United States
Department of
Agriculture

Forest Service

Pacific Northwest
Research Station

Research Note
PNW-444 June
1986

Resource Partitioning Among Woodpeckers in Northeastern Oregon

Evelyn L. Bull, Steven R. Peterson, and Jack Ward Thomas

Abstract

Eight species of woodpeckers coexist in conifer forests in northeastern Oregon: northern flicker *(Colaptes auratus);* yellow-bellied *(Sphyrapicus varius)* and Williamson's *(S. thyroideus)* sapsuckers; and pileated *(Dryocopus pileatus),* hairy *(Picoides villosus),* white-headed (P. *albolarvatus),* three-toed (P. *tridactylus),* and black-backed (P. *arcticus)* woodpeckers. Tree diameter was the most important factor considered in selection of nest trees by northern flickers, Williamson's sapsuckers, and pileated and hairy woodpeckers. These species partitioned the nest habitat by occupying different forest stands or conditions of nest trees. Pileated woodpeckers occurred in grand fir *(Abies grandis* (Dougl. ex D. Don) Lindl.) stands and nested in snags dead 10 or more years. The same stands were used by Williamson's sapsuckers which nested in live or recently dead trees. Northern flickers and hairy woodpeckers nested in ponderosa pine *(Pinus ponderosa* Doug, ex Laws.) forests but flickers used larger snags.

Foraging habitat and strategies differed. Only the pileated woodpecker excavated extensively in dead wood—particularly in downed wood and in grand fir forests. Northern flickers fed on the ground in open forests or grasslands. Live trees were used by Williamson's sapsuckers and white-headed woodpeckers. Sapsuckers drilled sapwells in Douglas-fir *(Pseudotsuga menzeisii* (Mirb.) Franco) and the white-headed woodpecker gleaned on ponderosa pine trunks and ate seeds. The remaining three species foraged by scaling, but the three-toed woodpecker fed exclusively in lodgepole pine *(Pinus contorta* Dougl. ex Loud.) stands. The hairy and black-backed woodpeckers scaled on similar trees in ponderosa pine stands. Hairy woodpeckers occasionally foraged on limbs and cones; black-backed woodpeckers used neither.

Theoretically, nesting should have occurred when maximum food was available; however, hairy and black-backed woodpeckers, species most similar in their feeding habitat and strategies, fledged their young the earliest and the latest, respectively. This temporal separation could reduce competition.

Keywords: Woodpeckers, birds, wildlife habitat.

EVELYN L. BULL is research wildlife biologist and JACK WARD THOMAS is chief research wildlife biologist, Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, Route 2, Box 2315, LaGrande, Oregon 97850. STEVEN R. PETERSON is Chief of Game Research, Alaska Department of Fish and Game, Juneau, Alaska 99802.

Introduction

Eight species of woodpeckers coexist in the coniferous forests of the Blue Mountains of northeastern Oregon. Because these woodpeckers are insectivorous and excavate nest cavities in dead trees, a potential for competition exists. Theoretically, two species cannot coexist over time using the limited resources in identical ways because one eventually replaces the other (Schoener 1974). Through coevolution, the environment can be partitioned so each species occupies a separate niche and competition is avoided (Darlington 1972). Partitioning occurs if the species use: (1) different resources; (2) the same resource in different places; or (3) the same resource at different times (MacArthur 1958). The objectives of the study were to compare nesting habitat, foraging, and breeding phenology among eight woodpecker species.

Study Area

The study was conducted in the 11,400-ha Starkey Experimental Forest, Wallowa-Whitman National Forest, an area representative of the central Blue Mountains. Located 35 km southwest of La Grande, Oregon, Starkey Experimental Forest is characterized by undulating uplands dissected by moderately to steeply walled drainages and elevations of 1070-1525 m. Annual precipitation averages 50 cm, of which nearly half is snow. Snow is on the ground from November through March.

Strickler (1966) describes the soils and vegetation. Soils originated from basalt and pumicite. Vegetation is closely associated with soil type and depth, and habitats have developed in a mosaic. Three habitats—open forest, dense forest, and grassland—are described by Edgerton and Smith (1971). Burr's (1960) classification was used to identify forest types at Starkey as: (1) open ponderosa pine *(Pinus ponderosa* Dougl. ex Laws.), (2) ponderosa pine-Douglas-fir *(Pseudotsuga menzeisii* (Mirb.) Franco), (3) Douglas-fir-grand fir *(Abies grandis* (Dougl. ex D. Don) Lindl.)-ponderosa pine, and (4) grand fir-Douglas-fir-western larch *(Larix occidentalis* Nutt.).

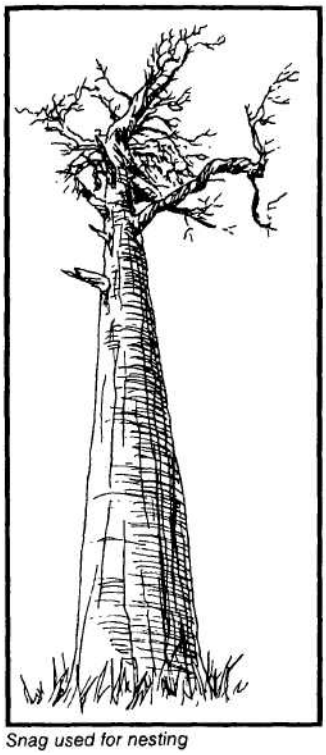
Fire suppression and selective timber harvesting in the 1930's resulted in stand structure unlike that of even-aged stands. Multilayered canopies with some much larger trees characterize most stands. As these large trees die or are cut, favorable conditions allow new tree establishment. Over time, this has created multilayered stands with numerous patches of young, even-aged trees and a few large, overmature trees.

In the 1970's an outbreak of mountain pine beetle *{Dendroctonus ponderosae)* occurred that infested over 200,000 ha in the Blue Mountains (Crookston and others 1977). The outbreak peaked in 1977 in the Starkey Experimental Forest killing thousands of lodgepole and ponderosa pines. These dead trees were present throughout the study.

Methods

Nesting

We searched for nests of eight woodpecker species: northern flicker *(Colaptes auratus);* yellow-bellied *(Sphyrapicus varius)* and Williamson's (S. *thyroideus)* sapsuckers; and pileated *(Dryocopus pileatus),* hairy *(Picoides villosus),* white-headed (P. *albolarvatus),* three-toed (P. *tridactylus),* and black-backed (P. *arcticus)* woodpeckers between 15 April and 15 July 1976,1977, and 1978 by hiking or riding horseback along routes of travel some 0.5 km apart. Travel was in proportion to the area occupied by each forest type. Nests containing an incubating adult or nestlings were considered active. Characteristics of the nest tree and habitat in 0.1-ha plots surrounding the nest were recorded. Nest tree characteristics included; nest height; exposure; amount and direction of tree lean; species; condition (live or dead); diameter at breast height (d.b.h.); height; and percent of the branches, bark, needles, and top remaining. Habitat characteristics included; density of the live stems, dead trees, and stumps; basal ar0a;percent of canopy closure and number of canopy layers, and heights; ground cover height, type, and coverage,; slope gradient and aspect; distance to$_t$ a clearing and to water: average size. and percent of cover $_i$of dead and downed material {logs}'forest type; and landform (slope ridge or draw)



Snag used for nesting

In June and July 1978 we checked nests each week for eggs, nestlings, fledged young, or nest failures. We considered young to be fledged if the cavity was vacant and the nestlings had been within a week of fledging age at the last observation.

To characterize the habitat available to woodpeckers, we sampled forest areas along 48 transects, each 805 m long and containing 10 sample points at 70-m intervals. Transects were located using an 805-m grid placed on a map of the study area. Starting points were selected from a random numbers table, and cardinal directions assigned systematically for each transect. At each sample point we recorded habitat characteristics described earlier for nest tree location in a 0.1-ha plot. The same characteristics measured at nest trees were measured at sample points.

Chi-square analysis(P ^0.05) was used to compare nesting habitat characteristics to the general forest condition. We made comparisons only for those woodpecker species for which 10 or more nests were located in dead trees.

