal species are dependent on woodpecker holes (Short 1979).

There is limited information on species of woodpeckers, their population status, and habitat needs in the subalpine forest community typical of some Wyoming forests (Salt 1957, Scott et al. 1982, Smith 1980). We describe the relationship among timber harvest, snag retention and woodpeckers in the lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forest typical of the Medicine Bow National Forest in southeastern Wyoming. Within the forest are habitats created by timber harvest before a snag policy was adopted as well as habitat created by timber harvest after snag-policy adoption.

The goal of this study was to determine the effects of clearcutting and the snag-retention policy on habitat use by woodpeckers in the Medicine Bow National Forest. The objectives developed to complete this study were: (1) to identify and describe habitats available and habitats used by woodpeckers, (2) to describe the characteristics of specific sites used by woodpeckers, and (3) to determine if correlations exist among the forests' timber harvest and snag practices, retention, and foraging and nesting sites of woodpeckers.

METHODS

Study area.—The study sites were located in the Snowy Range of the Medicine Bow National Forest, 50–80 km west of Laramie, Wyoming. Eight study sites were selected for the 1991 field season and six study sites were selected for the 1992 field season (Fig. 1). Elevation of the study sites ranged from 2499 to 3139 m.

The Snowy Range is dominated by lodgepole pine with small stands of

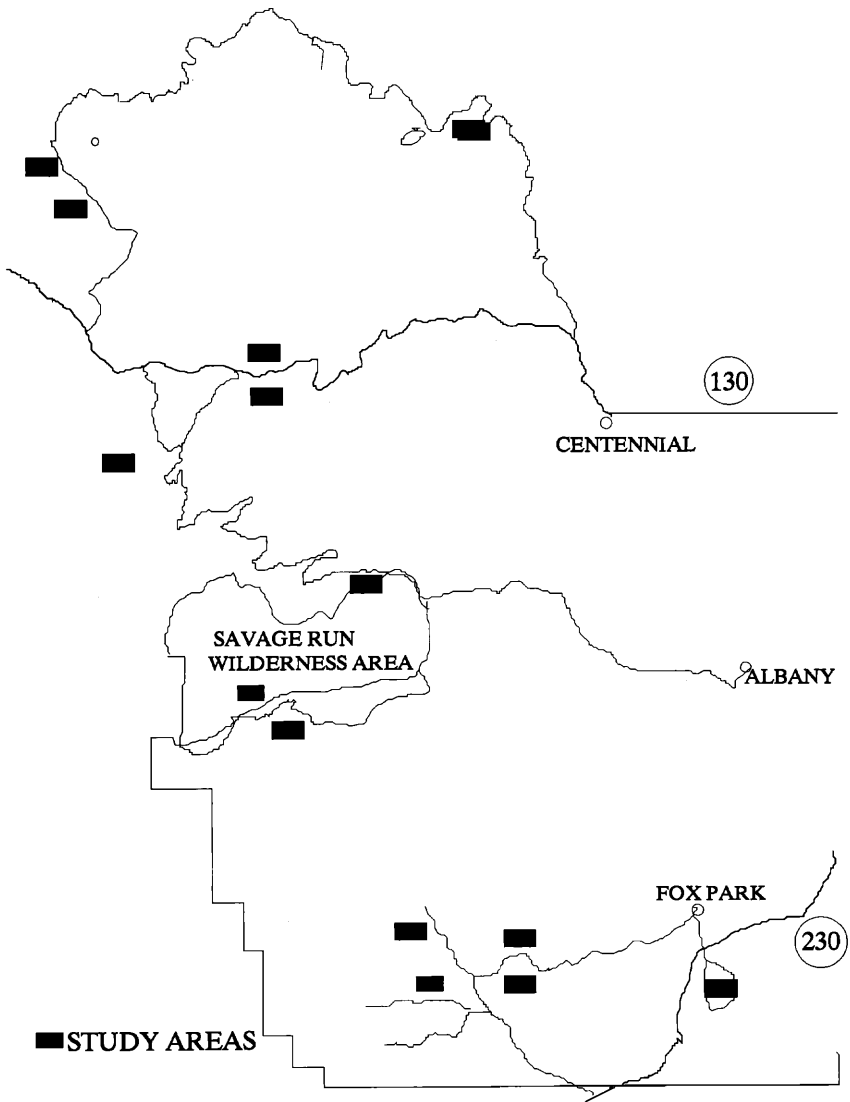


FIGURE 1. Location of the study sites in the Snowy Range from the 1991 and 1992 field seasons.

