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Habitat Use Among Woodpeckers in Forest Burns

Mary A. Harris
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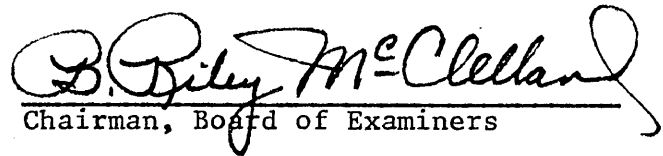HABITAT USE AMONG WOODPECKERS

IN FOREST BURNS

by

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Avian community composition, woodpecker foraging, and woodpecker
nest-site selection were studied on commercial forest land in two
coniferous forest burns near Missoula, Montana. Both burns were
characterized by a concentration of woodpeckers, particularly of
the genus Picoides. This concentration was present in response to
the abundance in bark- and wood-boring beetle larvae in the fire-
damaged trees. A decline in woodpeckers was observed three years
post-fire. This decline coincided with the emergence of wood-
boring beetles. As woodpeckers declined Mountain Bluebirds
(Sialia currucoides) and House Wrens (Troglodytes aedon) increased
within the burns, possibly in response to the increase in nest
sites and openness. Similarity in avifaunas of the burns and
adjacent unburned forests increased with vegetation regeneration.
    Foraging parameters studied for the Hairy (P. villosus), Black-
backed Three-toed (P. arcticus), and Northern Three-toed (P. tri-
dactylus) woodpeckers included tree species, tree size, technique,
and height use. The first three apparently facilitated inter-
specific niche partitioning and the latter intersexual partition-
ing. These separations were related to the distribution of trees
in single-species clumps of one size class.
    A strong sexual dimorphism was found for Black-backed (96%) and
a less marked dimorphism for Northern (85%) Three-toed Woodpeckers.
The size differences may allow niche partitioning by the sexes
through acquisition of different prey. This was supported by the
corresponding distributions of cerambicids with foraging locations
of the woodpeckers.
    The two three-toed woodpeckers nested in the smallest diameter
trees, the Common Flicker (Colaptes auratus) in the largest, and
the Hairy in the intermediate. All species used western larch
(Larix occidentalis) in a greater proportion than was available.
The two three-toed species nested in the densest stands of trees.
    Management suggestions for salvage logging following fire
include leaving selected western larch and as many trees of at
least 34 cm dbh as possible. Leaving uncut patches within burns
is also recommended.

ACKNOWLEDGEMENTS

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CHAPTER I

A COMPARISON OF BIRDS IN EARLY POST-FIRE CONIFEROUS

FOREST AND ADJACENT UNBURNED FOREST

Introduction

Fire is a natural agent in the forests of the northern Rocky

Mountains, creating a mosaic of avian habitats. Strikingly different

habitats of burned and unburned forest provide contrast; in addition

the variation among the burns is large. In some areas mixtures of

fire-killed and live trees remain after a fire; at other sites fires

totally consume the canopy and leave a forest of blackened snags. As

forest regeneration progresses following fire the area is utilized by

a changing avifauna (Bock and Lynch 1970, Taylor and Barmore 1980).

Several species of birds concentrate in forest burns the first

few years following fires (Stoddard 1963). Woodpeckers are attracted

to recent burns by the abundance of bark- and wood-boring beetle

larvae found within the fire-killed trees (Blackford 1955, Bock and

Lynch 1970, Taylor and Barmore 1980).

During the summers of 1977 and 1979 two fires occurred in forests

near Missoula, Montana. Portions of each burn were salvage logged

following the fires. This paper compares the avifaunas of the two

burns, the cut and uncut portions of the burns, and the adjacent

unburned forest.

Study Sites

Pattee Canyon

Pattee Canyon, a residential and recreational area, lies 3 km to the southeast of Missoula, Montana. In July, 1977 a fire burned 480 ha on the north-facing slopes of the canyon between elevations of 1100 and 1700 m. The area was forested primarily by Douglas-fir (Pseudo-tsuga menziesii), ponderosa pine (Pinus ponderosa), and western larch (Larix occidentalis), listed in order of decreasing abundance.

Following the fire two 70 ha portions of the burn were logged (Fig. 1). The westernmost area was clearcut and the area near the base of the canyon was thinned, leaving 125 trees standing per hectare. Throughout the remainder of the burn fire-killed trees were left standing with an average density of 1043 trees/ha.

Mill Creek

Mill Creek is 45 km southwest of Missoula. A fire occurred on 120 ha of north- and northwest-facing slopes between elevations of 1300 and 1400 m in August 1979. The tree species composition at this site was similar to that at Pattee Canyon (Table 1).

Table 1. Tree species composition (%) at each study site.

	Douglas-fir	Ponderosa Pine	Western Larch
Pattee Canyon	73.3	16.7	10.0
Mill Creek	77.0	15.8	7.2
Average	75.1	16.3	8.6

This area is owned by Champion International and, except for the steep hillside at the eastern side of the burn, was salvage logged following the fire (Fig. 2). Both live and fire-killed trees remained in an average density of 855 trees/ha within the cut portion of the burn. The trees on the uncut hillside were primarily fire-killed and stood in a density of 970/ha.

Methods

To estimate avian densities I walked fixed width (120 m) line transects 500 m in length. The paucity of understory and tree crown foliage within the burns facilitated detection of birds. I maintained the same width along the transects in the unburned forest where the avian density estimates are probably low because of decreased visibility in a habitat with an intact understory and crown.

I located three transects at Pattee Canyon; one in the cut portion of the burn, one in the uncut burn, and the third in the adjacent unburned forest (Fig. 1). I also located a transect 8 km farther up the canyon from the burn to serve as a control with which to compare spillover of species from the burn into the adjacent unburned forest.

At Mill Creek I located four transects. One transect was located in each of the following sites: the cut portion of the burn, the uncut portion, the adjacent unburned forest, and the eastern edge of the burn (Fig. 2).

I walked transects between 0700 and 0800 on mornings when there was little wind or rain. Each transect was covered from 2 to 6 times each breeding season (Table 2). To compare the avifaunas of the various transects I used Renkonen's (Huhta 1979) index of similarity:

Figure 1. The Pattee Canyon burn is outlined, with shading
indicating the areas that were salvage logged. The
two .5 km line transects within the burn are shown in
addition to the transect through the adjacent
unburned forest.

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Figure 2. The Mill Creek burn is outlined, the shaded portion
           representing the logged area. The four .5 km transects
           are shown.

Table 2. Number of birds per 40 ha (as averaged over all transect repetitions) along transects at Pattee Canyon and Mill creek.

	Pattee Canyon									Mill Creek					
	control	adjacent		burned cut			burned uncut			adjacent		edge	burned cut		uncut
	1981	1979	1981	1979	1980	1981	1979	1980	1981	1980	1981	1980	1980	1981	1981
Goshawk (Accipiter gentilis)	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Red-tailed Hawk (Buteo jamaicensis)	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
American Kestrel (Falco sparverius)	-	-	-	1	7	11	-	-	-	-	-	+	-	-	-
Ruffed Grouse (Bonasa umbellus)	-	2	-	-	-	-	-	-	2	-	-	-	-	-	-
Morning Dove (Zenaida macroura)	-	-	-	1	-	-	3	-	-	-	-	-	3	-	-
Common Nighthawk (Chordeiles minor)	-	-	-	-	3	2	-	-	-	-	-	-	+	-	-
White-throated Swift (Aeronautes saxatalis)	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Calliope Hummingbird (Stellula calliope)	-	-	-	-	7	-	1	-	3	3	-	2	-	-	-
Pileated Woodpecker (Dryocopus pileatus)	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+
Lewis' Woodpecker (Melanerpes lewis)	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-
Yellow-bellied Sapsucker (Sphyrapicus varius)	-	-	-	-	-	-	-	-	-	-	-	12	-	-	-
Williamson's Sapsucker (Sphyrapicus thyroideus)	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
Hairy Woodpecker (Picoides villosus)	7	2	7	6	-	-	3	10	5	-	-	8	19	13	3
Downy Woodpecker (Picoides pubescens)	-	-	-	-	-	-	-	-	2	-	2	-	-	-	-
Black-backed Three-toed Woodpecker (P. arcticus)	-	3	2	6	3	7	15	3	3	-	-	-	7	2	14
Northern Three-toed Woodpecker (P. tridactylus)	-	-	-	1	-	-	1	10	-	-	-	-	-	-	-
Hammond's Flycatcher (Empidonax hammondii)	5	-	2	-	-	-	1	-	-	-	-	5	-	3	2
Western Wood Pewee (Contopus sordidulus)	-	-	-	-	-	-	-	-	18	-	-	-	-	-	-
Olive-sided Flycatcher (Nutallornis borealis)	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-
Steller's Jay (Cyanocitta stelleri)	-	-	-	-	-	-	1	-	-	-	-	-	-	-	r
Common Raven (Corvus corax)	-	1	-	1	-	-	-	-	-	-	2	-	-	2	3
Clark's Nutcracker (Nucifraga columbiana)	-	-	-	-	-	-	1	-	-	10	-	-	4	-	3
Chickadee (Parus atricapillus or gambeli)*	13	22	13	-	-	-	1	-	-	10	8	10	-	-	2
Red-breasted Nuthatch (Sitta canadensis)	11	24	34	-	-			-	3	13	22	8	-	2	12
White-breasted Nuthatch (Sitta carolinensis)	2	-	4	-	-	-	-	-	-	-	-	-	-	-	-

Species															
Brown Creeper (Certhia familiaris)	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
House Wren (Troglodytes aedon)	-	-	-	2	-	-	4	7	2	-	-	-	1	-	-
American Robin (Turdus migratorius)	9	8	40	21	13	43	16	14	30	7	8	10	12	35	7
Varied Thrush (Ixoreus naevius)	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Swainson's Thrush (Catharus ustulatus)	-	4	9	-	-	-	4	-	-	-	-	-	-	-	-
Mountain Bluebird (Sialia currucoides)	-	-	-	10	17	18	5	17	20	-	2	3	16	17	2
Townsend's Solitaire (Myadestes townsendi)	2	-	-	-	-	-	-	-	-	-	7	3	-	3	8
Starling (Sturnus vulgaris)	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-
Golden-crowned Kinglet (Regulus satrapa)	2	1	-	-	-	-	-	-	-	-	5	-	-	-	-
Ruby-crowned Kinglet (Regulus calendula)	5	1	16	-	-	-	-	-	-	3	17	3	-	-	-
Solitary Vireo (Vireo solitarius)	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
Warbling Vireo (Vireo gilvus)	-	3	2	-	-	-	-	-	-	-	-	-	-	-	-
Orange-crowned Warbler (Vermivora celata)	-	1	-	-	-	-	-	-	-	-	3	2	-	-	-
Yellow-rumped Warbler (Dendroica coronata)	34	13	13	-	-	-	4	-	4	34	12	24	3	14	10
Townsend's Warbler (Dendroica townsendi)	-	-	-	-	-	-	-	-	-	7	3	-	-	-	-
MacGillvray's Warbler (Oporornis tolmiei)	-	5	-	2	3	2	3	7	-	-	2	3	3	-	-
Brewer's Blackbird (Euphagus cyanocephalus)	-	-	2	-	-	-	-	-	-	3	-	8	1	-	-
Western Tanager (Praanga ludoviciana)	2	19	16	-	-	-	4	-	-	7	5	7	-	5	5
Lazuli Bunting (Passerina amoena)	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-
Evening Grosbeak (Hesperiphona vespertina)	22	54	236	-	-	-	-	-	-	-	-	3	-	-	-
Dark-eyed Junco (Junco hyemalis)	13	24	38	16	60	85	20	27	69	37	15	22	31	37	32
Chipping Sparrow (Spizella passerina)	31	42	61	3	17	11	11	3	15	37	89	44	19	45	39
Cassin's Finch (Carpedacus cassinii)	-	1	-	-	-	-	5	-	3	-	3	-	4	5	5
Pine Siskin (Spinus pinus)	11	2	-	-	27	2	20	40	7	27	20	25	12	8	22
Red Crossbill (Loxia curvirostra)	2	3	20	-	-	-	-	-	-	30	-	-	-	-	-
total number of birds/40 ha	173	238	286	83	163	183	143	138	197	228	228	212	145	201	149
number of species	17	22	18	13	12	10	23	10	18	14	19	22	15	14	17
number of transect runs	3	6	3	6	2	3	5	2	4	2	4	4	5	4	5

*I often heard but did not see chickadees and was unable to differentiate between Black-capped and Mountain Chickadees by their vocalizations.