A stepwise discriminant function analysis was used (Klecka 1975) to determine habitat characteristics that best discriminated between use and nonuse for nesting by four species. This analysis was used only for a species with at least 50 nests in dead trees. Only woodpecker nests located prior to 1979 were used in the analysis. For three of these four woodpecker species, less than 8 percent of the nests were in live trees. Therefore we limited our analysis to nests in dead trees. Characteristics that emerged from the analysis with significant F-values (P^0.01) were considered good discriminators. This same analysis was used by Conner and Adkisson (1976) to distinguish nesting habitat among woodpecker species.

Foraging

We observed woodpecker feeding activities on eight 50-ha plots once each month from September 1976 to September 1977. Each 3-hour observation period took place within 6 hours of sunrise in order to include periods of intense feeding activity. Individual woodpeckers were observed for a maximum of 15 minutes to prevent sampling bias (Williams 1975). A new feeding site was recorded each time a woodpecker under observation moved between trees or more than 1 m on the same tree. Foraging behavior and habitat characteristics were recorded at each feeding site along a 2000-m circular route through the plot. Recorded characteristics included: forest type; landform (ridge, slope, or draw); tree species; tree condition (alive or dead), height of trees, length of logs; percent of bark, branches, and needles on tree; feeding location (trunk, branch, or ground); and height at which the bird was feeding. To obtain a sample of available habitat, we measured habitat characteristics using the point-center quarter method (Cottam and Curtis 1956) at 80 points (for trees and snags) and 40 points (for logs and stumps) spaced equidistance along the circular route.

Feeding activity was classified as: scaling—prying off layers of bark to get at insects in the superficial bark; excavation—digging into the wood; gleaning—searching over the trunk and limb surfaces; flycatching—pursuit of insects during flight; sapsucking—eating sap or cambium; ground foraging—feeding on the ground or digging in the soil for insects; and seed harvesting—extraction of seeds from cones (Jackman 1975).

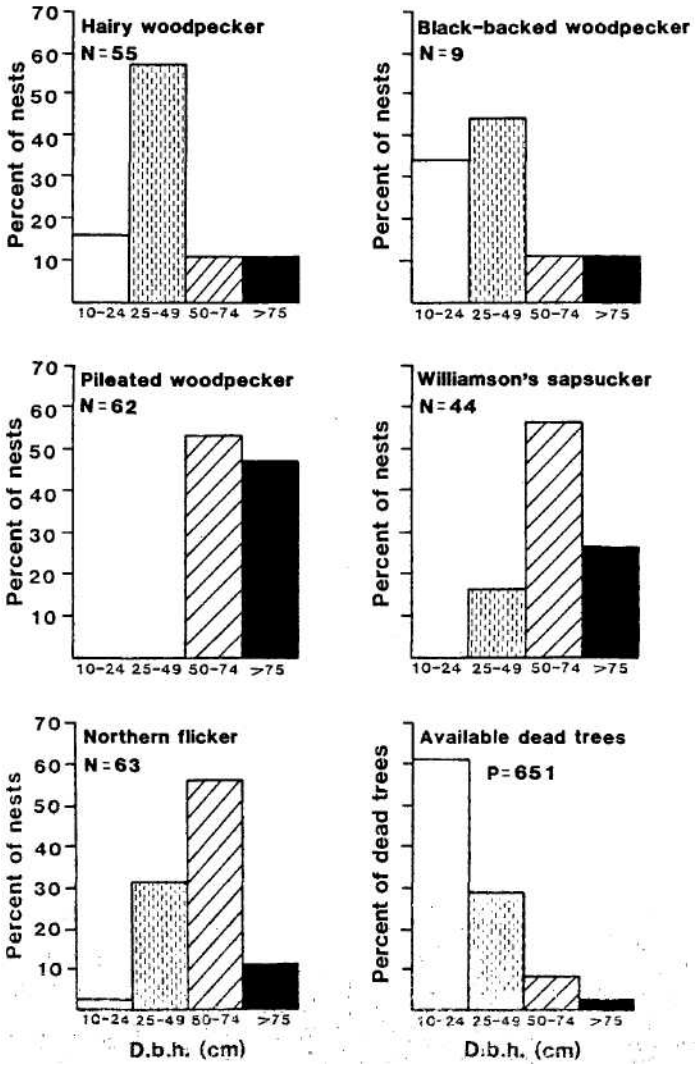
Discriminant function analysis was used to distinguish feeding habitat among seven woodpecker species, and to compare characteristics at feeding sites with the available habitat. Minimum sample size was 25; significant F-values were originally $P \leq 0.05$ but were reduced to $P \leq 0.01$ when nearly all the variables considered showed significance. Analyses were done by condition class (dead trees, live trees, or logs). Chi-square analysis was used to compare feeding habitat variables with available habitat ($P \leq 0.01$ and a minimum of 10 observations).

Results and Discussion

Nesting

Pileated woodpecker.—Pileated woodpeckers nested almost exclusively in dead ponderosa pine and western larch, although one nest was found in a live grand fir. They selected the largest dead trees available to nest in (fig. 1, table 1); 58 percent of the nest trees had broken tops. Less than 25 percent of the original limbs and bark remained in 76 percent and 58 percent of the nest trees, respectively, which suggested that the trees had been dead at least 10 years.

We tested characteristics of 63 nests in available dead trees and compared these with nests of other woodpeckers (table 1). The characteristics of nest trees were significantly different ($P \leq 0.01$) than random choice would indicate. Diameter at breast height and percent of bark, broken tops, and branches were the best discriminators ($P \leq 0.01$) between dead trees used and those not used for nesting.



Rgure.1.—Diameter at breast height (d.b.h.) of dead trees used for nesting by five woodpecker species and of a sample of available dead .trees. N is the number of nest trees and P is the number of dead trees.

Table 1—Frequency and mean (standard deviation) of measurements of nest tree characteristics for 5 woodpecker species

Characteristic	Pileated woodpecker	Hairy woodpecker	Northern flicker	Williamson's sapsucker	Black-backed woodpecker	Available snags
Tree species: 1/	* 2/	*	*	*		
Ponderosa pine	60	68	81	40	67	48
Lodgepole pine	0	17	3	0	27	24
Western larch	39	10	3	41	6	9
Douglas-fir	0	5	13	10		16
Grand fir	1	0	0	9	0	3
Diameter at breast height (cm)	76 (13.3)*	42 (21.6)*	56 (17.1)*	70 (26.4)*	37 (21.1)	27 (16.9)
Tree diameter at nest (cm)	57 (12.7)	26 (11.3)	46 (16.8)	43 (19.5)	30 (6.9)	--
Height (m)	28 (9.1)*	15 (9.8)*	15 (9.2)*	24 (10.1)*	19 (9.9)*	14 (6.8)
Hole height (m)	15 (5.6)	8 (6.0)	8 (6.2)	15 (7.1)	5 (6.2)	--
Percent bark	34 (33.9)*	84 (29.2)*	66 (39.7)*	87 (21.0)	97 (6.7)	91 (23.7)
Percent branches	25 (29.0)*	59 (35.5)*	34 (36.7)*	61 (35.6)*	85 (27.9)	68 (36.0)
Percent needles	4 (17.8)	10 (27.2)	10 (28.7)	42 (45.1)	43 (48.5)	6 (19.6)
Percent top broken	12 (16.2)*	20 (26.5)*	33 (29.5)*	14 (21.1)*	0.3 (1.3)	9 (22.4)
Lean	7 (7.0)*	6 (8.0)	9 (8.4)	6 (7.6)	6 (9.0)	5 (6.6)
Sample size	63	59	68	86	15	652

1/ Percent of nest trees by tree species; remaining characteristics are averages.

2/ Asterisks identify variables used in significantly different frequencies ($P \leq 0.01$) from available dead trees.