quaking aspen at lower and middle elevations (2500–2700 m). Lodgepole pine can persist as a stable community (Loope and Gruell 1973); however, Engelmann spruce and subalpine fir are considered the climax species in most areas (Daubenmire 1943).

Each study site consisted of approximately 2.54 km² of forest containing

clearcuts. When possible, study-site boundaries were established along natural borders such as ridges and streams. Otherwise, boundaries were established along clearcut edges or along lines established by compass bearings. The study sites contained few roads. No other human-made disturbances such as recreation areas or new road construction were present.

Clearcuts within study sites were approximately the same age, which ensured that there were few successional differences in the clearcuts that could affect bird use of the study sites. Non-s snag sites were study sites in which stands were clearcut without a snag-retention policy. As a result, no snags were retained in clearcuts. Combination sites contained both clearcuts with retained snags and clearcuts without retained snags.

Bird surveys.—A series of variable length transects was used to survey each study site. The orientations of the transects were chosen randomly from one of the four boundaries. Each transect began at that randomly chosen, study-site boundary (ridge, road, compass bearing) and proceeded across the study site to the opposite boundary. Transects were spaced at 200-m intervals perpendicular to the line of travel until the entire study site, including forested and clearcut areas, was surveyed. Transects within each study site were surveyed three times from May through August.

Woodpecker searches were conducted daily from 0630 to 1130 and from 1700 to 2030 hours. Three to five days were required to survey all the transects in a study site once. Observers stopped for 3 min at 300-m intervals to make stationary searches for woodpeckers. Upon locating a woodpecker or woodpecker nest, slope and aspect of the location were recorded, and distances to the nearest road, clearcut and water were measured. In addition, the snag class (Thomas et al. 1979), dbh, height, canopy height, hardness and species of tree used by the woodpecker were recorded. Tree height and minimum leaf-canopy height were determined with a clinometer. Tree hardness was judged as hard, firm or soft from a sample taken from the substrate with a Djos 250 increment bore.

Vegetation measurements.—General habitats of the study sites were determined with the aid of U.S. Forest Service stand-classification maps and U.S. Department of Agriculture National Computer Center data for the Medicine Bow National Forest. Characteristics recorded on the data sheet included forest type, stand size class, management activity and year of activity completion.

Vegetation and topographic characteristics were sampled at each location of woodpecker activity. Sampling techniques for these locations were adapted from James and Shugart (1970), with forest sampling additions by Noon (1981). Accordingly, site characteristics were defined within a 0.04-ha circular plot centered at the location of woodpecker activity.

We determined the average tree-canopy cover and ground cover by viewing canopy and ground vegetation through an ocular tube at 10 points each along both the north to south and east to west diameter lines of the circular plot. Percent of total ground cover for the dominant life forms (Noon 1981) was estimated from four 20 × 50 cm Daubenmire frames located randomly within the 0.04-ha plots. The dominant shrubs

were placed visually in categories from common to rare. The distribution of both shrub and ground cover was placed in categories from evenly dispersed clumps to small clumps. We estimated density of coniferous and deciduous shrub stems for the plot along the north to south and east to west diameter lines, as described by Noon (1981).

A density board was placed at each intersection of the circle perimeter and each cardinal direction to determine foliage volume. Log dispersion was determined within the plot by means of the point-quarter distance method. The species and dbh for every tree, defined as having a ≥ 3 dbh cm, within the circular plot was recorded.