+Members of these species were observed, but their densities were not estimated because of the species' large territory sizes.

-Indicates species not observed.

$$PS = \sum_{i=1}^{n} \min(P_{1i}, P_{2i}), \text{ where}$$

PS is percentage similarity, P_{1i} is the proportion of the ith species

on transect 1 (= $\frac{n_{1i}}{N_1}$) and P_{2i} the proportion of the ith species on

transect 2. The proportions were taken from average counts over all

repetitions of each transect. I used this method instead of a diversity

index to facilitate a species by species comparison of two transects

instead of a total number of species comparison. After computing the

percent similarity of two transects, I ranked all comparisons and

determined which transects' avifaunas were most similar and which were

most dissimilar. Therefore, in reporting the results and in the dis-

cussion, the degree of similarity is relative, based on this ranking

system.

Results

A high percent similarity existed between the cut and uncut burn

transects at each study site (Table 3). At Pattee Canyon the similarity

between these two areas increased from 1979 to 1981. The similarity

between transects within the Pattee Canyon burn and the adjacent

unburned forest also increased over the years. However, the percent

similarity was low between the burns and adjacent unburned areas.

The two study sites were relatively similar in the avifaunas of the

adjacent unburned areas except for the presence of a large number of

Evening Grosbeaks at Pattee Canyon in 1979 (Table 2). At Mill Creek the

avifauna along the edge of the burn was also similar to that of the

adjacent unburned forest.

Table 3. Comparisons of similarity among transects at Pattee Canyon (PC) and Mill Creek (MC) (% similarity) (Huhta 1979).

	PC control 1981	PC adjacent 1981	PC cut burn 1979	PC cut burn 1981	PC uncut burn 1979	PC uncut burn 1980	PC uncut burn 1981	MC cut burn 1980	MC cut burn 1981	MC edge 1980	MC uncut burn 1981
PC adjacent 1979		.26		.38							
PC adjacent 1981	.58		.32			.47					
PC cut burn 1979				.61							
PC cut burn 1980					.60						
PC cut burn 1981		.65				.71					
PC uncut burn 1979											
PC uncut burn 1980											
PC uncut burn 1981				.63							
MC adjacent 1980								.52	.66		
MC adjacent 1981	.60*							.51			.56
MC cut burn 1980									.51		
MC cut burn 1981		.46						.73			.62
MC edge 1980											
MC uncut burn 1981				.58							

*Evening Grosbeaks were excluded from this comparison because of the transient flocks present in Pattee Canyon in 1979.

The bird communities found within the two burns were dissimilar. The highest percent similarity among the comparisons of transects from both burns was for the uncut portions of the burns at two years post-fire (1979 for Pattee Canyon and 1981 for Mill Creek).

During 1979 at Pattee Canyon and 1980 at Mill Creek the Hairy, Black-backed Three-toed, and Northern Three-toed woodpeckers and the Common Flicker were concentrated within the burns (Table 2). The Northern Three-toed Woodpecker was present only prior to mid-April at Mill Creek in 1980. At Pattee Canyon an overall decline in the numbers of woodpeckers occurred in 1981.

Mountain Bluebirds increased in numbers within both burns over the years of this study. At Pattee Canyon the House Wren also increased within the burn and was present in greater numbers than my density estimates indicate due to its late arrival. American Robins, Dark-eyed Juncos, and Chipping Sparrows were present in increasing numbers from 1979 to 1981 along all transects in Pattee Canyon.

Discussion

The avifaunas within the two burns were characterized by the presence of a concentration of woodpeckers. Similar concentrations of woodpeckers within burns have been reported by several authors (Blackford 1955, Bock and Lynch 1970, Theberge 1976, Gniadek 1977, Taylor and Barmore 1980). These birds were numerous at Pattee Canyon in 1979 and Mill Creek in 1980. The Christmas bird count from 1978 indicated that the concentration was present within the Pattee Canyon burn the first winter following the fire (Marks, pers. comm.). The decline of these birds at each burn at approximately three years post-fire

coincides with the decline of beetle larvae found within the scorched trees. Similar declines in the number of woodpeckers within other burns have also been attributed to the concomitant drop in beetle larvae (Blackford 1955, Bock and Lynch 1970, Taylor and Barmore 1980).

Prior to the overall woodpecker decline at Mill Creek I observed the disappearance of one particular species, the Northern Three-toed Woodpecker. This species was present at this burn and appeared paired during February, 1980. I continued to observe the Northern Three-toed at Mill Creek until mid-April after which this species was no longer present. The other two Picoides woodpeckers, the Hairy and Black-backed Three-toed, remained and nested. However, I observed the abandonment of three of five nests located that year.

During the breeding season of 1980 at Mill Creek, insects were abundant within the fire-damaged trees and food scarcity did not seem to be a limiting factor. The time at which the Northern Three-toed Woodpecker disappeared coincided with the period of nest-site selection and excavation by the woodpeckers. Within the Pattee Canyon burn all three Picoides woodpeckers remained and nested in 1979 and 1980. At this site, however, a smaller proportion of the burn had been salvage logged following the fire than at Mill Creek, possibly leaving a greater number of suitable nest trees for the woodpeckers. Among the Hairy, Black-backed Three-toed, and Northern Three-toed woodpeckers the latter is perhaps the weakest excavator due to its small bill (Ridgway 1914). At Mill Creek where suitable nest sites appeared to be less abundant than at Pattee Canyon the Northern Three-toed may have left the burn due to increased competition with the Hairy and Black-

backed Three-toed woodpeckers for the limited nest sites.

The Mountain Bluebird and the House Wren each increased in numbers within the burns during the years of this study. Bock and Lynch (1970) observed the Mountain Bluebird in large numbers at a burn in California 5, 6, and 7 years post-fire as did Gniadek (1977) at a one year post-fire burn in Yellowstone National Park. Niemi (1978) noted an increase in House Wrens in the Boundary Waters Canoe Area following fire. Both species nest in cavities excavated by other species. In my study areas these species nested in old woodpecker holes. The House Wren also nested in the jagged ends of windthrown trees which were becoming more numerous as the fire-killed trees aged. As more trees fell the area was becoming more open and possibly attracting more of the types of insects on which each of these bird species forages.

The similarity between the two treatments within the burn increased from 1979 to 1981 as woodpeckers declined and the American Robin, Dark-eyed Junco, and Chipping Sparrow increased. Taylor and Barmore (1980) also observed an increase in these species in first through third year post-fire habitats. As the understory within the burns regenerated, an increase in insects, seeds, and cover also occurred, the latter of which Gniadek (1977) pointed out to be important to juncos in early post-fire habitat. All three of these species forage on the ground and may have increased in numbers in response to these habitat changes.

As regeneration of the understory proceeded within each burn the similarity between the avifaunas of the burned and adjacent unburned

transects increased. During the years of this study numerous standing trees within each burn provided a canopy without foliage. Comparing the similarities in breeding bird populations between a burn at 8 and at 15 years post-fire with an adjacent unburned forest area Bock and Lynch (1970) reported a decline in similarity. They pointed out, however, that by 15 years after the fire the habitat had few standing dead trees and was becoming a dense brush field.

Although the avifaunas of the adjacent unburned forest at both study sites were relatively similar, those of the burns were not. I believe this was a result of the difference in the number of trees remaining per hectare following logging at each site and the difference in severity of the fires which resulted in differing numbers of live trees remaining at each site. A greater number of birds requiring live trees for either feeding or nesting (Yellow-rumped Warbler, Western Tanager, Cassin's Finch) were present within the Mill Creek burn than within the Pattee Canyon burn. Bock and Lynch (1970) found these species at a burn 5, 6, and 7 years post-fire and attributed their presence to pockets of live trees which survived the fire.

After 50 years of fire suppression the role fire has played in the evolution of the forests of western North American has become clear (Weaver 1974). In some forests in which light periodic fires occurred for hundreds of years, fire suppression in the last half a century allowed shade tolerant species of trees to proliferate and fuels to accumulate, increasing the likelihood of a more destructive fire. The use of prescribed fires in forest management and allowing naturally occurring fires to burn in selected wildlands will not only

improve the health of the forest, but will provide a continuing array of avian habitats. This study indicates the importance of early post-fire habitat for several species of hole-nesting birds, particularly the two three-toed woodpeckers and the Mountain Bluebird.

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CHAPTER II

FORAGING SITE PARTITIONING AMONG WOODPECKERS
IN FOREST BURNS

Introduction

    Lack (1944) stressed that no two species with identical foraging

habits can occupy the same area. Some differences in feeding habits

must exist when similar species are sympatric. Rand (1952) expanded

this hypothesis suggesting that the sexes within a species may exhibit

different foraging habits to further reduce competition. He observed

that secondary sexual characters aid species in avoiding mismating

and that the less conspicuous dimorphisms "may also serve as adaptation

for slightly different foods." In addition, he indicated the impor-

tance of the reduction in competition during the breeding season when

the members of a pair may be restricted to a smaller area surrounding

a nest.

    Woodpeckers display a high degree of sexual dimorphism in trophic

structures such as bill size (Selander and Giller 1963). These sexual

differences may be related to a divergence in niche utilization. Field

studies of several North American woodpeckers have supported this

hypothesis: Kilham (1965, 1970), Jackson (1970), Kisiel (1972), Travis

(1977), and Williams (1980) for the Hairy (Picoides villosus) and

Downy (P. pubescens) woodpeckers; Ligon (1968), Morse (1972), and

Hooper and Lennartz (1981) for the Red-cockaded (P. borealis) Wood-

pecker; Kock et al. (1970) for the White-headed (P. albolarvatus)

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Woodpecker; and Austin (1976) for the Ladder-backed (P. scalaris)

Woodpecker.

Three species of Picoides woodpeckers; Hairy, Black-backed, Three-
toed (P. arcticus), and Northern Three-toed (P. tridactylus), concen-
trated in two forest burns near Missoula, Montana. Similar aggrega-
tions of woodpeckers have been reported across North America (Blackford
1955, Koplin 1969, Bock and Lynch 1970, Heinselman 1973, Theberge 1976,
Gniadek 1977, Lowe et al. 1978). Woodpeckers generally appear during
the first year following the fire and persist through the third year
(Bock et al. 1978, Taylor and Barmore 1980). The woodpeckers concen-
trate in response to the large numbers of bark- and wood-boring
beetle larvae found in the fire-weakened or killed trees. The
abandonment of these areas by woodpeckers after the first few years
following fire coincides with the decline in numbers of beetle larvae.

During the breeding seasons of 1979-1981 I observed the foraging
behaviors of the males and females of the three woodpecker species
concentrated in the two burns. The objectives of this study were to:
1) determine the densities of the woodpeckers within the burns;
2) determine if interspecific and intersexual niche partitioning was
occurring; and 3) describe the species distributions of the insects
within the burns and relate these to the foraging patterns of the
woodpeckers.