Table 2—Average (standard deviation) measurements at nest sites for 5 woodpecker species

Measurement	Pileated woodpecker	Hairy woodpecker	Northern flicker	Williamson's sapsucker	Black-backed woodpecker	Available habitat
Live stem density (number/0.1 ha)	38 (16.4)* 1/	13 (10.5)*	15 (12.3)	22 (15.0)*	17 (16.5)*	19 (12.8)
Dead stem density (number/0.1 ha)	7 (6.5)*	11 (11.5)*	5 (5.8)	6 (6.1)*	18 (18.9)*	5 (8.6)
Basal area (m^2/ha)	30 (15.6)*	18 (10.3)*	14 (8.7)*	19 (10.2)*	20 (11.9)*	45 (19.4)
Percent canopy	74 (22.4)	39 (26.1)	35 (23.5)	60 (26.2)	46 (25.5)	64 (26.8)
Lower canopy height (m)	14 (4.2)	11 (4.5)	11 (4.3)	13 (4.5)	10 (3.2)	10 (4.0)
Upper canopy height (m)	28 (5.3)*	22 (8.3)*	25 (7.0)	27 (6.3)*	22 (8.1)	24 (6.0)
Percent ground cover	46 (27.2)*	57 (25.0)*	59 (27.2)*	54 (28.2)*	58 (31.1)	36 (23.6)
Distance to water (m)	514 (429.1)*	638 (580.6)*	489 (473.0)*	330 (449.0)*	609 (417.2)	317 (207.3)
Distance to clearing (m)	38 (64.7)	11 (21.1)	12 (21.6)	20 (34.7)	9 (10.8)	26 (35.6)
Number of stumps (number/0.1 ha)	1 (2.2)*	3 (5.2)*	3 (3.8)*	3 (3.0)*	2 (2.7)*	8 (10.0)
Percent logs	13 (12.0)	9 (11.8)*	7 (5.3)*	10 (9.0)	6 (6.1)*	13 (11.3)
Size logs (cm)	24 (13.6)	24 (11.6)	33 (15.0)*	31 (14.9)*	23 (7.0)	21 (11.1)
Slope gradient	20 (11.3)	10 (10.5)*	14 (14.3)*	17 (14.6)	12 (10.1)	20 (15.6)
Sample size	63	59	68	86	15	367

1/ Asterisks identify variables used 1n significantly different frequencies ($P \leq 10.01$) from available habitat.

Many habitat characteristics in the 0.1 -ha plot surrounding a tree occurred in significantly different frequencies than if selected at random from available habitat (table 2). Five variables (stem density, upper canopy height, ground cover type, basal area, and stump density) best discriminated between nest sites and systematically sampled plots throughout the habitat. Eighty-three percent of the nests occurred in grand fir forest types (fig. 2), and 95 percent were in stands with at least two canopy levels. Two-thirds of the nest sites contained more than 75 percent canopy closure. Grass or forb vegetation predominated (92 percent) at nest sites. More dead trees and live trees over 30 cm d.b.h. (diameter at breast height) occurred at nest sites than at sample plots in grand fir types. Fewer than five stumps occurred in 95 percent of the nest habitats.

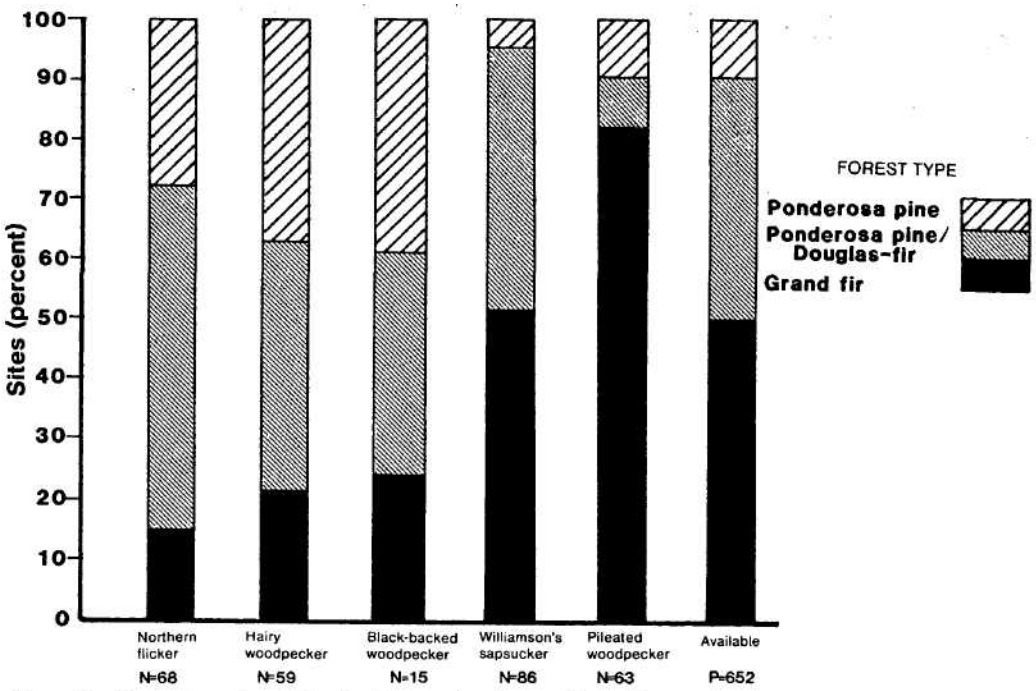


Figure 2.—Percentage of nest sites for five woodpecker species and of available habitat by forest type. N is the number of nest sites and P is the number of sample sites.

Hairy woodpecker.—Ninety-three percent of 59 hairy woodpecker nests were located in dead trees. Ponderosa pine made up the greatest percentage of nest trees, although all tree species except grand fir were used (table 1). D.b.h. and the percent of top broken off were the best discriminators between dead trees used and those not used. Raphael and White (1984) report similar findings. Snags 25 to 50 cm d.b.h. were preferred (fig. 1). Fifty-one percent of the nest trees had broken tops. The mean amount of bark and limbs remaining were 84 and 59 percent, respectively, which suggested that nest trees had been dead less than 5 years.

Characteristics of the habitat around nest trees were significantly different than those of available habitat (table 2). Basal area was the best discriminator between used and available habitat. Seventy-eight percent of the nests occurred in the ponderosa pine forest types (fig. 2). Ridges, low slope gradients, and southerly exposures were preferred. Hairy woodpeckers nested in relatively open stands with low basal areas (x = 17 m7ha), low stem densities (x = 13 per 0.1 ha), and open canopies (table 2). Densities of dead trees at nest sites were higher than densities at sampled plots in the ponderosa pine-associated forest types. About three-fourths of the nest sites contained more than five dead trees per 0.1 ha, less than five stumps per 0.1 ha, and very little dead and downed woody material. Although we observed hairy woodpeckers excavating nests at a later date than most other species (fig. 3), their young fledged the earliest (fig. 4). Forty-seven percent of the nests had young fledge during the week of *22* June.

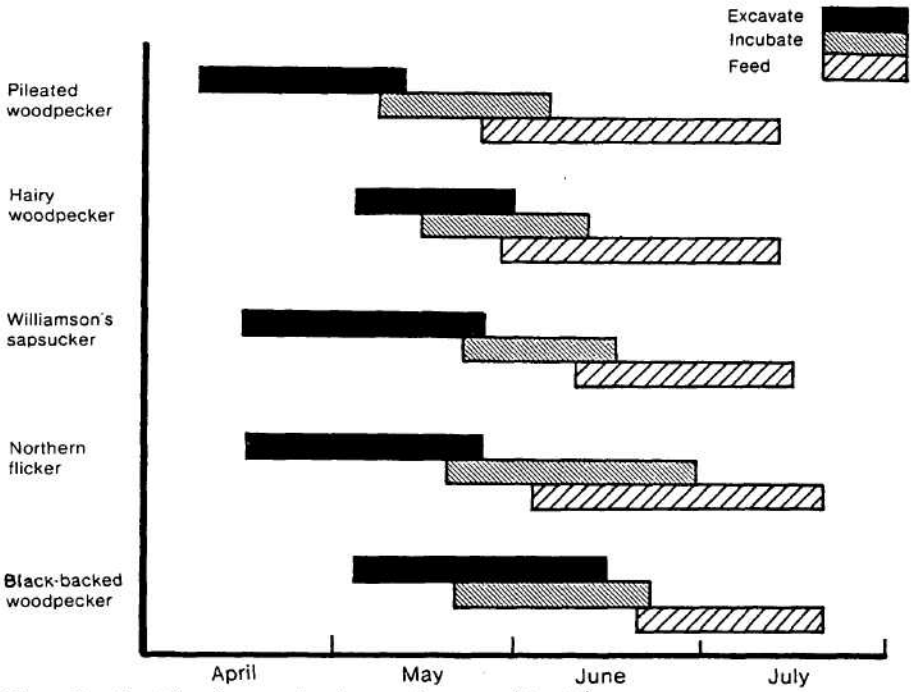


Figure 3.—The dates five woodpecker species were observed excavating, incubating, and feeding nestlings.