Random sampling to determine the vegetation characteristics of each study site was performed using the same sampling techniques as those used for woodpecker activity sites (0.04-ha circular plots) at 348 points. Sample locations were determined using a stratified-random method along a baseline. Sample locations followed the transects established for woodpecker surveys. A random number determined the starting point of the sampling scheme along a boundary of the study site.

Data analysis.—Vegetation variables were measured at 348 random locations within 14 study sites. Pearson product-moment correlation coefficients were calculated for each pair of vegetation variables. One variable of any pair of highly correlated variables ($r \geq 0.7$, $P < 0.01$) was eliminated from further analysis.

Cluster analysis combined all random samples from all study sites to define general forest types across the study sites (BMDP Statistical Software, Inc. 1991). A direct discriminant analysis (SPSS Inc. 1990) was used to verify that these forest types actually defined distinct forest types.

Mann-Whitney U tests or Kruskal-Wallis tests were used in the comparison of means when data sets were non-parametric. Otherwise, t -tests and ANOVA were used. Significance was inferred at $P \leq 0.05$. Comparison of 95% confidence intervals was used to suggest differences between groups with very different sample sizes when one of the groups had ≤ 10 samples (SAS Institute, Inc. 1989).

We used stepwise discriminant function analysis (SPSS Inc. 1990), Wilkes method, with 32 continuous vegetation variables to describe nesting habitat, habitat not used for nesting and foraging habitat of woodpeckers. Stepwise discriminant function analysis determined the best discriminating function between groups. The Wilkes method was used to maximize the separation between two groups. A randomly generated subsample of 70 unused habitat locations was compared to the nesting habitat locations to attain more equal sample sizes. Three groups of 70 unused habitat locations were generated and each group was discriminated against the nesting habitat locations.

Stepwise discriminant function analysis was used to make several other comparisons. Fifty samples of unused aspen habitat and 33 samples of nesting habitat were analyzed in a stepwise discriminant function analysis to determine which vegetation characteristics identified use or non-use of an aspen stand. Fifty-six and 31 samples of foraging by Hairy Wood-

peckers (*Picoides villosus*) (American Ornithologists' Union 1983) and Three-toed Woodpeckers (*P. tridactylus*), respectively, were used to distinguish the habitat used for foraging by the two species.

RESULTS

Forest types.—Cluster analysis delineated seven habitat types. Lodgepole pine characteristics identified five of the forest types, reflecting the dominance of lodgepole pine in our study sites. The young lodgepole forest type consisted of saplings and seedlings commonly present after disturbances such as clearcutting. The dense lodgepole forest type was characterized by dense stands of 10–15 cm dbh lodgepole trees with similar size snags and no understory trees. The open lodgepole forest type was characterized by widely spaced, 10–20-cm dbh lodgepole trees with few snags and no understory trees. Multiple layers of tree canopy dominated by mature lodgepole trees identified the multiple story lodgepole forest type. The final lodgepole forest type, mature lodgepole, was dominated by lodgepole trees >20 cm dbh. The spruce/fir forest type contained multiple canopies of Engelmann spruce and subalpine fir trees. The aspen forest type was identified as stands of aspen trees with occasional spruce, fir or lodgepole trees.

Nesting.—We located nests of 13 Hairy Woodpeckers, 13 Yellow-bellied Sapsuckers (*Sphyrapicus varius*, red-naped subspecies), three Williamson's Sapsuckers (*Sphyrapicus thyroideus*), three Northern Flickers (*Colaptes auratus*), and one Downy Woodpecker (*Picoides pubescens*). Discriminant function analysis classified each of the 33 woodpecker nests into one of the seven forest types with 90% correct classification. Three nests were located in the mature lodgepole forest type, three in the spruce/fir forest type and 27 in the aspen forest type. Two nests were located in lodgepole pine snags, one in an Engelmann spruce snag and 30 in aspen trees.

Increment bore samples showed 25 of the 30 aspen trees had heart rot. Conks and other visible signs of heart rot were present on many of the nesting trees. None of these aspen trees were snags. A few did have dead but not broken tops. Often nests were in or just below these dead tops.