Study Areas

The Pattee Canyon burn, composed almost entirely of privately
owned land, lies 3 km southeast of Missoula, Montana. In July, 1977
a fire burned 480 ha on the north-facing slopes of the canyon between

elevations of 1100 and 1700 m. The area was forested primarily by three species of conifers: Douglas-fir (Pseudotsuga menziesii), ponderosa pine (Pinus ponderosa), and western larch (Larix occidentalis), listed in order of decreasing abundance.

The second study site was at Mill Creek, 45 km southwest of Missoula. A fire occurred in this area during August, 1979 and covered 120 ha of north- and northwest-facing slopes between 1300 and 1400 m elevation. The area was similar in tree species composition to the Pattee Canyon study site (Table 1, Chp. 1). Mill Creek is owned by Champion International and was salvage logged following the fire.

Methods

From April through July, 1979 and 1980 I studied woodpecker foraging and density in Pattee Canyon. During the breeding season of 1981 I continued the density study at this site. At Mill Creek work was conducted during the breeding seasons of 1980 and 1981 from April through July.

To estimate avian densities I walked fixed-width (120 m) line transects 500 m in length. After walking several transects and recording lateral distances from the transect line to woodpeckers observed I determined that all woodpeckers to a distance of 60 m to either side of the line were detected (Emlen 1971). During the breeding season, most woodpeckers are easily detected by their vocalizations and drumming. In addition, detection was facilitated by the paucity of understory vegetation and tree crown foliage at the study sites following the fires.

I walked transects between 0700 and 0800 on mornings when there was little or no wind and rain. Within the Pattee Canyon burn two transects were run 11, 4, and 7 times during the breeding seasons of 1979, 1980, and 1981, respectively. During the breeding seasons of 1980 and 1981 I ran two transects within the burn at Mill Creek four times each. During the final study season at Mill Creek three transect counts were made in a similar (tree species composition and age) unburned forest area.

Available tree species and numbers at both study sites were determined by recording the vegetation in 0.04 ha circular plots (James and Shugart 1970). Plots were located at 100 m intervals along the transect routes. Within each plot I recorded species and diameter and distribution of size classes available by tree species at each study site.

When a foraging woodpecker was located I characterized feeding bouts by recording the following data: 1) species and sex of the woodpecker, 2) species of tree (foraging site substrate), 3) dbh of the tree, 4) height of the foraging bird above ground, and 5) feeding technique employed by the woodpecker. Feeding techniques were categorized as: 1) scaling (removal of bark flakes by tangential blows), 2) pecking (a series of perpendicular blows), 3) gleaning (removal of a food item from the surface of the foraging substrate), or 4) probing (tongue insertion into a bark crevice or beetle-larva tunnel unaccompanied by any other technique) (Hogstad 1977). A new feeding bout was initiated when the woodpecker flew to another tree. During individual bouts if the bird changed techniques or height I would record this as

well. I followed individuals until they flew out of sight.

I used a chi-square test to determine interspecific and inter-
sexual differences in tree species use as compared to expected use as
based on availability estimates. If the differences were statistically
significant (p < .05) I calculated confidence intervals using a Bon-
ferroni Z statistic to determine which tree species were being used in
a greater/lesser proportion than that which was available (Neu et al.
1974). I used Student's t-test to determine differences among the
three woodpecker species in mean tree sizes and foraging heights used.

To determine if three-toed woodpeckers are sexually dimorphic,
I measured the culmen (to base), tarsus, wing, and tail of 63 museum
skins (Baldwin et al. 1931). I calculated coefficients of difference
from the equation of Mayr et al. (1953);

$$CD = \frac{M_m - M_f}{S.D._f + S.D._m}$$

where M_m and M_f are the means for the male and female, respectively,
and $S.D._m$ and $S.D._f$ the standard deviations for the same. I then used
the table provided by Mayer et al. (1953) to express this value in
terms of equal or joint nonoverlap, e.g. where 90% of the population
of males is not overlapped by 90% of the population of females, which
the authors suggest as the traditional level of subspecific difference.
Following Selander (1965) I have applied this method to estimating the
joint nonoverlap between males and females of subspecies of woodpeckers.

During the spring of 1980 I cut 24 trees at Mill Creek to determine
the species and distributions of insects within the fire damaged trees.

I divided the study area into nine subunits. From each subunit I took three trees; Douglas-fir, ponderosa pine, and western larch, all selected on the basis of size (average dbh within the subunit) and accessibility. Not all tree species were present in all subunits.

After felling each tree I cut sections (average 71 cm length) from the lower, middle, and upper thirds relative to the individual tree's height. I loosely enclosed each section in window screening and placed them indoors. The following spring I opened the screen bags and collected the adult insects which had emerged from each section. I then stripped the bark, collecting additional adults and larvae. At this time I also counted all insect-emergence holes in each section.

After identifying the insects from each tree section I used the Kruskal-Wallis test, a nonparametric ranking procedure, to run one-way analyses of variance (Sokal and Rolf 1981). If there were significant differences in means of the summed ranks of the various insect species among the three tree species or the three height categories, I employed the Dunn (1964) multiple comparison procedure to determine which sets of data differed.

Results

Woodpecker Densities

During 1979 34 woodpeckers/40 ha were present in the Pattee Canyon burn (Table 4). The following year I observed only 23 woodpeckers/40 ha; the number declined to 15 in 1981. Along the control transect in the unburned forest area I observed 8 woodpeckers/40 ha in 1979. The

Table 4. Woodpecker densities by species within and adjacent to the two burns (number of woodpeckers/40 ha).

	Pattee Canyon					Mill Creek			
	unburned		burned			unburned		burned	
	1979	1980	1979	1980	1981	1980	1981	1980	1981
Hairy Woodpecker	2	7	3	10	5	–	–	19	13
Black-backed Three-toed Woodpecker	3	2	15	3	3	–	–	7	2
Northern Three-toed Woodpecker	–	–	1*	10	–	–	–	–	–
Common Flicker	3	7	15	–	7	–	2	9	10

*Indicates species present within the burn in a greater density than that observed along this transect.
-Indicates species not observed.

concentration of woodpeckers in Pattee Canyon in 1979 was composed of the Common Flicker (Colaptes auratus), and the Hairy, Black-backed Three-toed and Northern Three-toed woodpeckers. By 1981 I seldom observed the latter species.

Within the Mill Creek burn 35 woodpeckers/40 ha were present in 1980 and 25/40 ha in 1981. Species at this site were the Pileated (Dryocopus pileatus), Hairy, and Black-backed Three-toed woodpeckers and the Common Flicker, the foremost of which was uncommon. Prior to mid-April, 1980 the Northern Three-toed Woodpecker was common at this study site. However, during the remainder of the breeding season that year and during the following breeding season I seldom observed this species.

Habitat Characterizations

The two study sites were very similar in tree species composition. Each site was forested primarily by Douglas-fir with a few ponderosa pine and western larch (Table 2, Chp. 1).

The distributions of size classes were not as similar as tree species composition for the two study areas (Fig. 3). At Pattee Canyon 76% of the trees were 6-15 cm whereas at Mill Creek the majority (56%) of the trees had diameters between 1 and 5 cm. At Pattee Canyon the mean dbh for each species of tree was statistically the same ($\bar{x}$ = 12.73, F = 2.74, df_1 = 2, df_2 = 257). At Mill Creek, however, the mean dbh of each tree species was significantly different, (F = 3.19, df_1 = 2, df_2 = 598), with Douglas-fir the largest (8.26 cm) followed by western larch (7.89 cm) and ponderosa pine (6.11 cm).

Tree Species Use

The utilization of the three tree species by each woodpecker species was very similar in both burns. The Hairy Woodpecker used all tree species in expected proportions (Table 5). Each three-toed species utilized Douglas-fir far less than it was available and used western larch in a much greater proportion than expected. This pattern was especially pronounced for the Northern Three-toed Woodpecker.

Few significant differences in tree species use between the sexes of each woodpecker species were observed. Differences that were detected were inconsistent from one study site to the other. The female Hairy Woodpecker at Mill Creek exhibited the same pattern of

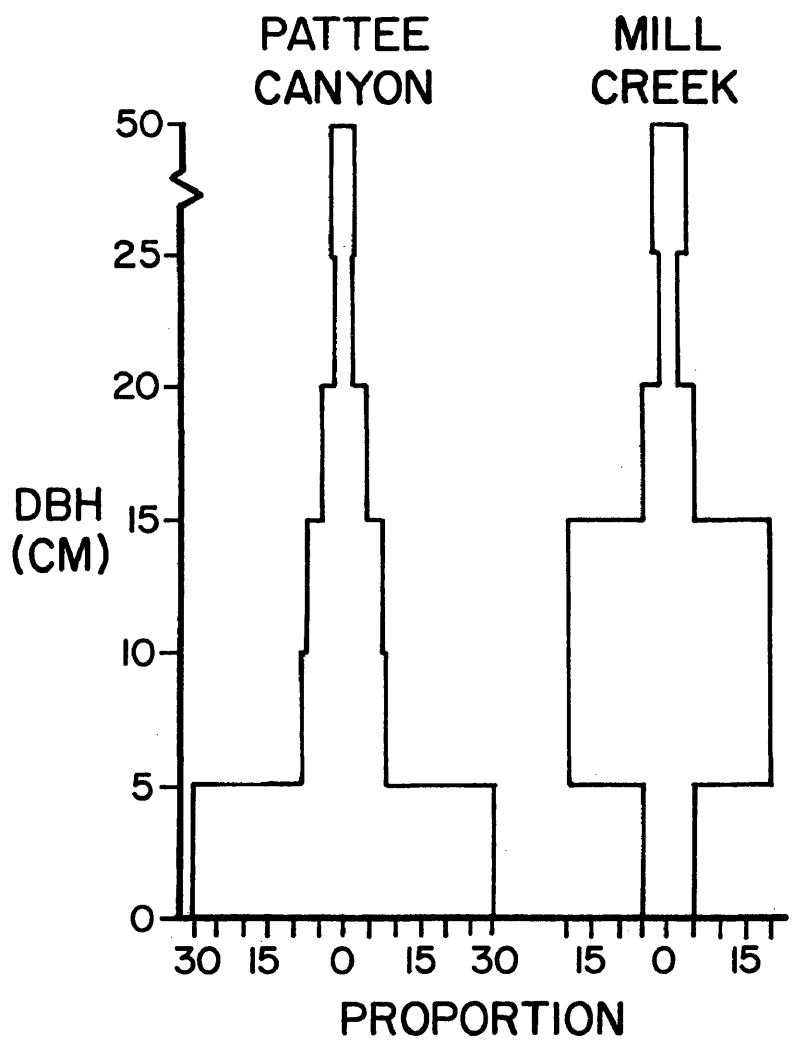Figure 3. Tree size availability at Pattee Canyon and Mill Creek.