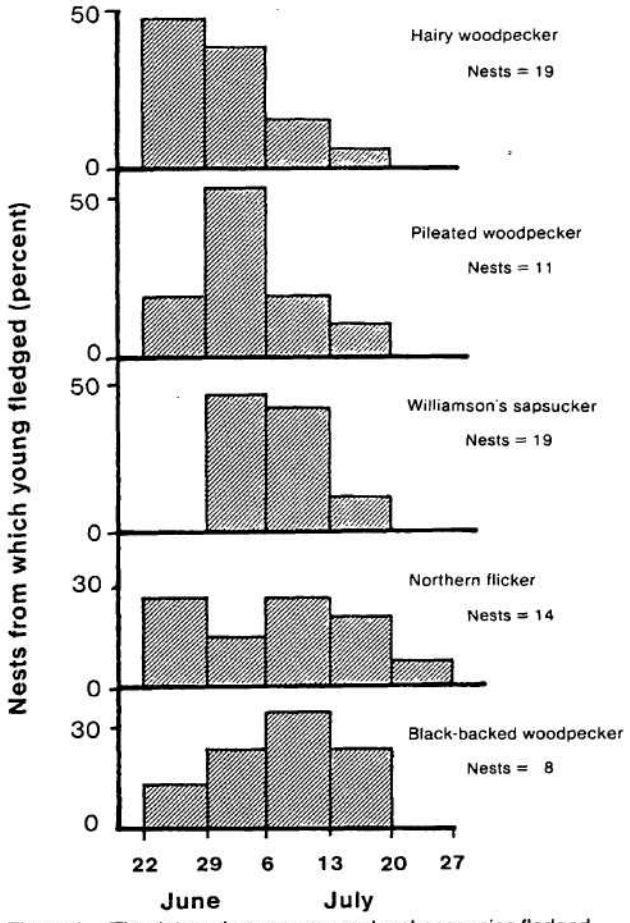


Figure 4.—The dates when young woodpecker species fledged.

Northern flicker

Northern flicker.—Ninety-five percent of 68 northern flicker nests occurred in dead trees. Ail the nest tree characteristics measured (except percent of needles) were significantly different from the characteristics of available dead trees (table 1). D.b.h. was the best discriminator between dead trees used and those not used.

Northern flickers frequently (79 percent) nested in ponderosa pine (table 1) and preferred snags greater than 50 cm d.b.h. (fig. 1). Seventy-one percent of the nest trees had broken tops, 72 percent had less than half their original limbs, and 68 percent had more than half the bark. Most nest trees had been dead more than 5 years.

Eighty-five percent of the nest trees were in ponderosa pine types (fig. 2). Ridgetops, slope gradients less than 10 percent, and southerly aspects were preferred. Basal areas was the best discriminator between used and unused habitat. Basal areas of less than 34 m^2/ha occurred at 67 of the 68 nest sites. Stem densities of less than 25 trees per hectare were selected. The low stem density and basal area influenced the high amount of herbaceous ground cover (59 percent) and low rate of canopy closure (35 percent). We believe ponderosa pine types provided open stands for nest sites adjacent to grasslands where the birds foraged.

Northern flickers had the greatest span in nesting and fledging dates of the woodpeckers (figs. 3 and 4).

Williamson's sapsucker.—Of 86 nests located for the Williamson's sapsucker, 51 percent occurred in dead trees and 49 percent in live trees. Western larch comprised the majority (62 percent) of the live trees with nests, although dead western larch, ponderosa pine, Douglas-fir, and grand fir were also used. All the measured characteristics of dead trees used for nesting, except percent of needles and amount of lean, were significantly different than those characteristics of available snags (table 1). D.b.h. was the best discriminator between dead trees used and dead trees available but unused.

Nest trees averaged 70 cm d.b.h., and 64 percent had broken tops. Most nest trees (73 percent) retained three-fourths of the original bark, and an average of 61 percent of the branches remained. Of the nests in dead trees, a d.b.h. greater than 50 cm was preferred (fig. 1). These conditions suggested that nest trees were alive or had been dead less than 3 years. Because the Williamson's sapsucker is a poor excavator (Spring 1965), it nests in live or recently dead trees with advanced decay in the heartwood (Erskine and McLaren 1972, Miller and others 1979, Shigo and Kilham 1968).

Although all forest types contained sapsuckers, 53 percent of the nests occurred in the grand fir types (fig. 2). Basal area was the best discriminator between used and unused habitat. This species preferred stands with less than 75 percent canopy closure, basal areas less than 34 m^2/ha, two or three canopy layers, and more than one dead tree per 0.1 ha. The surrounding habitat contained less than five stumps per 0.1 ha, shrub vegetation, and logs larger than 25 cm in diameter.

We suspect that most nests occurred in grand fir forest types because -these stands provide large, decayed, and deteriorating western larch and ponderosa pine suitable for nest sites. Live 'Douglas-fir trees were also abundant here and provided a source of sap. Williamson’s sapsuckers nested at a later date than some-of the woodpeckers (fig. 3) and fledged young primarily in July (fig. 4).

Black-backed woodpecker.—Sixty percent of the 15 black-backed woodpecker nests were in dead trees. Ponderosa pine, lodgepole pine, and western larch were used (table 1). Nests usually occurred in small-diameter (< 50-cm d.b.h.), tall (>15 m), recently dead (<5 years) trees. Ponderosa pine forest types contained 73 percent of the nest sites (fig. 2). Nests occurred in stands with a mean canopy closure of 46 percent and basal area of 20 m7ha. More than three-fourths of the nest sites contained less than five stumps per 0.1 ha, less than 10 percent log cover, and more than five dead trees per 0.1 ha.

The preference for small-diameter (<50 cm d.b.h.) (fig. 1) trees was unusual as most woodpeckers nested in larger dead trees (Mannan 1977, McClelland and others 1979, Raphael and White 1978, Scott 1978). Short (1974) states that the smaller woodpeckers reduce competition for their nests if they drill their cavities in trees too narrow for expansion by larger woodpeckers. McClelland and others (1979) think three-toed woodpeckers avoid drilling through the thick sapwood of large trees to get to the decayed heartwood. In most conifers, sapwood decays more rapidly than heartwood and should be more suitable for excavation. We believe the black-backed woodpecker prefers dead pines because pines have a thicker layer of sapwood than do other tree species of the same size. We also believe trees less than 50 cm d.b.h. are preferred because they contain a higher percentage of sapwood than do trees greater than 50 cm d.b.h., and this species often excavates nests in sapwood.

Black-backed woodpeckers nested and fledged young at a later date than the other four species. Young fledged from nests after 6 July at 63 percent of the nests.

Resource partitioning.—Although yellow-bellied sapsuckers and white-headed and three-toed woodpeckers nested in the study area, less than 10 nests were located and they are not discussed. Black-backed woodpeckers were not included in the discriminant analysis because we located too few nests.

Pileated and hairy woodpeckers, northern flickers, and Williamson's sapsuckers nested in dead trees averaging more than 40 cm d.b.h. and selected dead broken-topped ponderosa pines for their nests. There were, however, variations in tree condition, forest type, and other characteristics, which separated the habitat of each species.

The analysis correctly classified 67 percent of the nests in the appropriate species category. Forest type was the variable that best discriminated among nest sites of the four species. Use of forest type separated pileated woodpeckers and Williamson's sapsuckers (both used the grand fir types) from northern flickers and hairy woodpeckers (both used the open ponderosa pine types). Bark condition was the second-best discriminating variable and, in combination with forest type, distinguished among nest sites of all species. Pileated woodpeckers nested in dead trees with less bark than those used by Williamson's sapsuckers. Northern flickers nested in dead trees that had less bark than trees used by hairy woodpeckers. Including percent of needles, stem density, and d.b.h. also resulted in significant F-values.