Forest types were not used for nesting in proportion to forest type availability ($\chi^2 = 3.76$, $P < 0.001$) (Fig. 2). Comparison of 95% confidence intervals showed that the aspen forest type was disproportionately used for nesting, whereas the mature lodgepole and spruce/fir forest types were used in proportion to availability.

The mean dbh of nest trees (32.3 cm, 25.5 cm, 25.3 cm, and 28.7 cm for Hairy Woodpeckers, Yellow-bellied Sapsuckers, Northern Flickers, and Williamson's Sapsuckers, respectively) were significantly different ($H = 8.76$, $P = 0.03$). Yellow-bellied Sapsuckers, Williamson's Sapsuckers, and Northern Flickers had a similar mean dbh of nest trees ($H = 2.19$, $P = 0.33$), but mean dbh of Hairy Woodpecker nest trees was different from that of this combined group, 26.0 cm ($U = 54.50$, $P = 0.01$). As a result, we divided the nest trees into two groups: those used by Hairy Woodpeckers and those used by the combined group.

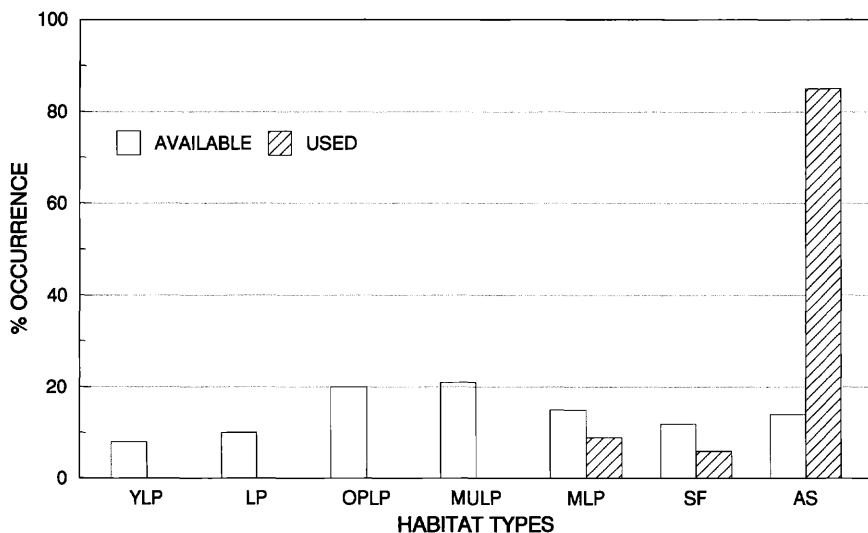


FIGURE 2. Nesting forest type use by all woodpeckers compared to forest type availability (YLP = Young Lodgepole Pine; LP = Dense Lodgepole Pine; OPLP = Open Lodgepole Pine; MULP = Multiple-story Lodgepole Pine; MLP = Mature Lodgepole Pine; SF = Spruce/Fir; AS = Aspen).

Hairy Woodpecker nest trees were larger than that of available aspen trees, 11.8 cm ($U = 772.0$, $P < 0.001$) and available snags, 9.0 cm ($U = 1114.0$, $P < 0.001$). The mean dbh of nest trees for the combined group was larger than that of available aspen trees ($U = 2507.0$, $P < 0.001$) and available snags ($U = 2860.0$, $P < 0.001$). Only 16% of the available aspen trees and 11% of the available snags were at least as large as the smallest tree used for nesting, an 18-cm-dbh aspen.

The number of nests in a study site was most strongly associated with the total basal area of aspen trees larger than 18 cm dbh in a study site ($r = 0.849$, $P < 0.01$). Number of aspen trees >18 cm dbh was chosen as a variable to reflect the availability of trees at least as large as the smallest tree (18 cm dbh) used for nesting by a downy woodpecker. The total basal area of aspen trees >18 cm dbh in a study site did not differ among snag, non-snag, and combination study sites ($H = 2.98$, $P = 0.22$).