Table 5. Tree species use by Hairy (H), Black-backed Three-toed (BB), and Northern Three-toed (N) woodpeckers.

tree species	proportion species on site (P_{i_o})	number of observations of woodpecker	proportion of observation (P_{i_o})	confidence interval on proportion of occurrence $(P_i)^a$ (95% family confidence coefficient)
H				
Pattee Canyon				
Douglas-fir	.73	10	.435	$.074 \leq P_1 \leq .796$
western larch	.10	8 ·	.348	$.000 \leq P_2 \leq .735$
ponderosa pine	.17	5	.217	$.000 \leq P_3 \leq .641$
Mill Creek				
Douglas-fir	.77	32	.571	$.000 \leq P_1 \leq 2.87$
western larch	.07	18	.322	$.069 \leq P_2 \leq .575$
ponderosa pine	.16	6	.107	$.000 \leq P_3 \leq .397$
BB				
Pattee Canyon				
Douglas-fir	.73	26	.413	$.191 \leq P_1 \leq .635*$
western larch	.10	30	.476	$.266 \leq P_2 \leq .686*$
ponderosa pine	.17	7	.111	$.000 \leq P_3 \leq .243$
Mill Creek				
Douglas-fir	.77	32	.386	$.188 \leq P_1 \leq .584*$
western larch	.07	47	.566	$.400 \leq P_2 \leq .732*$
ponderosa pine	.16	4	.048	$.000 \leq P_3 \leq .294$
N				
Pattee Canyon				
Douglas-fir	.73	10	.172	$.000 \leq P_1 \leq .446*$
western larch	.10	46	.793	$.656 \leq P_2 \leq .930*$
ponderosa pine	.17	2	.034	$.000 \leq P_3 \leq .329$
Mill Creek				
Douglas-fir	.77	1	.083	$.000 \leq P_1 \leq .718*$
western larch	.07	10	.834	$.563 \leq P_2 \leq 1.10*$
ponderosa pine	.16	1	.083	$.000 \leq P_3 \leq .718$

*Proportion tree species available (P_{i_o}) falls outside the confidence interval of use by the woodpecker.

^{a}Interval calculated by $\bar{p}_i \pm z_{(1 - \alpha/2k)} \sqrt{\bar{p}_i(1 - \bar{p}_i/n)}$ where $\alpha = .05$, $k = 3$. Comparison of interval with corresponding p_{i_o} determines over $(p_{i_o}$ falls below interval) or under $(p_{i_o}$ falls above interval) utilization.

tree use as the two three-toed species, using Douglas-fir less than expected (Table 6). The male and female Northern Three-toed Wood-peckers at Pattee Canyon differed only in the extent to which each under utilized Douglas-fir and over utilized western larch.

Table 6. Tree species use by male and female Hairy Woodpeckers at Mill Creek and male and female Northern Three-toed Wood-peckers at Pattee Canyon.

	proportion on site (P_{i_o})	number of observations of woodpecker	proportion of observation (P_{i_o})	confidence interval on proportion of occurrence $(P_i)^c$ 95% family confidence coefficient
			Hairy	
female				
Douglas-fir	.77	26	.722	$.520 \leq P_1 \leq .924$
western larch	.07	7	.195	$.000 \leq P_2 \leq .539$
ponderosa pine	.16	3	.083	$.000 \leq P_3 \leq .449$
male				
Douglas-fir	.77	6	.300	$.000 \leq P_1 \leq .730*$
western larch	.07	11	.550	$.205 \leq P_2 \leq .895*$
ponderosa pine	.16	3	.150	$.000 \leq P_3 \leq .624$
			Northern Three-toed	
female				
Douglas-fir	.73	10	.333	$.000 \leq P_1 \leq .767*$
western larch	.10	19	.633	$.379 \leq P_2 \leq .887*$
ponderosa pine	.17	1	.034	$.000 \leq P_3 \leq .451$
male				
Douglas-fir	.73	0	.000	-0-
western larch	.10	27	.964	$.882 \leq P_2 \leq 1.05*$
ponderosa pine	.17	1	.006	$.000 \leq P_3 \leq .181$

*Proportion tree species available (P_{i_o}) falls outside the confidence interval of use by the woodpecker.

^{c}Interval calculated by $\bar{P}_i \pm z_{(1-\alpha/2k)} \sqrt{\bar{P}_i(1-\bar{P}_i/n)}$ where $\alpha = .05$, k = 3. Comparison of interval with corresponding p_{i_o} determines over $(p_{i_o}$ falls below interval) or under $(p_{i_o}$ falls above interval) utilization.

Size Class Use

The mean size class (dbh) of trees used differed significantly
among all woodpecker species at both study sites except between the two
three-toed species at Mill Creek (Table 7, Fig. 4). The Hairy Wood-
pecker was most consistent from site to site in mean dbh use. The
Black-backed Three-toed Woodpecker differed the most. The intermediate
species in size class use at both sites was the Northern Three-toed
Woodpecker.

The only significant intersexual differences in mean dbh used were
in the Hairy Woodpecker at Pattee Canyon (Fig. 5) and the Northern
Three-toed Woodpecker at Mill Creek (Fig. 6). The males in each
instance used trees of a significantly greater diameter than the
females.

Foraging Height

Several differences in the mean foraging heights of males and
females of all three woodpecker species were observed (Table 7). Male
Hairy Woodpeckers foraged at significantly greater heights than females
at Mill Creek (Fig. 7). At Pattee Canyon, although the difference was
not statistically significant, the relationship was similar. The male
Black-backed Three-toed Woodpecker foraged at a mean height which was
significantly lower than the female at Pattee Canyon. Again the differ-
ence in mean heights was not statistically significant at the other
study site, but a similar relationship was observed. The relationship
in foraging heights of the male and female Northern Three-toed Wood-
pecker was inconsistent from site to site. At Pattee Canyon the male

Table 7. Interspecific and intersexual comparisons of foraging behaviors of Hairy, Black-backed Three-toed, and Northern Three-toed woodpeckers (means ± standard error).

species and sex	Mill Creek				Pattee Canyon			
	N	dbh(cm)	N	height(m)	N	dbh(cm)	N	height(m)
Hairy								
male	36	15.60 ± 1.06	38	9.48 ± 0.87	6	22.00 ± 1.84	16	3.24 ± 1.05
female	21	15.29 ± 0.96	26	6.64 ± 0.90	6	13.50 ± 2.63	9	2.78 ± 1.04
species mean	57	15.66 ± 0.73	64	8.33 ± 0.65	12	18.18 ± 2.04	25	3.15 ± 0.71
Black-backed								
male	47	13.00 ± 0.50	59	4.92 ± 0.53	17	25.06 ± 1.92	24	3.02 ± 0.47
female	32	13.72 ± 1.29	33	5.97 ± 0.80	17	26.82 ± 3.32	28	5.61 ± 0.73
species mean	79	12.45 ± 0.98	92	5.31 ± 0.45	34	25.51 ± 1.91	52	4.51 ± 0.50
Northern								
male	7	16.14 ± 1.83	8	6.86 ± 1.74	9	22.22 ± 1.14	29	2.12 ± 0.65
female	9	11.00 ± 1.27	11	5.71 ± 0.97	10	18.50 ± 2.09	26	4.56 ± 0.65
species mean	16	13.25 ± 1.23	19	6.20 ± 0.90	19	20.26 ± 1.30	55	3.81 ± 0.60

Brackets denote signifiant differences between means (Student's t-test p < 0.05).

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Figure 4. Tree size use by the Hairy, Black-backed Three-toed, and Northern Three-toed woodpeckers at each study site.

PATTEE CANYON

MILL CREEK

N=12   N=32   N=19   N=57   N=79   N=16

DBH (CM)

50
25
20
15
10
5
0

15 0 15   15 0 15   15 0 15   15 0 15   15 0 15   15 0 15
HAIRY BLACK-BACKED NORTHERN   HAIRY   BLACK-BACKED   NORTHERN

PROPORTION USE
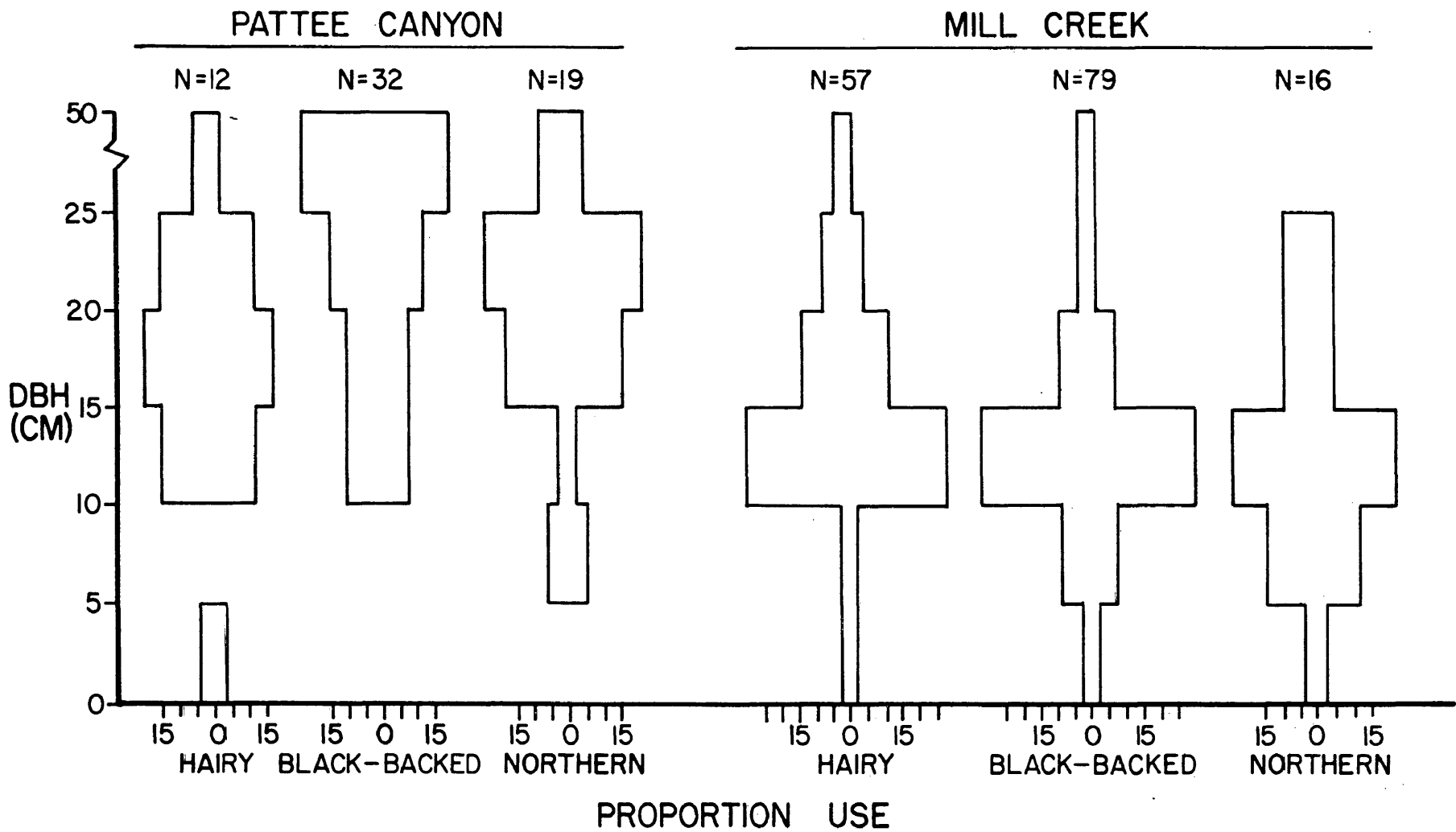
Figure 5.   Tree size use by male and female Hairy Woodpeckers at
            Pattee Canyon.