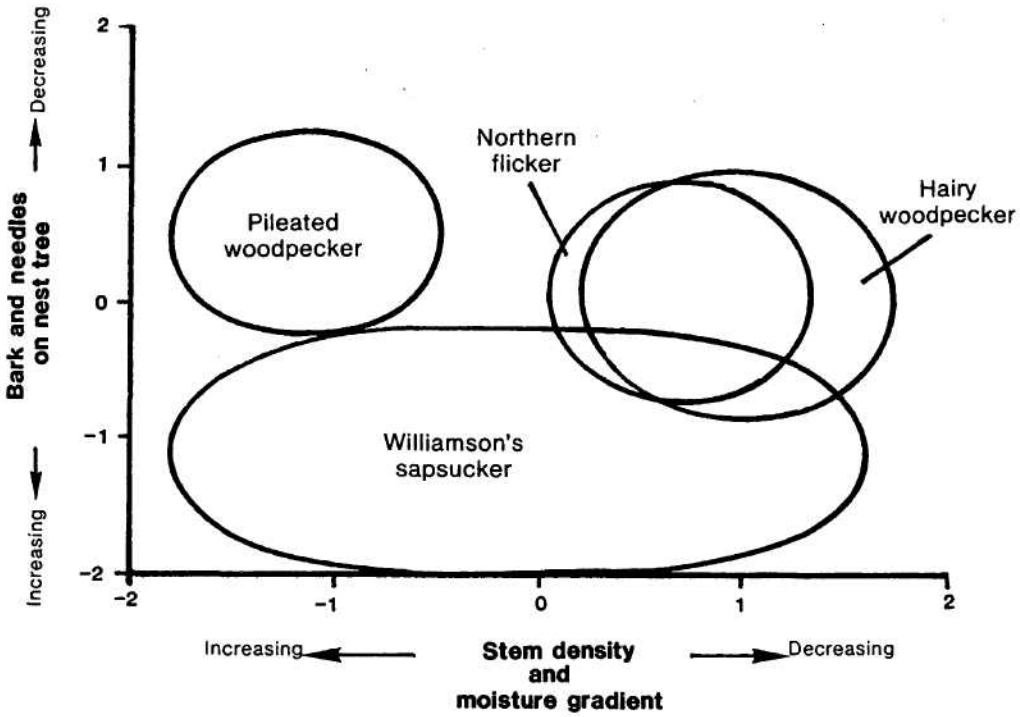


Figure 5.—Overlap in characteristics of the nest snag and habitat surrounding nests for four woodpecker species. The ellipses are described by the mean ± one standard deviation of the first (X-axis) and second (Y-axis) discriminant function scores of each species.

Each species' respective nesting niche was calculated with the mean and one standard deviation of the first and second discriminant function scores (fig. 5). Pileated woodpeckers nested in trees with less bark and needles and the area around nests had a higher moisture gradient and stem density than the trees and areas used by other woodpeckers. The moisture gradient was lowest in the ponderosa pine forest types, moderate in the Douglas-fir forest types, and highest in the grand fir forest types. Williamson's sapsuckers nested in stands with a wide range of moisture gradients and stem densities but nested in live or recently dead trees that retained a large portion of bark and needles. Nest trees of pileated woodpeckers and Williamson's sapsuckers could not be distinguished 6 to 7 percent of the time.

The greatest overlap in niche existed between hairy woodpeckers and northern flickers. Both nested in trees that retained little bark and needles and in stands with a lower moisture gradient (ponderosa pine forest type) and lower stem density than stands used by other species. Hairy woodpeckers had a larger niche and used slightly drier forest types than those used by northern flickers. Nest trees of these two species could not be distinguished 13 to 29 percent of the time. We believe these four species partitioned the habitat by using different forest types or by nesting in different types of trees in the same forest types.

Foraging

Pileated woodpecker.—During this study, pileated woodpeckers fed by excavating two-thirds of the time and by scaling the remainder of; the time (fig. 6). This species foraged in logs live trees, and dead trees 36,35, and 29 percent of the time, respectively (fig. 7): The grand fir forest types were preferred and contained 64 percent of the feeding sites.

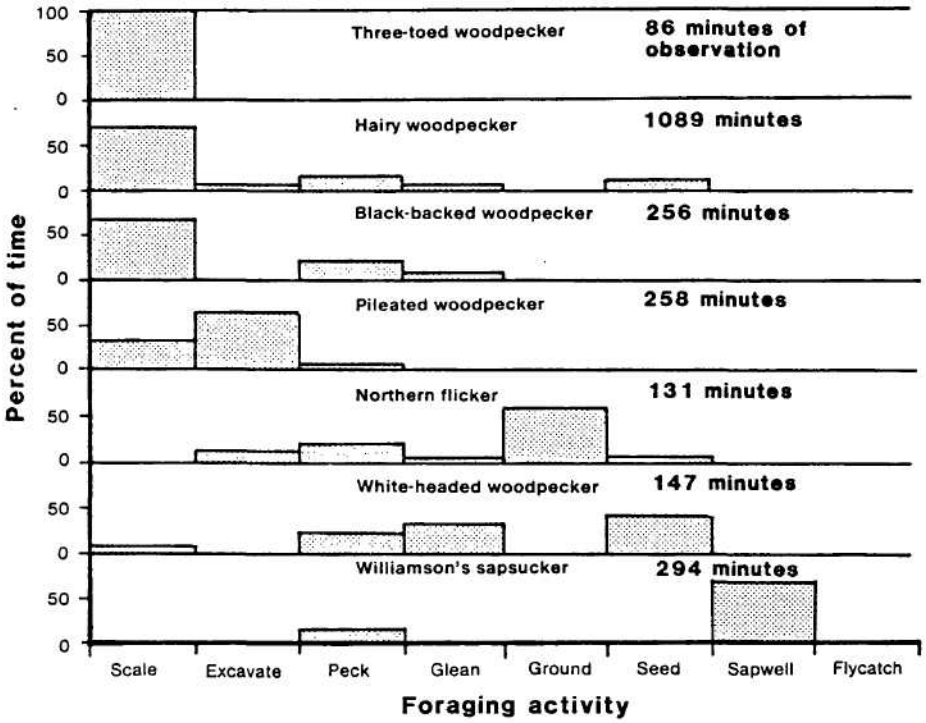


Figure 6.—Percentage of time seven woodpecker species engaged in foraging activities. Observations on any bird were limited to 15 minutes.

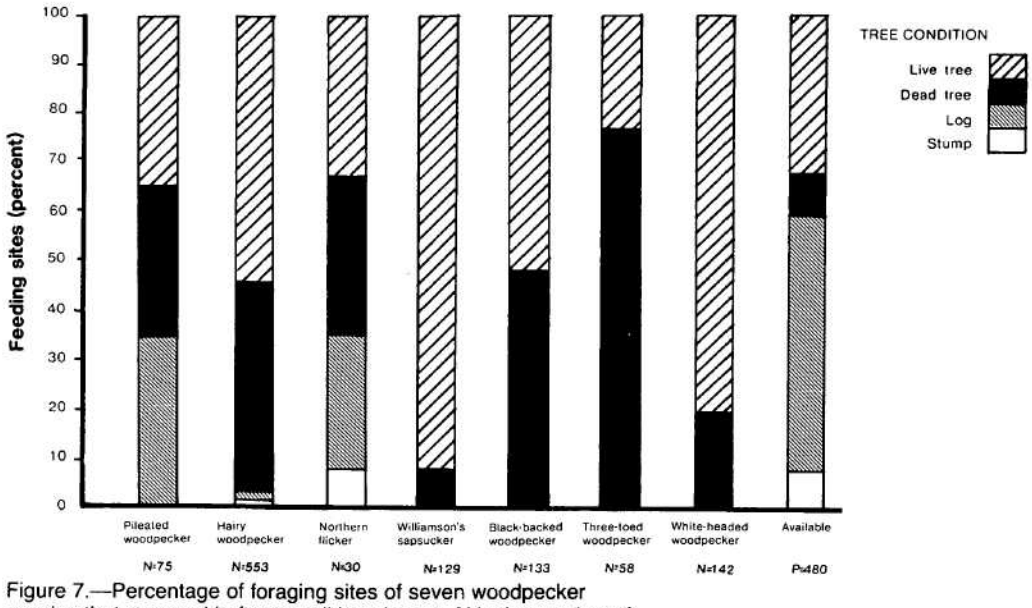


Figure 7.—Percentage of foraging sites of seven woodpecker species that occurred in four condition classes. N is the number of foraging sites and P is the number of sample sites.