Stepwise discriminant function analysis (P in = 0.05, P out = 0.051) separated habitat not used for nesting from nesting habitat, and accounted for 62%, 68%, and 69% of the variance within three groups of random samples, respectively. A single function was generated for each analysis (Table 1). Each of the functions significantly separated the random habitat group and the nesting habitat group ($P < 0.001$). The same variables contributed strongly to the single function in each analysis. The function depends on the variables constituting large aspen trees with abundant live vegetation in the ground cover or simply a mature aspen tree mead-

TABLE 1. Comparison of vegetation variables from discriminant function analysis of habitat not used for nesting and nesting habitat.

Variable	Structure coefficient			Group mean			
	Sample 1	Sample 2	Sample 3	Random habitat			Nesting habitat
				Sample 1	Sample 2	Sample 3	
% ground cover	0.601	0.732	0.611	34.6	34.1	37.2	73.6
Mean dbh of aspen	0.497	0.700	0.662	3.9	2.8	2.7	14.6
% ground covered with grass	0.475	0.586	0.532	10.2	9.6	11.4	39.2
Density of logs	0.377	0.520	0.322	65.0	67.4	72.8	89.5

ow. Respective group centroids for the function in each analysis were located at 2.08, 1.84 and 2.12 for nesting habitat, and -0.98 , -0.87 and -1.02 for unused habitat on a one dimensional scale. Discriminant function analysis was able to provide 91.2%, 92.2% and 92.2% correct classification, respectively, in each of the three analyses with a single function.

Foraging.—Fifty-six foraging locations of Hairy Woodpeckers, 31 of Three-toed Woodpeckers, nine of Yellow-bellied Sapsuckers, seven of Northern Flickers, and four of Williamson's Sapsuckers were identified within the study sites. Discriminant function analysis classified each of the samples into one of the seven forest types. Forest types were not used in proportion to availability by all woodpeckers combined ($\chi^2 = 29.8$, $P <$

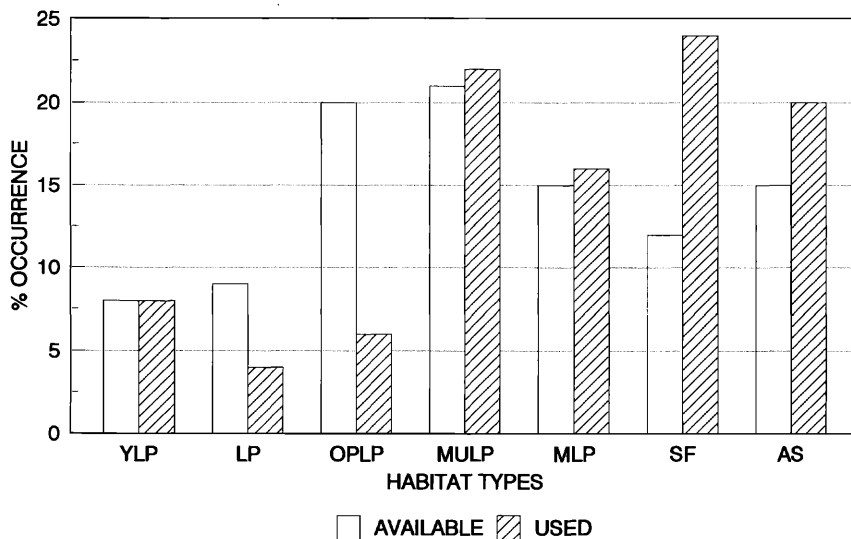


FIGURE 3. Foraging forest type use by all woodpeckers compared to forest type availability. (See Fig. 2 for abbreviations.)

0.001). The open lodgepole pine and dense lodgepole pine forest types were used less than available, the spruce/fir forest type was used more than available, and all other forest types were used in proportion to availability (Fig. 3). We saw one Black-backed Woodpecker (*Picoides arcticus*) but did not include it in our analysis.

Hairy Woodpeckers used the aspen forest type for foraging in greater proportion than available ($\chi^2 = 18.96$, $P < 0.05$). Three-toed Woodpeckers used the spruce/fir forest type in greater proportion than it was available ($\chi^2 = 35.85$, $P < 0.05$).