PATTEE CANYON
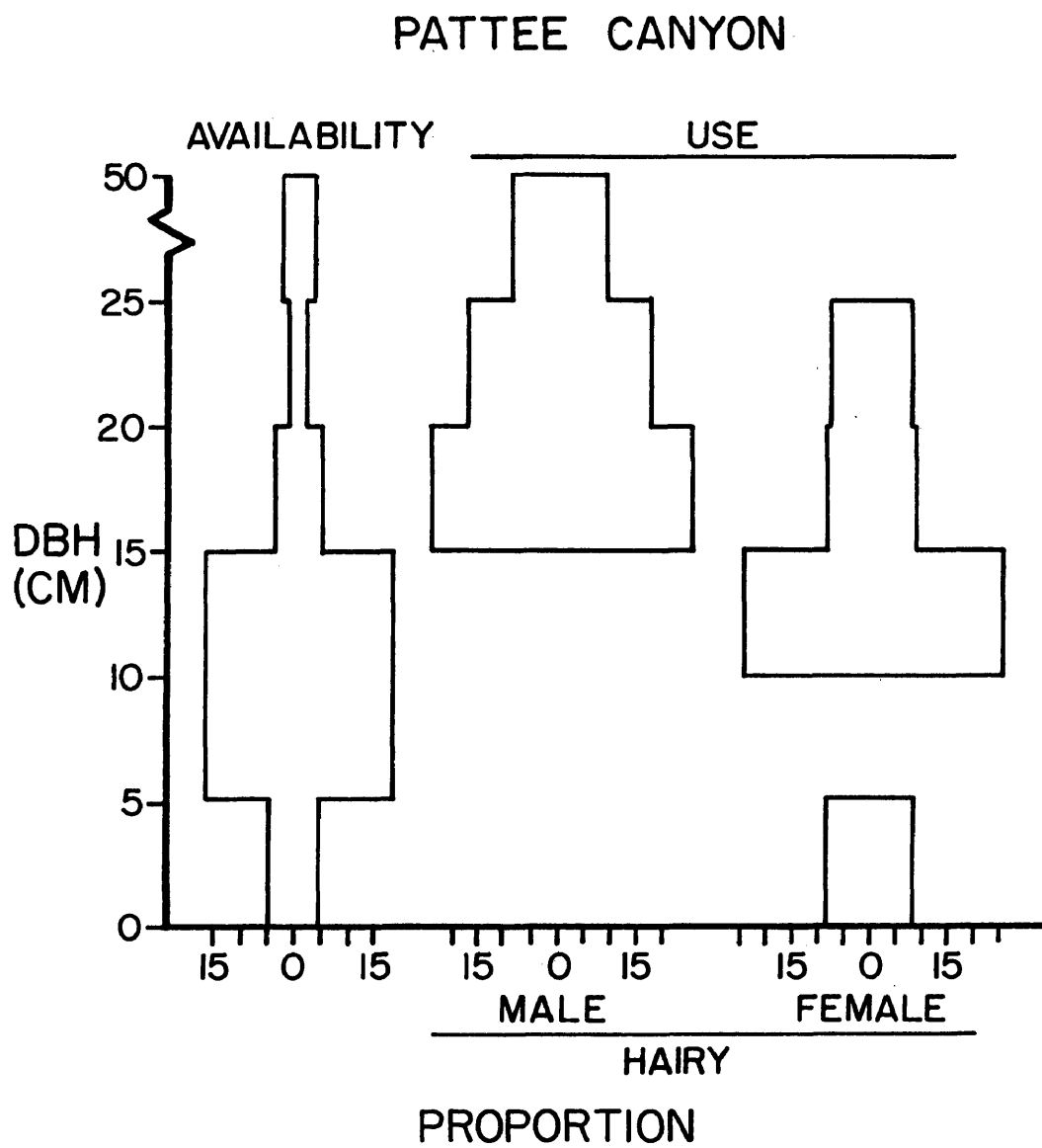
Figure 6. Tree size use by male and female Northern Three-toed Woodpeckers at Mill Creek.

MILL CREEK

PROPORTION
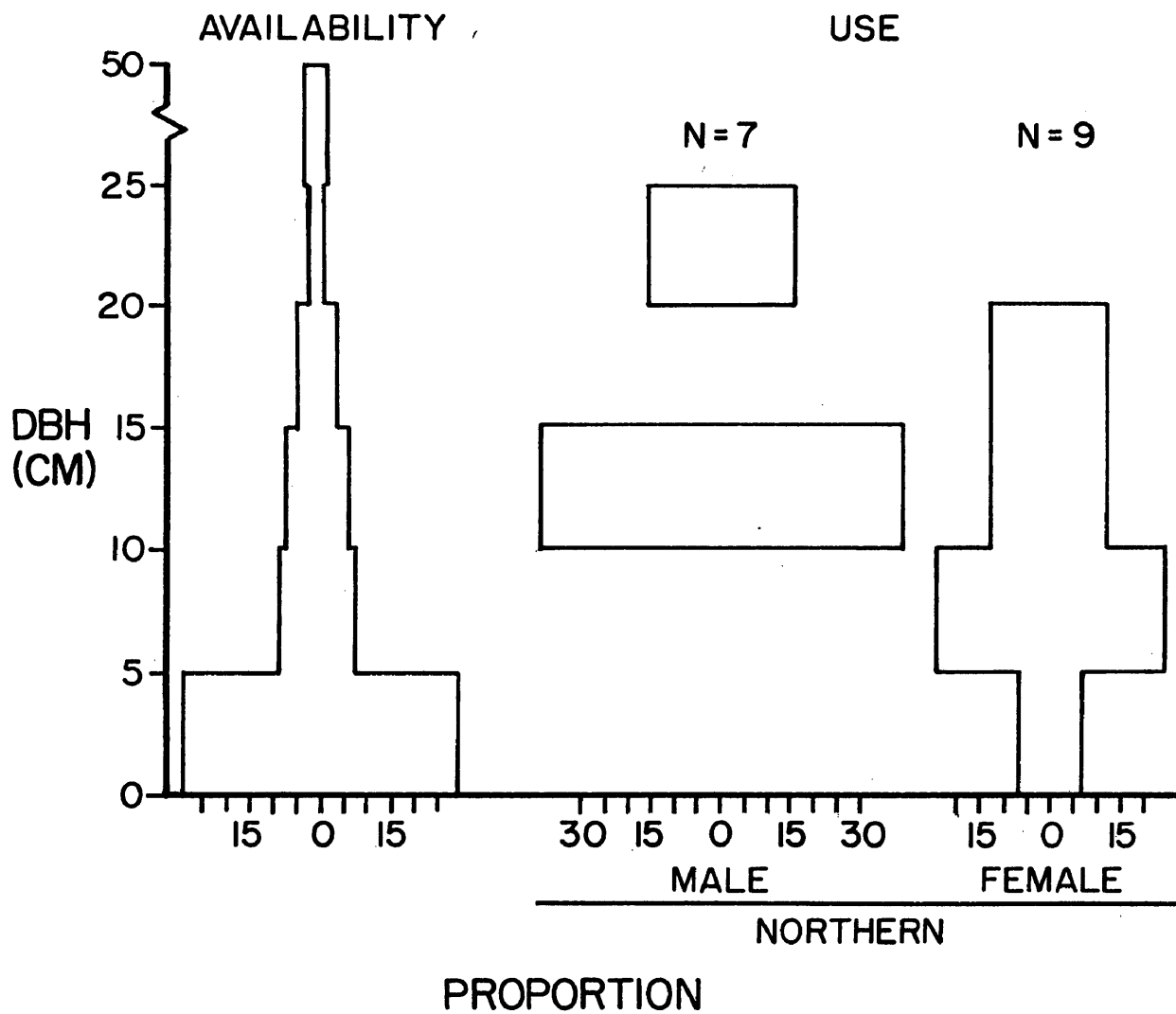
Figure 7. Foraging heights of male and female Hairy Woodpeckers
at Mill Creek. Areas within polygons represent %
observations at that height.

MILL CREEK

N = 38   N = 26

FORAGING HEIGHT (M)

13 +

10-12

7-9

4-6

0-3

15   0   15   15   0   15

MALE   FEMALE

PROPORTION USE
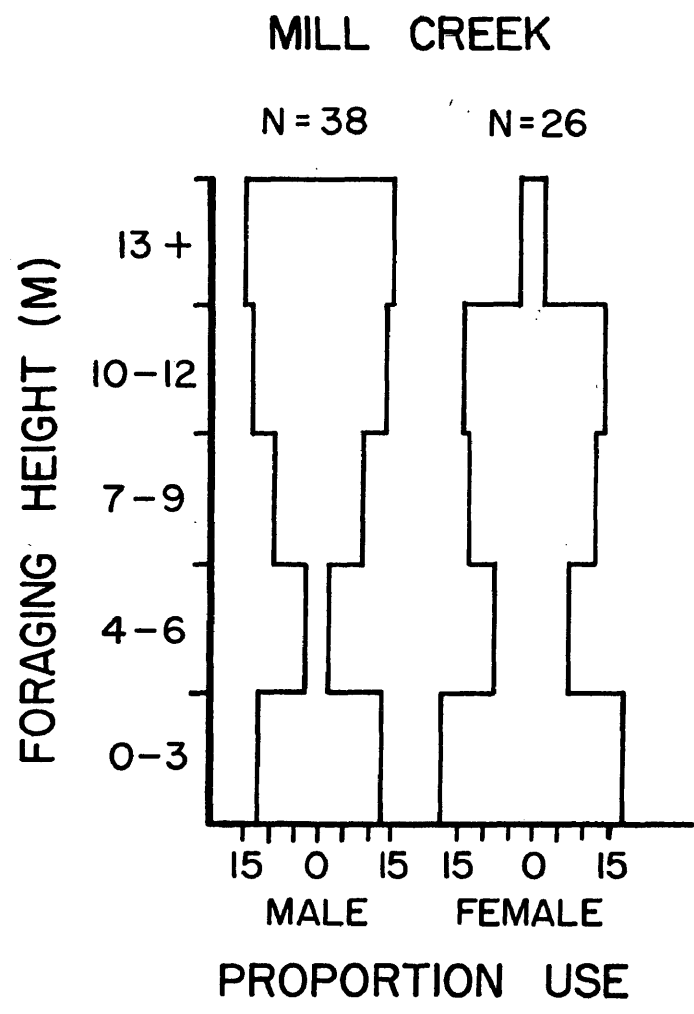
foraged at a significantly lower height than the female (Fig. 8). At

Mill Creek the sexes foraged at similar heights, the male's mean

slightly higher than the female's.

Only one significant interspecific difference in foraging heights

was observed. This difference occurred between the Hairy and the Black-

backed woodpeckers at Mill Creek. In this comparison the Hairy Wood-

pecker foraged at a mean height 3 m above that of the Black-backed

Three-toed Woodpecker (Table 7).

Foraging Technique

I observed no significant intersexual differences in foraging

technique among the three species of woodpeckers. Interspecific

differences, however, were observed. The Hairy and Black-backed Three-

toed woodpeckers each pecked 80% or more of the observed foraging bouts

(Table 8). The majority of the remaining time was spent probing by

the former species and scaling by the latter. The Northern Three-toed

Table 8. Foraging techniques used by each woodpecker species. Data
combined for both sites (% observations).

| woodpecker species | technique | | | N |
	pecking	scaling	probing	
Hairy	82	5	13	83
Black-backed Three-toed	80	19	1	137
Northern Three-toed	54	33	13	68

Figure 8. Foraging heights of male and female Black-backed and
          Northern Three-toed woodpeckers at Pattee Canyon.