Dead and downed material used as feeding sites were significantly different from available dead and downed material in d.b.h., length, and tree species. The discriminant analysis entered two variables (d.b.h. and forest type) that distinguished sites used for foraging from available sites. Pileated woodpeckers used Douglas-fir and western larch logs of large diameter (>25 cm) and long length (>15 m) disproportionately more than random selection would account for. Seventy-eight percent of the downed material used for foraging had less than one-fourth of the bark, branches, and needles remaining.

The amount of bark and branches remaining and the d.b.h. of dead trees used for feeding versus available dead trees were significantly different. D.b.h. and forest type distinguished between used and available dead trees. Dead trees greater than 50 cm d.b.h. with at least three-fourths of their bark but less than three-fourths of their branches characterized most of the feeding sites (75 percent) in dead trees. Dead trees retained an average of 12 percent of the needles. These conditions suggested that trees dead only long enough to lose some limbs but not much bark were preferred feeding sites. The approximate time span since death was 5 years. Mannan (1977) also reports foraging by this species on large-diameter snags.

Pileated woodpecker

Live trees used as feeding sites were significantly different from available live trees in d.b.h. and height. Large trees were preferred; 46 percent of the trees used for feeding were greater than 50 cm d.b.h., and 77 percent of the trees were taller than 15 m. Percent of bark was the best discriminator between trees used for feeding sites and available trees because portions of the bark had been removed as a result of the foraging activity.

Pileated woodpeckers fed extensively on carpenter ants *(Camponotus* sp.). Sanders (1970) found that carpenter ants nest only in logs, stumps, and dead trees greater than 30 cm in diameter and in live trees greater than 20 cm d.b.h. The ants use larger diameter material because the smaller diameter material lacks permanence, decays faster, and forces the ants to move more often. We suspect that pileated woodpeckers selected woody material greater than 25 cm in diameter because ants were more abundant there. In addition, larger diameter dead wood generally contains higher densities of woodborers because of additional surface area and moisture retention.[1/]

A third of the foraging by pileated woodpeckers consisted of scaling for bark beetles in and under the bark of live trees. We presume this woodpecker favored the larger diameter trees because these trees have higher densities of beetle larvae (Parker and Stevens 1979).

Although an analysis of pileated woodpecker fecal material collected at the Starkey Experimental Forest showed 95 percent of the diet consisted of carpenter ants in 1980-81 (Beckwith and Bull, 1985), a portion of the diet must have consisted of bark beetles in 1976-77 because pileated woodpeckers were observed scaling about a third of the time. The discrepancy was caused by a change in prey availability from 1976 to 1981. The mountain pine beetle population was at a peak in 1977, but by 1981 was at a iow level, We believe the woodpeckers preyed on the bark beetles when the beetles were abundant but changed to other prey when the beetles declined.

[1/]Personal communication, B.E. Wickman, Forestry and Range Sciences Laboratory. Route 2, Box 2315 Le Grande, Oregon 97850.

Black-backed woodpecker.—Black-backed woodpeckers scaled 72 percent of the time and pecked and gleaned the remainder of the time (fig. 6). All forest types were used and 97 percent of the foraging occurred on ridges. Live and dead trees were used in approximately equal proportions (fig. 7). Live lodgepole pine was preferred for foraging and was used 54 percent of the time. Tree species was the best discriminator between live trees used and those not used.

D.b.h., height, and percent of needles were significantly different for dead trees used for feeding from those of available dead trees. Percent of needles was the best discriminator between used and available dead trees. This species fed in trees that averaged 34 cm d.b.h. and 19 m tall, and retained 41 percent of their needles. The retention of needles suggested that the trees had been dead less than 2 years.

The larvae of wood-boring beetles make up three-quarters of the black-backed woodpecker's diet (Bent 1964). Wickman (1965) and Baldwin (1960) report this species feeding on woodborers *{Monochamus oregonensis)* and Engelmann spruce beetles *(Dendroctonus engelmanni).*

Three-toed woodpecker.—Three-toed woodpeckers acquired food exclusively by scaling (fig. 6), and 78 percent of the feeding sites were in dead trees (fig. 7). All characteristics of foraging sites except bark condition were significantly different than if the sites had been selected at random from available dead trees. Forest type and percent of needles remaining were the best discriminators between habitat used and not used. Three-toed woodpeckers scaled dead trees that averaged 24 cm d.b.h. and 18 m tall, and that retained most of their bark (93 percent), limbs (76 percent), and a portion of the needles (21 percent). These conditions describe trees that had been dead less than 3 yr. Koplin (1969) also observed this species feeding on insects in the bark of freshly killed trees. All feeding occurred on the trunk at an average height of 7 m (table 3). This species used grand fir types 69 percent of the time. All feeding activity took place on lodgepole pine trees and on flat terrain. Birds occurred only in grand fir forest types that contained lodgepole pine.

Table 3—Frequency and mean values (standard deviation) of tree characteristics used for foraging by 7 woodpecker species, condition classes combined

Characteristic	Pileated woodpecker	Black-backed woodpecker	Three-toed woodpecker	Hairy woodpecker	White-headed woodpecker	Williamson's sapsucker	Northern flicker
Tree species: 1/							
Ponderosa pine	27	37	--	51	100	30	40
Lodgepole pine	8	41	100	33	--	9	3
Western larch	18	10	--	5	--	14	7
Douglas-fir	39	10	--	5	--	47	50
Grand fir	8	2	--	5	--	--	--
D.b.h. (cm)	51 (26.1)	31 (16.0)	24 (6.7)	30 (15.1)	44 (14.8)	41 (18.6)	56 (11.8)
Height (m)	20 (12.1)	18 (8.6)	19 (4.5)	16 (7.2)	20 (5.9)	21 (8.1)	20 (10.0)
Percent bark	64 (42.6)	97 (7.1)	94 (6.0)	97 (9.8)	100 (1.1)	98 (9.9)	58 (47.4)
Percent branches	52 (44.8)	89 (23.9)	81 (20.2)	92 (18.7)	98 (5.3)	94 (19.4)	35 (37.0)
Percent needles	37 (47.2)	72 (40.6)	38 (43.5)	72 (38.8)	90 (27.5)	91 (25.4)	13 (26.0)
Foraging height	9 (7.9)	10 (6.8)	7 (3.5)	8 (5.9)	7 (5.0)	10 (6.2)	14 (8.9)
Sample size (number of trees)	75	133	58	553	142	129	30

1/ Percent of all foraging sites that occurred, by tree species. For other variables, means and standard deviations are presented.

White-headed woodpecker.—White-headed woodpeckers spent 41 percent of their time extracting seeds from pine cones (fig. 6). We assumed they were feeding on seeds although they could have been taking insects from the cones. As 80 percent of the foraging took place on live trees, we only analyzed feeding sites on live trees.

Forest type, d.b.h., and tree species at foraging sites were significantly different than if those sites had been selected at random from available habitat. Forest type was the best discriminator between used and available trees. Only ponderosa pine (table 3) and ponderosa pine forest types were used. The birds preferred trees greater than 25 cm d.b.h., and foraged on the lower 4 m of the trunk more than three-fourths of the time.

We suspect ponderosa pine was used because the layered bark provides crevices sheltering numerous insects. Larger trees (and areas lower down on the trunk) have greater surface area and deeper cracks, which presumably provide refuge for insects. In addition, trees over 25 cm d.b.h. are the best seed producers (Fowells and Schubert 1956).

Northern flicker.—Northern flickers spent 65 percent of their foraging time (fig. 6) on the ground and lesser amounts of time excavating, pecking, gleaning, and seed harvesting in live and dead trees, downed material, and stumps (fig. 7). This variety of strategies and condition classes portrays the versatile and opportunistic nature of this species.

In areas used for ground foraging, the vegetative ground cover and bare area averaged 52 and 40 percent, respectively; rock and downed material made up the remainder. Mean height of vegetation was 10 cm. Percent of low ground cover and height of ground vegetation may have enhanced the accessibility of prey species. Grasses, generally fescue *(Festuca* spp.) or pinegrass *(Calamagrostis rubescens),* dominated most (81 percent) of the feeding sites. Fifty-nine percent of these feeding sites occurred in ponderosa pine types. Lawrence (1967), Stallcup (1968), and Jackman (1975) also report that northern flickers feed extensively on the ground, primarily to search for ants.