Other woodpecker species foraged among several forest types. Northern Flickers and Yellow-bellied Sapsuckers foraged in mature lodgepole pine, multiple-story lodgepole pine, spruce/fir, aspen, and young lodgepole pine forest types. Williamson's Sapsuckers foraged in multiple-story lodgepole pine, lodgepole pine, and aspen forest types.

Substrates foraged by all woodpeckers were larger on average (28.2 cm dbh) than were the available substrates (11.2 cm dbh; $t = 11.43$, $P < 0.001$). Lodgepole pine trees used for foraging were larger on average (26.2 cm dbh) than were lodgepole pines available within the study sites (13.8 cm dbh; $U = 2868$, $P < 0.001$). Snags used for foraging were larger on average (29.9 cm dbh) than were available snags (9.0 cm dbh; $U = 1262$, $P < 0.001$). Aspen, Engelmann spruce and subalpine fir used for foraging were larger than were available trees (95% confidence intervals). Foraged logs were no larger than available logs on the basis of 95% confidence intervals.

Fourteen woodpeckers including Hairy Woodpeckers, Three-toed Woodpeckers, Williamson's Sapsuckers, Yellow-bellied Sapsuckers and Northern Flickers were seen foraging in clearcuts. Nine observations of foraging were within snag-retained clearcuts and five within clearcuts without retained snags. Three observations of foraging within each clearcut type were on logs. The mean size of three lodgepole pines and three snags used for foraging in snag-retained clearcuts was 19 cm dbh. The two lodgepole pines used in clearcuts without retained snags were 29 and 32 cm dbh.

DISCUSSION

Nesting.—Woodpeckers have been reported to nest in a variety of habitats (Thomas et al. 1979). Ninety percent of woodpecker nests were in aspen stands with distinct edges adjacent to lodgepole pine, spruce and fir, or sagebrush. Other biologists also have found that woodpeckers commonly nest in aspen stands (Flack 1976, Winternitz and Cahn 1983). Our results showed that aspen stands used for nesting contained larger aspen trees, large snags and more ground cover than unused aspen stands (Winternitz 1980). The aspen stands that contained nest trees had an average of 90/ha in the overstory. The smallest aspen tree used for nesting was 18 cm dbh, with an average size of aspen nest trees of 26.7 cm dbh. Only 11% of the available aspen trees were at least this large. The large size of

aspen nesting trees is comparable to results from Crockett and Hadow (1975) and Winternitz and Cahn (1983).

Aspen trees do not become large enough (>18 cm dbh) for woodpecker nesting until they are approximately 100 yr old (Winternitz and Cahn 1983). Most nests were in live, intact aspen trees with heartrot. Broken tops allow *Fomes* sp. to invade a tree and cause decay that facilitates woodpecker nesting (Conner et al. 1976), especially in conifers (McClelland and Frissell 1975). Scott et al. (1980) suggested, however, that the thin bark of aspen needed only a few scratches for infection to occur and, therefore, broken tops were not necessary for infection.

Large aspen trees with heartrot also were used as nest sites in the spruce/fir forest type. Much of the spruce/fir forest type contained a few aspen trees >18 cm dbh because aspen is often succeeded by spruce and fir. Two nests were found in 25 and 31 cm dbh aspen trees with heartrot in the spruce/fir forest type.

Snags within the forest seldom were used for nesting. Few snags existed in areas containing even-aged stands of mature lodgepole pine, which contained many large trees of the size suitable for nesting. Most snags available in the forest were <18 cm dbh, the size of the smallest tree used for nesting. Some lodgepole stands were composed of a few large trees, which were being replaced by stunted seedlings (Whipple and Dix 1979). Thus, there are not many large trees that could become large snags.

Nesting in the study sites corresponded to characteristics of aspen stands, regardless of the snag-retention policy within the study site. The strongest relationship showed that the number of nests on a study site increased as the amount of mature aspen on the site increased. Similar results were found by Flack (1976). The extent of mature aspen stands may be a limiting factor of woodpecker nesting in the Snowy Range.