PATTEE CANYON

FORAGING HEIGHT (M)

N=24   N=28   N=29   N=26

13 +
10-12
7-9
4-6
0-3

30 15 0 15 30   15 0 15   45 30 15 0 15 30 45   15 0 15

MALE   FEMALE   MALE   FEMALE

BLACK-BACKED   NORTHERN

PROPORTION USE
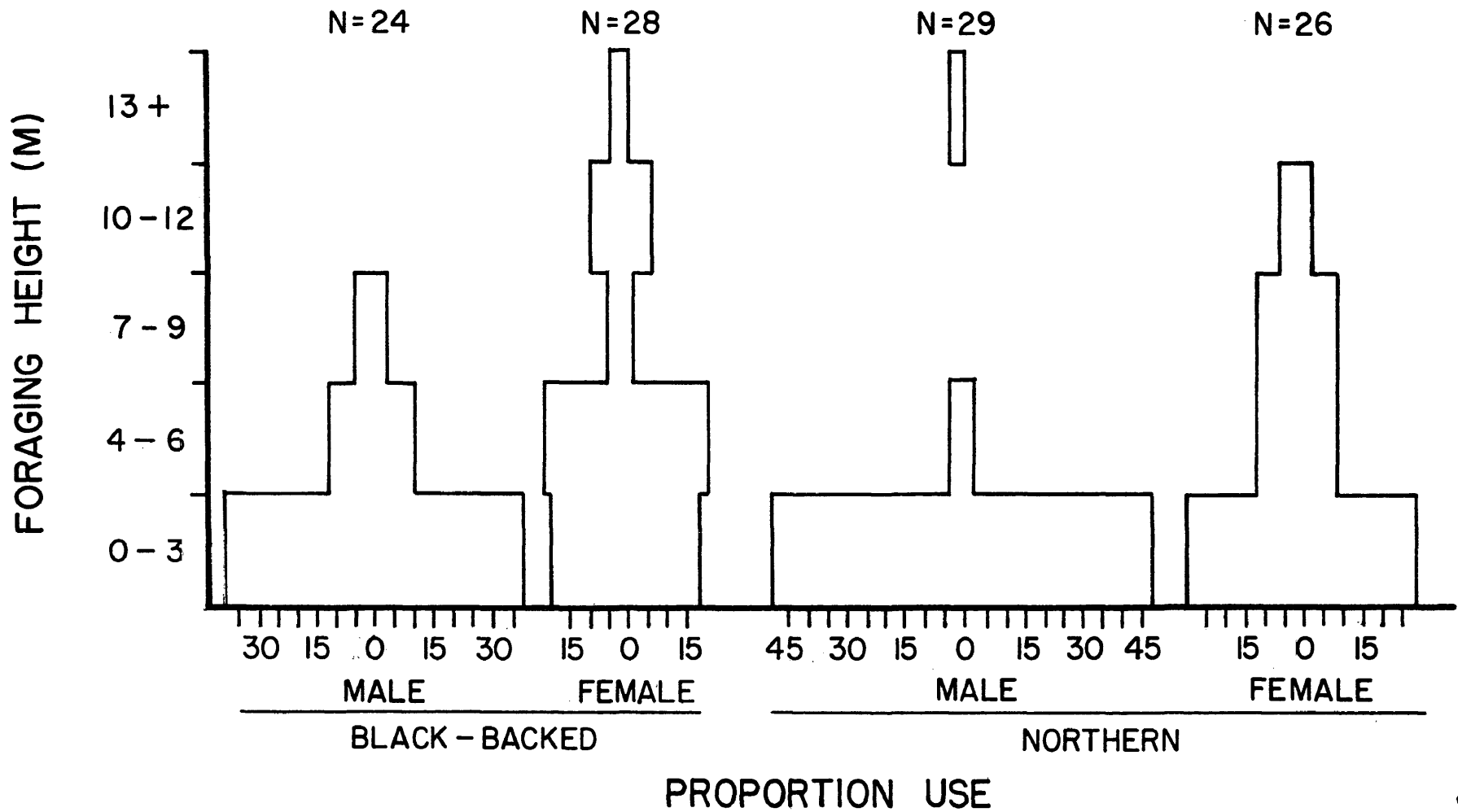
Woodpecker employed pecking far less and scaling far more than the
other two _Picoides_ woodpeckers.

Determination of Sexual Dimorphism

I grouped the museum specimens of the two three-toed woodpecker
species into subspecies based on their collection location (Bangs 1900,
Bent 1964). The two subspecies occurring in Montana are _P. arcticus
arcticus_ and _P. tridactylus dorsalis_; I measured five specimens of each
sex of the former and five males and four females of the latter sub-
species. All measurements, including those of specimens of subspecies
occurring elsewhere are included in Appendix A.

Many of the specimens were collected during molt, and the tail
consisted of pinfeathers. For this reason I did not include tail
measurements in my analysis.

Specimens of the subspecies of the Northern Three-toed Woodpecker
present on the study sites (_P. t. dorsalis_) displayed a low percentage
of joint nonoverlap. From my measurements of nine specimens of _P. t.
dorsalis_ I derived values of 75-80% joint nonoverlap in culmen length.
In addition, the joint nonoverlap values for tarsus and wing lengths
were both below 75%. Bangs (1900) listed measurements of five males
and five females of this subspecies. From the means and standard
deviations derived from these measurements I calculated joint nonoverlap
for the culmen and wing to be at least 85%.

For the ten specimens of _P. a. arcticus_ I measured, the joint non-
overlap for the sexes was less than 75% for both culmen and wing length.
By taking the means and standard deviations for Bangs' (1900)

measurements of 30 specimens (19 males and 11 females) I derived quite different values. Joint nonoverlap for the culmen was 92%, the tarsus 93%, and the wing greater than 96%.

Insect Distributions

Coleopterans were the most numerous insects in the wood with an overall total six times greater than all other insect orders combined. Members of three families were most common: Buprestidae, Cerambicidae, Scolytidae. Hymenopterans present included members of the families Siricidae, Braconidae, and Aulacidae (Table 9).

Among the cerambicids $\underline{Xylotrechus}$ $\underline{longitarsus}$ was the most common. This species occurred in the lower and middle sections of western larch (Kruskal-Wallis H_2 = 7.891, Dunn's (1964) multiple comparison procedure). $\underline{Monochamus}$ $\underline{scutellatus}$, the next most numerous cerambicid, occurred with equal frequency in the upper and middle sections of all three tree species.

The flat-headed woodborers, buprestids, occurred in significantly greater numbers in Douglas-fir and western larch than in ponderosa pine. Of the 103 adults I collected, 97 were in lower sections of the tree.

The most numerous coleopterans were bark beetles (Scolytidae) of the genus $\underline{Dendroctonus}$. Of the 114 individuals 104 occurred in ponderosa pine at all heights. $\underline{Ips}$ also occurred most commonly in ponderosa pine (84 of 92 individuals). This genus attacked the upper sections of the trees.

$\underline{Scolytus}$ were present in only three tree sections of Douglas-fir,

Table 9. Insects found in tree species and sections taken from Mill Creek approximately one year post-fire (May 1980).

family or species	tree species			tree section			totals
	Douglas-fir	ponderosa pine	western larch	upper	middle	lower	
Aradidae	10	7	3	3	1	16	20
Buprestidae							
Melanophila acuminata and M. drumondi	52	4	47	2	5	96	103
larvae	14	1	18	6	9	18	33
Eunemidae (Melasidae)							
Cleridae	0	2	1	0	1	2	3
Trogositidae (Ostomidae)	6	2	3	0	0	11	11
Cerambicidae							
Rhagium inquisitor	0	1	0	0	0	1	1
Tetropium velutiuum	0	0	8	3	3	2	8
Xylotrechus longitarsus	11	7	25	0	14	19	33
Acanthocinus obliquus	0	9	0	3	5	1	9
Monochamus scutellatus	7	11	2	5	14	1	20
larvae	62	41	55	52	42	59	153
Crysomelidae	0	4	0	1	0	3	4
Scolytidae							
Dendroctonus sp.	1	104	9	21	12	81	114
Ips pini	0	84	4	43	6	43	92
Scolytus sp.	86	0	0	15	2	69	86
Lonchaeidae	2	44	3	9	17	23	49
Siricidae	1	6	8	4	2	9	15
Braconidae	12	1	7	1	10	9	20
Aulacidae	4	0	7	0	0	11	11

each section from a different height category. Two of the sections of Douglas-fir in which these beetles occurred were from the same bole.

In addition to collecting adult and larval insects I counted buprestid, cerambicid, and scolytid emergence holes. The combined sections had totals of 271, 259, and 2086 holes, respectively. The frequency at which I observed both flat- and round-headed woodborer emergence holes was statistically the same for all tree species and section heights. However, bark-beetle emergence holes were present in far greater numbers in ponderosa pine sections at each height category.

The dipterans (family Lonchaeidae) were located predominantly in ponderosa pine sections. The hymenopterans and the hemipteran I collected did not occur predominantly in any one tree species or height category.

Discussion

The foraging behavior of a single species of woodpecker may vary from one study to another as a result of several factors. Jackson (1970) pointed out the influence of food abundance on niche partitioning. Stomach content analyses for the Northern Three-toed Woodpecker reported by Beal (1911), Stallcup (1962), and Koplin (1967) indicated a large degree of variation in diet. Also, the presence or absence and densities of congeners may greatly effect the foraging strategies of a species from one location to another.

Of the foraging parameters in this study--tree species use, tree size use, foraging method, and foraging height--the first three appear to aid the species in niche partitioning; the latter may allow the

sexes to segregate their activities.

Tree Species and Foraging Technique

At both study sites Hairy Woodpeckers were more general in their use of tree species than were the two three-toed woodpecker species. Koplin (1969) found the Hairy to be the most generalized species using each tree species with similar frequency. He observed the Northern Three-toed Woodpecker 72% of the time on Engelmann spruce (Picea engel-manii), the dominant tree species. I found the Northern feeding on western larch, a species comprising only 8.5% of the available trees, an average of 82% of the observations. In tree species use the Northern was the most specialized of the three woodpecker species in this study.

I believe the observed differences in foraging technique employed by the three woodpecker species were a consequence of their tree species use. All three woodpecker species pecked the majority of the time, but differed in technique used in the remaining observations. The remainder of the foraging bouts were spent probing by Hairy Woodpeckers with little (5%) of their time spent scaling. The pattern was quite different for the two three-toed species. Each of these woodpeckers employed scaling in the greatest number of remaining feeding observations, the Northern spent almost twice as much time scaling as the Black-backed Three-toed Woodpecker. Both of the three-toed species, particularly the Northern, used western larch more than the other two conifers. Following scorching, the bark of this tree species is easily removed by scaling. The bark of ponderosa pine will also flake off, but far less readily than western larch whereas scorched Douglas-fir bark

strongly adheres to the wood. Hogstad (1977) reported scaling as the technique most often employed by the Northern Three-toed Woodpecker and also related this to the condition of the trees on which the birds foraged.

I observed only two instances in which significant differences in tree species use by the sexes occurred. In the first case female Hairy Woodpeckers displayed a pattern of use more similar to that of the three-toed species than that of male Hairy Woodpeckers. Kilham (1965) noted a similar observation when he described tree species use by Black-backed Three-toed Woodpeckers. He observed Black-backs feeding on elms (Ulmus spp.) and white pine (P. strobus), two tree types "especially attractive to females of D. villosus" at his study sites (p. 142).

The Northern Three-toed Woodpecker displayed the other instance of divergence of the sexes in their utilization of the three tree species. Both sexes favored western larch, but the female did so almost to the total exclusion of the other tree species: 27 of 28 observed foraging bouts.

Tree Size Class

Interspecific differences in tree size use were more numerous than intersexual differences. The only comparison of woodpecker species pairings at either site which did not reveal a statistically significant difference in mean dbh was between the two three-toed species at Mill Creek. This may be a result of the contracted distribution of size classes available at this site. At Mill Creek 56% of the trees available had diameters between 1 and 5 cm (Fig. 3). Trees

of this small size are not often attacked by wood- and bark-inhabiting insects (Furniss and Carolin 1977). In the majority of the observed feeding bouts both three-toed woodpeckers utilized trees with diameters between 11 and 15 cm (the Black-backed 58% and the Northern 43%). At Pattee Canyon, where the sample size was six times greater than at Mill Creek, I detected a significant difference in mean dbh use between the two three-toed woodpeckers (Table 7). At this site the distribution of tree sizes was less skewed than that at Mill Creek. In addition, over-lap values in tree size class use were greater for Mill Creek across all woodpecker pairings than those for Pattee Canyon.