Williamson's sapsucker.—Both the Williamson's and yellow-bellied sapsuckers occurred in the study area, but we never observed the latter species foraging, so our comments are restricted to the Williamson's sapsucker. Sapsuckers fed at sap wells three-fourths of the time and pecked or gleaned the rest of the time (fig. 6). Tate (1973), Jackman (1975), and McClelland (1977) report extensive use of sap; Stallcup (1968) observed this species gathering ants on trunks and eating phloem.

We analyzed only feeding sites in live trees because 93 percent of the foraging occurred there. Tree species, d.b.h., and height were significantly different at foraging sites than if sites had been selected at random from available live trees. D.b.h. was the best discriminator of the three variables that distinguished between feeding sites and available habitat. Douglas-fir and western larch trees were preferred for feeding and were used 46 and 14 percent of the time, respectively. Trees had a mean d.b.h. and feeding height of 21 cm and 10 m, respectively (table 3): Grand fir forest types contained half the foraging sites. The high foraging height enabled the birds to reach the phloem through a thin layer of bark even though the trees were larger and thick barked at the base (Oliver 1970), Both Stallcup (1968) and Oliver (1970) report sapsuckers using ponderosa pine trees extensively; their study areas were, however, stands solely of ponderosa pine.

Hairy woodpecker.—Scaling was the predominant feeding activity (75 percent) of hairy woodpeckers; pecking, seed harvesting, and gleaning comprised the remainder (fig. 6). The two ponderosa pine forest types contained 59 percent of the feeding sites, although the grand fir forest types were used in a greater proportion than their occurrence at Starkey. Ridges were also used in greater frequency than expected. Live and dead trees were used, respectively, 55 and 42 percent of the time as feeding sites (fig. 7).

Hairy woodpeckers preferred to feed in live lodgepole pine and western larch and used ponderosa pine in proportion to its occurrence. Tree species was the best discriminator between used and unused trees. The hairy woodpecker showed a preference for trees greater than 25 cm d.b.h. Of the feeding sites recorded in dead trees, 67 percent occurred in ponderosa pine. Dead trees greater than 25 cm d.b.h. and 15 m tall were preferred. Dead trees retaining more than three-fourths of their bark and limbs were used most of the time (82 percent). Dead trees used for foraging retained an average of 47 percent of the needles, which suggested that these trees had been dead 1 -3 years.

Resource partitioning.—During this study we detected four ways that woodpeckers partition resources: (1) they use different substrates, (2) they occupy different forest types, (3) they use different foraging techniques, and (4) they use resources at different times (young fledged at different times).

We included nine habitat variables in the discriminant function analysis to determine which variables could distinguish the foraging habitats among the seven woodpecker species. The analysis correctly classified 42 percent of the feeding sites according to species. Eight of the nine variables had significant F-values (P^O.01). Percent of bark was selected as the best discriminator. This variable alone, however, could not separate feeding sites of pileated woodpeckers and northern flickers or of those species that fed on live trees or recently dead trees.

When d.b.h., the second-best discriminator, was considered, feeding sites of white-headed woodpeckers could be distinguished from those of all other species except Williamson's sapsuckers. By including tree condition in the analysis, feeding sites of pileated woodpeckers and northern flickers could be distinguished because the former species fed in dead and downed woody material. When forest type was included, Williamson's sapsuckers were separated from the white-headed woodpeckers; the former preferred grand fir forest types and the latter fed exclusively in ponderosa pine forest types. Even when land form and tree species were considered, significant differences (P^O.01) were not detected between hairy and black-backed woodpeckers.

The foraging niche of each species was calculated using the mean and one standard deviation of the first two discriminant functions (fig. 8). Considerable overlap occurred among most species and particularly between the hairy and black-backed woodpeckers. This analysis did not include, however, foraging activities or locations on trunk or limb as variables, both of which can separate species ecologically.

Different foraging activities presumably result in the acquisition of different prey (Williams 1975). Foraging activities were significantly different among all woodpecker species except the hairy and black-backed woodpeckers. In Illinois, Williams (1975) found the foraging activities of four woodpecker species to be significantly different and felt this allowed coexistence by reducing competition for food. Differentiation of foraging behavior was the major factor that permitted different woodpecker species to coexist in ponderosa pine forests in Colorado (Stallcup 1968). In California, Raphael (1980) and Raphael and White (1984) found that foraging methods, rather than differences in microhabitat, are responsible for the foraging segregation of a group of cavity nesters.

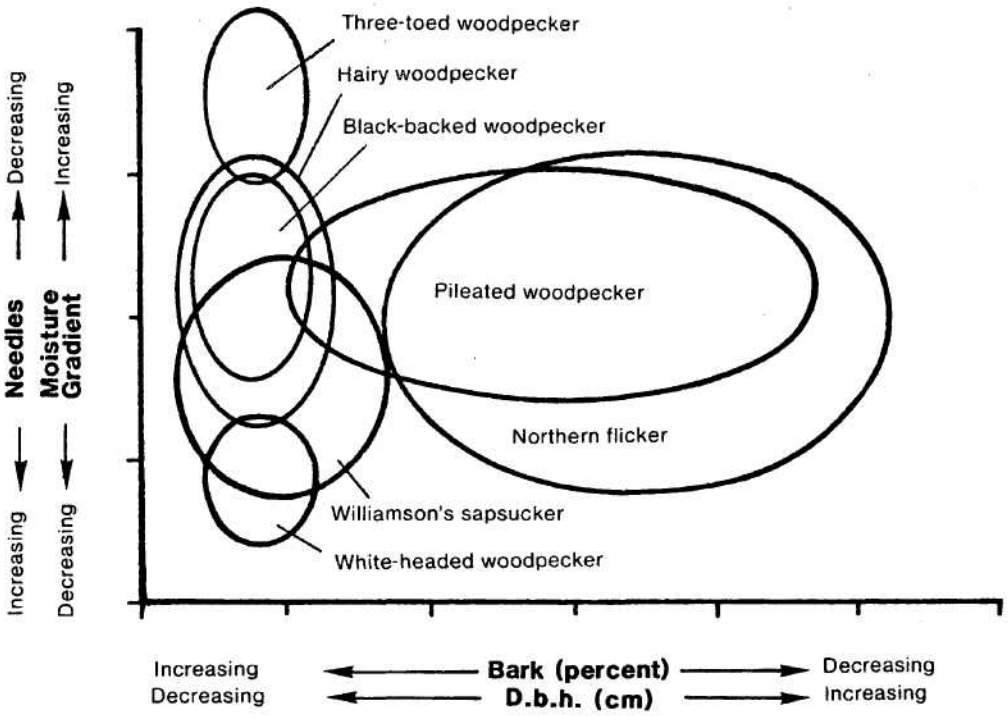


Figure 8.—Niche overlap in woodpecker use of live, dead standing, and downed trees for feeding. Ellipses are described by the mean ± one standard deviation of the first (X-axis) and second (Y-axis) discriminant function scores of each species.

The hairy and black-backed woodpeckers used similar habitats and foraging activities during our study. Feeding location was the primary habitat difference between hairy and black-backed woodpeckers as the latter species foraged only on trunks. The hairy woodpecker scaled and pecked on branches 27 percent of the time.

Another means of partitioning is temporal separation of resource utilization. Hairy woodpeckers fledged young the earliest and black-backed woodpeckers fledged young the latest of the woodpecker species. This temporal difference in breeding phenology may augment the demand for food at different times by these two species.

Habitat partitioning and foraging strategies acted to separate the feeding habitat of seven species. Hairy and black-backed woodpeckers showed the most overlap as both fed in the same habitat with the same strategies. We suspect some competition could exist between these two species if resources were limited.

Implications for **Management**

Managers of public forest land in the United States have begun to pay attention to inaintaining 'population, ieveis of cavity nesting birds in managed forests (Davis and others. 1983). Most management action has been predicated on simple management models that involve the species, size/numbers, a*nd* distribution, of snags (see Thomas and others 1379 as an example). The information from-this study indicates, how the primary excavators (woodpeckers) partition and exploit habital. Those insights reveal the attributes of habitat; beyond snags that are -important to the individual species.