Foraging.—The variety of forest types used for foraging should be expected (Conner and Crawford 1974, Knight 1958, Mannan et al 1980, Shook and Baldwin 1970, Thomas et al. 1979). Woodpeckers are opportunistic foragers that eat berries, fruits and seeds, as well as insects (Short 1982). In addition, woodpeckers forage on a variety of substrates including live trees, snags, logs and stumps. All of these substrates can be found in each forest type. We commonly observed foraging on lodgepole trees. This observation probably was related to the high lodgepole pine frequency in the forest and not foraging substrate. Trees used for foraging were larger than average, which could improve foraging efficiency as larger trees and snags contain higher concentrations of insects (Parker and Stevens 1979).

We saw woodpeckers foraging on 48 snags in our study sites, suggesting snags are an important component of woodpecker habitat. Snags used for foraging were found in each of the forest types. Snags retained within clearcuts were used for foraging, as were logs and stumps. It is known that snags provide necessary foraging sites in winter when snow cover conceals ground foraging sites (Thomas et al. 1979).

Snags in clearcuts provide foraging sites where slash has been burned

or in lodgepole pine stands, which characteristically have small amounts of dead timber. Also, in clearcuts, snags provide foraging sites for Hairy Woodpeckers and Three-toed Woodpeckers, which do not commonly glean insects from logs and slash. Other species of birds also use the snags for foraging.

The results of our study suggest that availability of snags was not an important factor for woodpecker nesting. Only three snags were used for nesting and these were not retained within clearcuts. Retained snags may not have been excavated because they were in exposed sites, however. Snags in the middle of clearcuts do not have the protection from wind, heat and precipitation that is provided by a group of live trees. The retained snags were often smaller than the minimum size (>18 cm dbh) used for nesting. Snags retained on the edge of the forest or within the forest would, in all likelihood, increase nesting and foraging sites for woodpeckers if the snags were >18 cm dbh.

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LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. 6th ed. American Ornithologists Union, Washington, D.C. 377 pp.
- BEAVER, D. L. 1972. Avian species diversity and habitat use in forests on the Sierra Nevada, California. Ph.D. thesis. Univ. California, Berkeley, California. 206 pp.
- BMDP STATISTICAL SOFTWARE, INC. 1991. SOLO Statistical System. Los Angeles, California. 619 pp.
- BULL, E. L. 1983. Longevity of snags and their use by woodpeckers. Pp. 64-67, *in* J. W. Davis, G. A. Goodwin, and R. A. Ockenfels, eds. Snag habitat management: Proc. Symposium. USDA Forest Service Gen. Tech. Rep. RM-99. Fort Collins, Colorado.
- CONNER, R. N., AND H. S. CRAWFORD. 1974. Woodpecker foraging in Appalachian clearcuts. *J. For.* 72:564-566.
- , O. K. MILLER, AND C. S. ADKISSON. 1976. Woodpecker dependence on trees infected by fungal heart rots. *Wilson Bull.* 88:575-581.
- CROCKETT, A. B., AND H. H. HADOW. 1975. Nest site selection by Williamson and Red-naped Sapsuckers. *Condor* 77:365-368.
- DAUBENMIRE, R. F. 1943. Vegetation zonation in the Rocky Mountains. *Bot. Rev.* 9:326-387.
- FLACK, J. A. D. 1976. Bird populations of aspen forests in western North America. *Ornithol. Monogr.* No. 19. 97 pp.
- JAMES, F. C., AND H. H. SHUGART. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727-736.
- KNIGHT, F. B. 1958. The effects of woodpeckers on populations of the Engelmann spruce beetle. *J. Econ. Ent.* 51:603-607.
- LOOPE, L. L., AND G. E. GRUELL. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. *Quat. Res.* 3:425-443.
- MANNAN, R. W., E. C. MESLOW, AND H. M. WIGHT. 1980. Use of snags by birds in Douglas fir forests, western Oregon. *J. Wildl. Manage.* 44:787-797.
- MCCLELLAND, B. R., AND S. S. FRISSELL. 1975. Identifying forest snags useful for hole-nesting birds. *J. For.* 73:414-417.
- NOON, B. R. 1981. Techniques for sampling avian habitats. Pp. 42-52, *in* D. E. Capen, ed. The use of multivariate statistics in studies of wildlife habitat: Proc. Workshop. USDA Forest Service Gen. Tech. Rep. RM-87. Fort Collins, Colorado.