The Northern Three-toed Woodpecker at Mill Creek displayed one of the two statistically significant intersexual differences in size class use. The males used significantly larger trees than the females. Hogstad (1976) observed the same intersexual relationship for the Northern in Norway. The other significant difference in size class use by the sexes occurred with the Hairy Woodpecker at Pattee Canyon where males foraged on significantly larger trees than females. The intrinsic significance of each of these intersexual differences in tree size class use is questionable due to nonindependence among the observations; only two birds were observed in each case.

Foraging Height

I found a greater number of differences between the sexes of the three woodpecker species in foraging height in contrast to tree species, foraging technique, and size class use all for which inter-specific differences were more numerous than intersexual. The only

significant interspecific difference in mean foraging heights was between the Hairy and the Black-backed Three-toed Woodpeckers at Mill Creek. In his study of the two three-toed woodpeckers Short (1974, p. 7) reported "that Northern Three-toed Woodpeckers foraged higher in trees...than Black-backs," but presented no supporting data. In contrast, I observed no significant differences between the two three-toed woodpeckers in regard to foraging height.

The intersexual differences in foraging height were numerous at both study sites and occurred within all three woodpecker species. In this study Hairy Woodpecker males foraged higher on the trees than females. Ligon (1968) and Hooper and Lennartz (1981) all observed a similar relationship in the foraging heights of male and female Red-cockaded Woodpeckers (P. borealis). Except at Mill Creek, where my observations of the Northern Three-toed Woodpecker were limited, males of both three-toed species foraged significantly lower than females. Bull (1980) observed no differences in foraging heights of the two three-toed species. Hogstad (1976) found that male Northern Three-toed Woodpeckers in Norway foraged at a lower height than females. Male Nuttal's Woodpeckers (P. nutallii) were also reported to forage lower than females (Jenkins 1979).

Sexual Dimorphism and Prey Acquisition

The apparent lack of significant sexual dimorphism in the specimens of Black-backed Three-toed Woodpeckers (P. a. arcticus) I measured is probably a product of sample size. Bangs (1900) listed measurements of 30 specimens of the subspecies, three times the number I was able to examine. For this reason I believe the degree

of joint nonoverlap I calculated from his data is more representative of this species. The consistency in the coefficients of difference (and joint nonoverlap values) for all parameters; culmen, wing, and tarsus, implies the high degree of sexual dimorphism is not limited to trophic structures. Based on these results the Black-backed Three-toed Woodpecker appears to be highly sexually dimorphic, comparable to the Hairy Woodpecker in degree of dimorphism (Selander 1965, Holmgren 1979).

The 75-80% joint nonoverlap in culmen length I report for the sexes of the Northern Three-toed Woodpecker (P. t. dorsalis) is in agreement with Koplin's (1967) findings for the subspecies. P. t. dorsalis exhibits a greater degree of joint nonoverlap in culmen than in wing or tarsus length. Hogstad (1976) reported similar findings for P. t. tridactylus. The greater degree of dimorphism in trophic structures may be related to a divergence in foraging behavior between the sexes (Selander and Giller 1963).

The intersexual difference in culmen length may allow the acquisition of different prey (Austin 1976). After analyzing the stomach contents of male and female Hairy, Downy, and Northern Three-toed woodpeckers Massey and Wygant (1954) reported a greater proportion of beetles in the stomachs of the males of all three species. Williams (1980) observed male and female Downy Woodpeckers taking different prey: males took ants while females took homopterans and spiders.

Beal (1911) found wood-boring beetles (buprestids and cerambicids) comprised 64 and 61% of the diets of the Black-backed and Northern Three-toed Woodpeckers, respectively, based on stomach content

analyses. Cerambicids were more numerous than buprestids in the tree sections I examined. The species of cerambicids that occurred most frequently, Xylotrechus longitarsus, was found in sections of larch. The two three-toed woodpeckers and the female Hairy Woodpeckers, through their extensive use of larch, may have been specializing on this insect.

The flat-headed woodborers, the buprestids, occurred almost exclusively in Douglas-fir and western larch. These beetles appeared to specialize along the height gradient, occurring in the lower tree sections 94% of the time. Again, this could be related to the lower foraging heights at which I observed both male three-toeds and female Hairy Woodpeckers. Hogstad (1977) also found that cerambicid and scolytid numbers decreased as height above ground increased, which may have been related to the lower height at which he observed male Northern Three-toed Woodpeckers foraging.

Distributions of the insects among the tree species and heights in this study may be related to observed differences in the foraging behaviors of the three woodpecker species. Further study may correlate tree diameter with insect distributions and woodpecker foraging patterns.

Conclusion

The foraging behaviors of many species of North American wood-peckers have been studied. Austin (1976) summarized the results of 13 studies of the foraging behaviors of eight species of Picoides woodpeckers. He noted whether significant intersexual differences

in plant species, technique, or site (position on foraging substrate) were observed. Results conflicted for each species studied, which is to be expected when comparing birds from different areas (Kilham 1965). However, the parameter for which the sexes of all species studied were most often found to differ in their use was foraging site, which is comparable to my measurement of height.

The results of my study were consistent with this trend. Foraging height differed most often between the sexes. The other parameters appeared to be used to separate the species rather than the sexes within a species.

This difference in the foraging behaviors of the sexes of the three woodpecker species may be related to the pattern of tree growth I have observed at my study sites. The three conifers at my study sites often grew in aggregations of trees of the same species and age, which in turn resulted in trees of similar size within a clump. The sexes of each of the three woodpeckers used the same tree species, employed the same foraging techniques (which appeared to be matched to the foraging site substrate), and used trees of similar size classes. If the members of a pair of woodpeckers were foraging together this was to be expected in forest as described above. The members of a pair of woodpeckers may forage together differing little in their use of tree species, size class, and method, yet stratifying themselves vertically. The ability to partition the niche in this manner is particularly valuable to a pair of woodpeckers during the breeding season when it may "enable them to work the more limited resources of their immediate environment to best advantage in the task of feeding themselves and young" (Kilham 1965, p. 144).

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CHAPTER III

NEST-SITE SELECTION AMONG WOODPECKERS

IN FOREST BURNS

Introduction

Large numbers of wood- and bark-boring beetles are attracted to

recently burned forests. Woodpeckers concentrating in response to

these insect infestations have been reported by Blackford (1955), Bock

and Lynch (1970), and Taylor and Barmore (1980).

During 1979-1981, woodpecker concentrations were studied near

Missoula, Montana in two areas which had recently burned. Hairy

(Picoides villosus), Black-backed Three-toed (P. arcticus), and Northern

Three-toed (P. tridactylus) woodpeckers and the Common Flicker

(Colaptes auratus) nested within the Pattee Canyon and Mill Creek burns.

This paper presents a comparison of nest sites selected by these

woodpeckers.

Study Sites

In July, 1977 a fire burned 480 ha along the north-facing slopes

of Pattee Canyon, which lies 3 km to the southeast of Missoula,

Montana. The canyon forest was composed of (in order of decreasing

abundance) Douglas-fir (Pseudotsuga mensiezii), ponderosa pine (Pinus

ponderosa), and western larch (Larix occidentalis). All trees, except

a few pockets within ravines, were killed by the fire and remained

standing. Mean density of trees was 1040 per hectare. A 25 ha area was

thinned following the fire leaving 125 trees per hectare.

Mill Creek is 45 km southwest of Missoula. In August, 1979 a fire burned 120 ha of forest similar in composition to Pattee Canyon (Table 2, Chp. 1). The area was salvage logged following the fires and approximately 830 trees per hectare remained.

Methods

During the breeding seasons in 1979, 1980, and 1981 at Pattee Canyon and 1980 and 1981 at Mill Creek, I located active (containing eggs or nestlings) woodpecker nests by following adults and listening for excavation sounds or vocalizing young. At the time of nest location I collected excavation chips at the base of the nest trees of the three Picoides woodpeckers. I analyzed these chips to determine their specific gravity as an indication of the presence of decay. The chips at the nest of Common Flickers were all from visibly decayed wood.

After the young had fledged I recorded species and diameter at breast height (dbh) for each nest tree and all trees within a 0.04 ha circular plot surrounding the nest. I also recorded height and orientation of nest holes. To derive estimates of nest tree availability I made similar characterizatons of six plots at intervals of 100 m along transects in each of the following: the uncut and cut portions of the Pattee Canyon burn and the uncut, cut, and edge areas of the Mill Creek burn.

I used the Mann-Whitney U test to determine if the differences among the woodpecker species in mean dbh of nest tree, hole height, and density of trees at the nest sites were significant (Daniel 1978).

The chi-square test of goodness of fit determined if the woodpeckers were using the tree species in proportion to their availabilities. By computing confidence intervals with the Bonferoni Z statistic (Neu et al. 1974) an assessment of use compared to availability by woodpeckers of specific tree species was made.

Results and Discussion

Tree species availabilities were similar at the two study sites. I therefore used averages for all use and availability comparisons and combined nests from both sites. I located a total of 32 nests: 14 Hairy, 6 Black-backed Three-toed, 3 Northern Three-toed, and 9 Common Flicker nests.

A significantly greater number of nest holes was located in western larch and fewer in Douglas-fir than expected based on availability ($x^2 = 56.97$, df = 2) (Table 10). McClelland et al. (1979) observed a similar preference by woodpeckers for western larch. In

Table 10. Tree species used by woodpeckers for nesting. Nests from both study sites considered simultaneously.

	Douglas-fir	Ponderosa Pine	Western Larch
Hairy	3	4	7
Black-backed Three-toed	2	1	3
Northern Three-toed	2	0	1
Common Flicker	3	2	4

the analysis by bird species, only the Hairy Woodpecker showed a statistically significant deviation in tree species use compared to availability (x^2 = 42.90, df = 2). Here again, western larch was utilized more often than expected (Table 10). The other three species also used western larch more often than expected when tested together. McClelland (1977, p. 123) related the high degree of use of western larch by woodpeckers to this species' "comparative absence of sapwood decay." Unlike Douglas-fir, western larch maintains a hard shell of sapwood while the heart wood decays creating an "ideal" nesting site for excavators.

Analysis of excavation chips indicated that 87% of the nest sites were in decayed wood. Only two Hairy and two Black-backed Three-toed nests were located in apparently sound wood. Of the four species of woodpeckers considered in this study the Hairy and Black-backed Three-toed are the strongest excavators (Spring 1965).

The three Picoides woodpeckers utilized nesting trees of similar diameters (Mann Whitney U, α = .05)(Table 11). All three species differed significantly from the Common Flicker, which tended to use trees of a greater dbh. This pattern is not surprising when the relative sizes of the birds and their respective nest cavities are considered: Hairy, Black-backed Three-toed, and Northern Three-toed cavities are approximately 11.3 cm wide while the Common Flicker's is 18.8 cm (Harrison 1978).

The two three-toed species were similar in all nest site characteristics (Table 2). Each species nested in small trees at low heights. Considering the inverse relationship between tree diameter

Table 11. Means (± standard error) of nest site parameters for each species of woodpecker.

	N	dbh nest tree (cm)	nest hole height (m)	no. trees/ha at nest site
Hairy Woodpecker	14	28.02 ± 3.92	6.18 ± 3.74	933.33 ± 209.40
Black-backed Three-toed Woodpecker	6	23.33 ± 2.81	3.70 ± 0.46	1170.83 ± 137.14
Northern Three-toed Woodpecker	3	21.33 ± 5.46	3.80 ± 1.50	1141.67 ± 193.82
Common Flicker	9	34.33 ± 4.29	6.16 ± 1.76	400.56 ± 146.40

Brackets denote significant differences in means (Mann-Whitney U test, Daniel 1978).

and height along the trunk it is probably necessary for these birds to excavate nearer the base when small trees are used so that the nest cavity can be accommodated. Short (1979) pointed out that larger woodpeckers occasionally take over and enlarge the nest sites of smaller woodpeckers. He speculated that by excavating in small diameter trees the smaller woodpeckers may be mitigating this form of competition.