Most currently used models, such as those of Thomas and others (1979) and Davis and others (1983), assume that if snags are available in appropriate sizes, numbers, and distribution, then the natural succession or the guided growth of the managed forest will produce adequate habitat conditions for the woodpeckers and the secondary cavity nesters that use the abandoned cavities. This assumption is probably correct. If adequate habitat is not provided, however, for all the sympatric species of woodpeckers, more specific habitat models can be derived from such information as presented here.

Acknowledgments

The authors wish to acknowledge significant contributions by Edward O. Garton and Arthur D. Partridge, University of Idaho; personnel at the Intermountain Forest and Range Experiment Station, Moscow; and Amy Bull who assisted with field work.

English Equivalents

1 centimeter (cm) = 0.39 inch
1 meter (m) = 39.37 inches or 3.28 feet
1 kilometer (km) = 0.62 mile
1 hectare (ha) = 2.47 acres
1 square meter per hectare (m7ha) = 4.33560 square feet per acre

Literature Cited

Baldwin, Paul H. Overwintering of woodpeckers in bark beetle-infested spruce-fir forests of Colorado. In: Proceedings, 12th international ornithological congress; [date of conference unknown]; [location of conference unknown]. Helsinki: [publisher unknown]; **1960;** 12(1): 71-84.

Beckwith, Roy C.; Bull, Evelyn L. Scat analysis to identify the arthropod component of a woodpecker's diet. The Murrelet. 66(3): 90-92; **1985.**

Bent, Arthur Cleveland. Life histories of North American woodpeckers. New York: Dover Publ., Inc.; **1964.** 334 **p.**

Burr, James A. Soil survey, Starkey Experimental Forest and Range, Union and Umatilla Counties, Oregon. [Location of publisher unknown]: U.S. Department of Agriculture, Soil Conservation Service and Forest Service; **1960.** 32 **p.**

Conner, Richard N.; Adkisson, Curtis S. Discriminant function analysis: a possible aid in determining the impact of forest management on woodpecker nesting habitat. Forest Science. 22(2): 122-127; **1976.**

Cottam, Grant; Curtis, J.T. The use of distance measures in phytosociologist sampling. Ecology. 37(3): 451-460; **1956.**

Crookston, Nicolas L.; Stark, Ronald W.; Adams, David L. Outbreaks of the mountain pine beetle in lodgepole pine forests—1945-1975. Moscow, ID: University of Idaho, College of Forestry, Wildlife and Range Sciences; **1977.** 7 p.

Darlington, P.J., Jr. Competition, competitive repulsion, and coexistence. Proceedings of the National Academy of Science. 69(11): 3151-3155; **1972.**

Davis, Jerry W.; Goodwin, Gregory A.; Ockenfels, Richard A., tech. coords. Snag habitat management: proceedings of the symposium. Gen. Tech. Rep. RM-99. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; **1983.** 226 **p.**

Edgerton, Paul J.; Smith, Justin G. Seasonal forage use by deer and elk on the Starkey Experimental Forest and Range, Oregon. Res. Pap. PNW-112. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1971.**12 **p.**

Erskine, Anthony J.; McLaren, William 0. Sapsucker nest holes and their use by other species. Canadian Field Naturalist. 86: 357-361; **1972.**

Fowells, H.A.; Schubert, G.H. Seed crops of forest trees in the pine region of California. Tech. Bull. 1150. [Location of publisher unknown]: U.S. Department of Agriculture; **1956.** 48 **p.**

Jackman, Siri Marion. Woodpeckers of the Pacific Northwest: their characteristics and their role in the forests. Corvallis, OR: Oregon State University; **1975.** 147 p. M.S. thesis.

Klecka, William R. Discriminant analysis. In: SPSS statistical package for the social sciences. 2d ed. New York: McGraw-Hill Book Co.; **1975:** 434-467.

Koplin, James R. The numerical responses of woodpeckers to insect prey in a subalpine forest in Colorado. Condor. 71(4): 436-438; **1969.**

Lawrence, Louise de Kiriline. A comparative life history study of four species of woodpeckers. Ornithological Monographs. 5:1-156; **1967.**

MacArthur, Robert H. Population ecology of some warblers of northeastern coniferous forests. Ecology. 39(4): 599-617; **1958.**

Mannan, Robert William. Use of snags by birds, Douglas-fir region, western Oregon. Corvallis, OR: Oregon State University; **1977.**114 p. M.S. thesis.

McClelland, B. Riley. Relationships between hole-nesting birds, forest snags, and decay in western larch-Douglas-fir forests of the northern Rocky Mountains. Missoula, MT: University of Montana; **1977.** 496 **p.**

McClelland, B. Riley; Frissell, Sidney S.; Fisher, William C; Halvorson, Curtis H. Habitat management for hole-nesting birds in forests of western larch and Douglas-fir. Journal of Forestry. 77(8): 480-483; **1979.**

Miller, Eileen; Partridge, Arthur D.; Bull, Evelyn L. The relationship of primary cavity nesters and decay. Transactions of the Northeast Wildlife Society. 36: 60-68; **1979.**

Oliver, William W. The feeding pattern of sapsuckers on ponderosa pine in northeastern California. Condor. 72(2): 241; **1979.**

Parker, Douglas L.; Stevens, Robert E. Mountain pine beetle infestation characteristics in ponderosa pine, Kaibab Plateau, Arizona, 1975-77. Res. Note RM-367. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experimental Station; **1979. 4 p.**

Raphael, Martin G. Utilization of standing dead trees by breeding birds at Sagehen Creek, California. Berkeley, CA: University of California. **1980.** 195 p. Ph.D. dissertation.

Raphael, Martin G.; White, Marshall. Snags, wildlife, and forest management in the Sierra Nevada. Cal-Neva Wildlife. 1978:23-41.

Raphael, Martin G.; **White, Marshall.** Use of snags: by cavity nesting birds in the Sierra , Nevada. Wildlife Monograph: 86.; Washington, DC: The Wfldlife Society; **1984.** 66 p.

Sanders, C.J. The distribution of carpenter ant colonies in the spruce-fir forest of northwestern Ontario. Ecology. $1(5): 865-873; **1970**

Schoener, Thomas W. Resource partitioning in ecological communities. Science. 185: 27-39; **1974.**

Scott, Virgil E. Characteristics of ponderosa pine snags used by cavity-nesting birds in Arizona. Journal of Forestry. 76(1): 26-28; **1978.**

Shigo, Alex L; Kilham, Lawrence. Sapsuckers and *Formes igniarius* var. *populinus.* Res. Note NE-48. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. **1968. 2 p.**

Short, Lester L. Habits and interactions of North American three-toed woodpeckers *(Picoides arcticus* and *Picoides tridaetylus).* American Museum Novitates 2547: 1-42; **1974.**

Spring, Lowell W. Climbing and pecking adaptations in some North American woodpeckers. Condor. 67(6): 457-488; **1965.**

Stallcup, Patricia L. Spatio-temporal relationships of nuthatches and woodpeckers in ponderosa pine forests of Colorado. Ecology. 49(5): 831-843; **1968.**

Strickler, Gerald S. Soil and vegetation on the Starkey Experimental Forest and Range. Society of American Forestry Proceedings. 1965: 27-30; **1966.**

Tate, James, Jr. Methods and annual sequence of foraging by the sapsucker. Auk. 90(4): 840-856; **1973.**

Thomas, Jack Ward; Anderson, Ralph G.; Maser, Chris; Bull, Evelyn L. Snags. In: Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington. Agric. Handb. 553. Washington, DC: U.S. Department of Agriculture; **1979:** 60-77.

Wickman, Boyd E. Black-backed three-toed woodpecker, *Picoides arcticus,* predation on *Monochamus oregonensis.* Pan-Pacific Entomologist. 41(3): 162-164; **1965.**

Williams, Joseph B. Habitat utilization by four species of woodpeckers in a central Illinois woodland. American Midland Naturalist. 93(2): 354-367; **1975.**

Pacific Northwest Research Station
319 S.W. Pine St.
P.O. Box 3890
Portland, Oregon 97208

*GPO 694-328 (1986)

U.S. Department of Agriculture
Pacific Northwest Research Station
319 SW. Pine Street
P.O. BOX 3890
Portland, Oregon 97208

BULK RATE
POSTAGE+
FEES PAID
USDA-FS
PERMIT No, G-40

Official Business
Penalty for Private Use, $300

Do NOT detach label