- PARKER, D. L., AND R. E. STEVENS. 1979. Mountain pine beetle infestation characteristics in ponderosa pine, Kaibab Plateau, Arizona, 1975-77. USDA Forest Service Res. Note RM-367. 4 pp.
- RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildl. Monographs* 86:1-66.
- SALT, G. W. 1957. An analysis of the avifaunas in the Teton mountains and Jackson Hole, Wyoming. *Condor* 59:373-393.
- SAS INSTITUTE INC. 1988. SAS/STAT Users Guide, release 6.03 ed. SAS Institute Inc., Cary, North Carolina. 1029 pp.
- SCOTT, V. E. 1978. Characteristics of ponderosa pine snags used by cavity-nesting birds in Arizona. *J. For.* 76:26-28.
- . 1979. Bird response to snag removal in ponderosa pine. *J. For.* 77:26-28.
- , J. A. WHELAN, AND P. L. SVOBODA. 1980. Cavity-nesting birds and forest management. Pp. 311-324, in R. M. DeGraaf, ed. *Management of western forests and grasslands for nongame birds: Proc. Workshop. USDA Forest Service Gen. Tech. Rep. INT-86.* 535 pp.
- , G. L. CROUCH, AND J. A. WHELAN. 1982. Responses of birds and small mammals to clearcutting in a subalpine forest in central Colorado. USDA Forest Service Res. Note RM-422. Fort Collins, Colorado. 6 pp.
- SHOOK, R. S., AND P. H. BALDWIN. 1970. Woodpecker predation on bark beetles in Engelmann spruce logs as related to stand diversity. *Can. Entomol.* 102:1345-1354.
- SHORT, L. L. 1979. Burdens of the picid hole-excavating habit. *Wilson Bull.* 91:16-28.
- . 1982. Woodpeckers of the World. Delaware Mus. Nat. Hist. Monogr. Ser. No. 4. Greenville, Delaware. 676 pp.
- SMITH, K. G. 1980. Nongame birds of the Rocky Mountain spruce-fir forests and their management. Pp. 258-279, in R. M. DeGraaf, ed. *Management of western forests and grasslands for nongame birds: Proc. Workshop. USDA Forest Service Gen. Tech. Rep. INT-86.* 535 pp.
- SPSS INC. 1990. SPSS-X User Guide, release 4.0.1 edition. SPSS Inc. Chicago, Illinois. 1072 pp.
- THOMAS, J. W., R. J. MILLER, H. BLACK, J. E. RODRICK, AND C. MASER. 1979. Guidelines for maintaining and enhancing wildlife habitat in forest management in the Blue Mountains of Oregon and Washington. *Trans. N. Am. Wildl. Nat. Resour. Conf.* 41:452-476.
- WHIPPLE, S. A., AND R. L. DIX. 1979. Age structure and successional dynamics of a Colorado subalpine forest. *Am. Midl. Nat.* 101:142-158.
- WINTERNITZ, B. L. 1980. Birds in aspen. Pp. 247-257, in R. M. DeGraaf, ed. *Management of western forests and grasslands for nongame birds: Proc. Workshop. USDA Forest Service Gen. Tech. Rep. INT-86.* 535 pp.
- , AND H. CAHN. 1983. Nestholes in live and dead aspen. Pp. 102-106, in J. W. Davis, G. A. Goodwin, and R. A. Ockenfels, eds. *Snag Habitat Management: Proc. Symposium. USDA Forest Service Gen. Tech. Rep. RM-99.* Fort Collins, Colorado.

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