The Black-backed Three-toed and Northern Three-toed woodpeckers also nested in areas of comparable tree densities. Although the differences were not statistically significant, the two three-toed woodpeckers nested in areas of the highest tree densities when compared to Hairy Woodpeckers, which were intermediate, and Common Flickers which nested in the most open sites. Bull (1981) found Hairy Woodpeckers nesting in areas with fewer trees/ha than Common Flickers. McClelland (1977) found Northern Three-toed Woodpeckers nesting at sites of highest basal area followed by the Hairy and Black-backed

Three-toed woodpeckers and finally the Common Flicker.

There was a tendency among the woodpeckers in this study to orient their nest-cavity entrances to face east and avoid west:

$$east (NE + E + SE) = 59\% \ (19 \ nests)$$

$$north (NE + N + NW) = 34 \ (11)$$

$$west (NW + W + SW) = 19 \ (6)$$

$$south (SE + S + SW) = 38 \ (12)$$

A southeast orientation has been reported by several other authors (Bent 1939, Pynnonin 1939, Blume 1961, Lawrence 1967, Dennis 1969, McClelland 1978). However, other studies have reported orientations in directions other than south and east. Many explanations have been offered for nest hole orientation and McClelland (1977) provided a thorough review of these studies. An additional explanation is the possible tendency for the excavating adult to position itself in the sun. Most woodpeckers are residents and begin nest-hole excavation early in the spring. Days are still cool and mornings cold. By working on the sunny side of the tree the birds may be warming themselves. This could be a proximate factor which may have its evolutionary basis in the ultimate factor of increased warmth in the cavity for eggs and young, which some authors have suggested (Pynnonin 1939, Blume 1961, Lawrence 1967).

Among the Common Flicker and the Hairy, Black-backed Three-toed, and Northern Three-toed woodpeckers, the two three-toed species were most similar in nest-site selection within the Mill Creek and Pattee Canyon burns. Each of the three-toed woodpeckers nested in small

trees, at low heights, and in the densest stands of trees. There
was a strong tendency among the woodpeckers of these two burns to nest
in western larch far more often than expected considering the availa-
bility of this tree species. This indicates the importance of western
larch in providing suitable nesting-site substrate for woodpeckers
in early post-fire habitat in the forests of the northern Rocky
Mountains.

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CHAPTER IV

MANAGEMENT RECOMMENDATIONS

Background

Periodic fires have been an integral part of the northern Rocky

Mountain ecosystem for hundreds of years (Howe 1973, Weaver 1974).

Fires promote a mosaic of avian habitats which include recently burned

patches with standing dead trees, brush fields, and mature forests. A

succession of bird species able to utilize the various habitats

accompanies the vegetational succession following fire. Reports of

Blackford (1955), Bock and Lynch (1970), Theberge (1976), Gniadek

(1977), and Taylor and Barmore (1980) indicate that woodpeckers, par-

ticularly the Hairy (Picoides villosus), Black-backed Three-toed (P.

arcticus), and Northern Three-toed (P. tridactylus) readily exploit

early (1-4 years) post-fire habitat. These woodpeckers have been

considered an important component of the forest ecosystem in main-

taining potentially harmful insects at endemic levels (Massey and

Wygant 1954, Baldwin 1968, Beebe 1974).

Recommendations

This note proposes guidelines for post-fire logging which would

mitigate the loss of critical components of this heavily used wood-

pecker habitat. These recommendations have been developed from a

three-year breeding season study of habitat use by woodpeckers of early

post-fire burns near Missoula, Montana, as discussed in preceding

chapters.

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Recommendations include: 1) leaving western larch (Larix

occidentalis) where possible, 2) leaving as many trees with dbh of

at least 34 cm as possible, 3) leaving patches of uncut forest through-

out the burn, and 4) delaying logging operations until mid- to late

summer.

Rationale

Woodpeckers at the Pattee Canyon and Mill Creek burns near Missoula,

Montana, used western larch for nesting in a far greater proportion than

this species was available. This was particularly evident for the two

three-toed woodpeckers. In addition, the three-toed species foraged

primarily in western larch. McClelland (1977) suggested that hole

nesters adapted to the use of larch in order to remain within forest

burns as this species is usually the only large tree remaining

following fire. This adaptation appears particularly strong for the

Black-backed and Northern Three-toed woodpeckers, each of which is a

far less common species than the Hairy.

The two three-toed woodpeckers were able to successfully nest in

trees of dbh as small as 13 cm, although the average dbh of nest trees

was 22 cm. The Hairy Woodpecker and Common Flicker (Colaptes auratus)

used trees with an average dbh of 28 and 34 cm, respectively. High

stumping of trees over 35 cm dbh may insure nesting sites for flickers,

which tend to nest nearer to the ground than do other species.

Leaving several trees of diameters of at least 30 cm should be planned

in order to insure a supply of trees suitable for nesting and feeding

in by Hairy and three-toed woodpeckers.

Of the four woodpecker species nesting within my two study sites the three-toed species excavated their cavities within the densest stands of trees. The post-salvage nesting habitat could be enhanced for these woodpeckers by leaving patches of uncut forest throughout the burn.

The timing of timber salvage efforts may be critical to birds. Whenever possible, cutting and transporting trees should be avoided from mid-April through June. During this period woodpeckers are excavating nest cavities, incubating eggs, and feeding nestlings. The birds are restricted in their movements and if continually disturbed may abandon the nest. By July the woodpeckers are more mobile as the young have usually left the nest and disturbance in the area could be better tolerated.

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APPENDIX A

MORPHOLOGICAL MEASUREMENTS OF SPECIMENS OF

Picoides arcticus AND P. tridactylus

Appendix A. Measurements of museum specimens of Black-backed (Picoides arcticus) and Northern (P. tridactylus) Three-toed Woodpeckers. Linear measurements in mm, weight in gm. (M - male, F - female)

Species	Sex	Culmen	Tail	Tarsus	wing	Weight	Length	Collection Location
P. arcticus	M	34.94	80.91	20.47	130.28	-	-	Alaska
P. arcticus	M	30.77	84.62	20.28	130.20	73.5	-	Washington
P. arcticus	M	29.12	74.85	20.28	123.31	-	-	Ohio
P. arcticus	M	34.09	62.28	20.69	129.97	-	-	Washington
P. arcticus	M	34.13	60.89	21.12	128.57	-	-	Washington
P. arcticus	M	38.59	83.57	21.30	131.67	79	269	Washington
P. arcticus	M	30.83	72.37	21.26	127.62	-	-	Washington
P. arcticus	M	37.07	84.25	21.75	130.62	73.9	-	Montana
P. arcticus	M	33.49	83.65	20.50	132.13	-	243	Montana
P. arcticus	M	33.69	-	-	-	-	-	Montana
P. arcticus	F	32.63	87.59	21.97	129.40	-	254	Washington
P. arcticus	F	33.09	-	19.42	124.59	-	-	Washington
P. arcticus	F	31.19	70.83	19.33	122.43	64.1	-	Washington
P. arcticus	F	29.69	66.36	19.79	123.43	-	-	British Columbia
P. arcticus	F	32.74	81.34	20.71	128.17	67.5	-	Montana
P. arcticus	F	30.39	79.22	19.53	129.74	69	-	Montana
P. arcticus	F	31.18	76.62	20.12	124.48	-	-	Montana
P. arcticus	F	32.42	75.20	19.79	124.13	-	-	Montana
P. tridactylus	M	30.43	71.71	19.22	120.70	-	221	Washington
P. tridactylus	M	28.27	73.92	19.08	117.33	-	216	Washington
P. tridactylus	M	27.13	63.93	17.27	113.36	-	185	Washington
P. tridactylus	M	28.61	73.72	19.16	120.85	-	210	Washington
P. tridactylus	M	28.91	-	19.19	117.94	-	223	Washington
P. tridactylus	M	30.72	73.53	18.65	117.07	-	224	Washington
P. tridactylus	M	30.03	79.22	18.86	116.58	-	-	-
P. tridactylus	M	13.68	-	13.98	78.86	-	-	-
P. tridactylus	M	32.52	77.61	19.94	125.16	-	-	-
P. tridactylus	M	29.81	71.67	20.52	126.76	-	-	Montana
P. tridactylus	M	31.08	73.98	17.83	111.08	59.9	-	Quebec
P. tridactylus	M	30.09	76.93	15.34	121.27	-	-	Washington
P. tridactylus	M	31.46	75.90	17.22	116.66	-	230	Washington
P. tridactylus	M	29.75	68.17	20.07	113.06	50.5	225	Washington
P. tridactylus	M	33.32	74.71	18.04	115.82	-	-	Washington
P. tridactylus	M	31.17	66.03	19.23	115.23	55.7	213	Washington
P. tridactylus	M	31.32	-	21.67	113.63	-	207	Alaska
P. tridactylus	M	29.76	77.62	20.16	121.23	57.5	235	Washington
P. tridactylus	M	29.53	61.07	17.87	112.18	-	213	Yukon
P. tridactylus	M	32.38	76.53	18.13	120.00	-	-	Washington
P. tridactylus	M	-	73.27	18.45	114.54	-	-	Washington
P. tridactylus	M	35.52	81.62	19.96	124.17	-	-	U.S.S.R.
P. tridactylus	M	31.30	75.43	18.87	120.13	-	-	-
P. tridactylus	M	32.54	80.13	18.08	123.47	-	-	U.S.S.R.
P. tridactylus	M	31.23	76.77	17.43	115.32	-	-	Montana
P. tridactylus	M	30.52	75.14	18.78	117.58	-	-	Montana
P. tridactylus	M	30.13	-	-	119.29	55.6	-	Montana
P. tridactylus	M	29.96	80.76	18.77	125.33	58.1	-	Montana
P. tridactylus	M	31.11	72.36	19.69	117.59	-	222	Montana
P. tridactylus	F	27.21	69.03	17.32	114.63	52.4	-	Washington
P. tridactylus	F	27.20	68.45	19.15	110.36	-	-	Washington
P. tridactylus	F	26.05	59.95	11.62	116.35	-	197	Washington
P. tridactylus	F	27.82	73.49	18.48	116.83	-	216	Washington
P. tridactylus	F	24.12	76.87	18.07	113.88	-	210	Washington
P. tridactylus	F	30.00	76.13	17.10	116.47	-	-	-
P. tridactylus	F	27.71	71.76	19.52	124.18	-	203	Montana
P. tridactylus	F	27.56	72.47	20.54	119.04	-	191	Montana
P. tridactylus	F	23.17	69.75	17.82	116.46	-	218	Washington
P. tridactylus	F	25.69	73.25	12.46	110.20	-	-	Washington
P. tridactylus	F	27.48	73.17	13.04	107.98	51.00	214	Washington
P. tridactylus	F	27.53	71.80	11.87	114.22	-	226	Washington
P. tridactylus	F	21.34	58.38	16.59	110.26	-	214	Alaska
P. tridactylus	F	27.87	72.56	17.37	109.04	50.6	218	Washington
P. tridactylus	F	25.05	72.27	12.08	116.34	-	216	Washington
P. tridactylus	F	31.18	78.05	17.93	119.27	58.9	-	Montana
P. tridactylus	F	27.62	75.63	17.57	114.86	54.5	-	Montana

- Indicates information unavailable.