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Habitat Use by Cavity-Nesting Birds in the Okanogan National Forest, Washington

by

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Abstract

HABITAT USE BY CAVITY-NESTING BIRDS IN THE OKANOGAN NATIONAL FOREST, WASHINGTON

By Sarah J. Madsen

Chairperson of the Supervisory Committee: Professor David A. Manuwal,
College of Forest Resources

A study of cavity-nesting bird abundance, distribution, and habitat preferences was conducted in the Okanogan National Forest (ONF) during the spring and summer of 1983 and 1984. Study sites were selected to represent managed and unmanaged commercial forest conditions, major logging methods used in the ONF, and different policies concerning snag retention.

I found 176 nests of 15 cavity-nesting bird species, and focused nest site analyses on 89 nests of eight primary cavity-nesting (excavator) species. Nest tree and stand characteristics were compared among bird species and with sampled, available habitat using both univariate and multivariate analyses. I found 76% of the excavator nests in dead trees, 15% in defective live trees (with broken or dead tops), and 9% in intact live trees. Compared to available snags and defective live trees, nest trees were larger in diameter, were more likely to be ponderosa pine (Pinus ponderosa) or western larch (Larix occidentalis) than Douglas-fir (Pseudotsuga menziesii), and more often had a broken top and outward evidence of decay. Tree diameters

>53 cm dbh and heights >24 m were preferred. Mean nest tree diameters for six excavator species ranged from 44 cm dbh for the hairy woodpecker (*Picoides villosus*) to 84 cm dbh for the pileated woodpecker (*Dryocopus pileatus*), and the mean for all excavators was 65 cm dbh.

A higher proportion of excavator nests were found in unmanaged than managed sites, but nesting species composition varied among management types. The number of snags >53 cm dbh was higher in excavator nest stands than in sample plots of study site stand structure.

Characteristics of snags, stubs, and defective live trees with foraging evidence were compared with those of corresponding available trees. Similar to nest trees, western larch and ponderosa pine, diameters >53 cm dbh and heights >24 m were preferred.

Cavity-nesting bird abundance was highest in sites containing ≥3.5 snags >53 cm dbh/ha. Bird abundance increased in relation to snag density, and was most closely correlated with the density of snags >53 cm dbh. No difference was found in bird abundance in unmanaged sites and sites where high snag densities were retained during logging.

Management implications of the study, and specific recommendations concerning snag density, snag recruitment, and firewood cutting, are discussed.

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INTRODUCTION

Snags, or dead standing trees, have been a persistent concern to forest resource managers, but a considerable transition has occurred in the focus of this concern. During early years of commercial forestry in the United States, and until quite recently, dead trees were simply regarded as a "danger to the very health and existence of the forest" and "a class of useless and detrimental material" (Weaver 1921:507) that should be eliminated from forest lands. From the prevailing viewpoint of timber protection and production, snags were fire hazards, interfered with efficient silvicultural practices, harbored insect pests, and threatened the safety of forest workers. Consequently, studies were conducted to determine the most effective technique for snag disposal (Weaver 1921, Kolbe 1939), as well as how long these hazards remained standing in the forest (Keen 1929), and snag-felling became established as a routine procedure in timber management operations (Hawley and Smith 1954, Brown and Davis 1973).

In the past 10 years, however, there has been increased concern for the importance of maintaining snags as wildlife habitat in managed forests. Numerous studies during this period documented extensive use of snags by cavity-nesting birds for nest, roost, and forage sites, and also discussed the critical need for snag retention and management guidelines for these species (Jackman 1974; Balda 1975; Conner et al. 1975; McClelland and Frissell 1975; Bull and Meslow 1977; McClelland 1977; Bull 1978; Raphael and White 1978; Scott 1978; Evans and Conner 1979; Thomas et al. 1979; Mannan et al. 1980; Raphael and White 1984; Zarnowitz and Manuwal 1985). The beneficial role cavity-nesting birds may play in regulating populations of insects that damage and degrade trees grown for timber production (Otvos 1965, Beebe 1974, Kroll and Fleet 1979, Otvos 1979) has also received greater attention. Furthermore, many federal laws, such as the Multiple Use and Sustained Yield Act, Endangered Species Act, and the National Forest Management Act, now require that resource managers evaluate effects of forest land-use activities on wildlife habitat.

Despite the recognized need for snags as wildlife habitat, many forest management objectives and contraints, including maximizing timber production, meeting public demands for firewood, and complying with safety and fire protection standards, continuously conflict with snag management goals. Because of these conflicts, and concern for snag attrition associated with past and present management practices, forest managers need specific information about cavity-nesting bird habitat requirements that will be useful in forest planning and management. Except for limited anecdotal accounts (Burdick 1944, Wing 1944, Jewett et al. 1953), forest managers lacked such information for cavity-nesting birds in the Okanogan National Forest (ONF).

The primary objectives of this study were to:

(1) Describe habitat characteristics of nest and forage sites used by cavity-nesting bird species.

(2) Compare forest structural features of available habitat with those of selected habitat.

(3) Determine the relative abundance and distribution of cavity-nesting birds among unmanaged and managed commercial forest types.

(4) Examine relationships between the relative abundance of cavity-nesting birds and the presence of dead standing and down wood, and

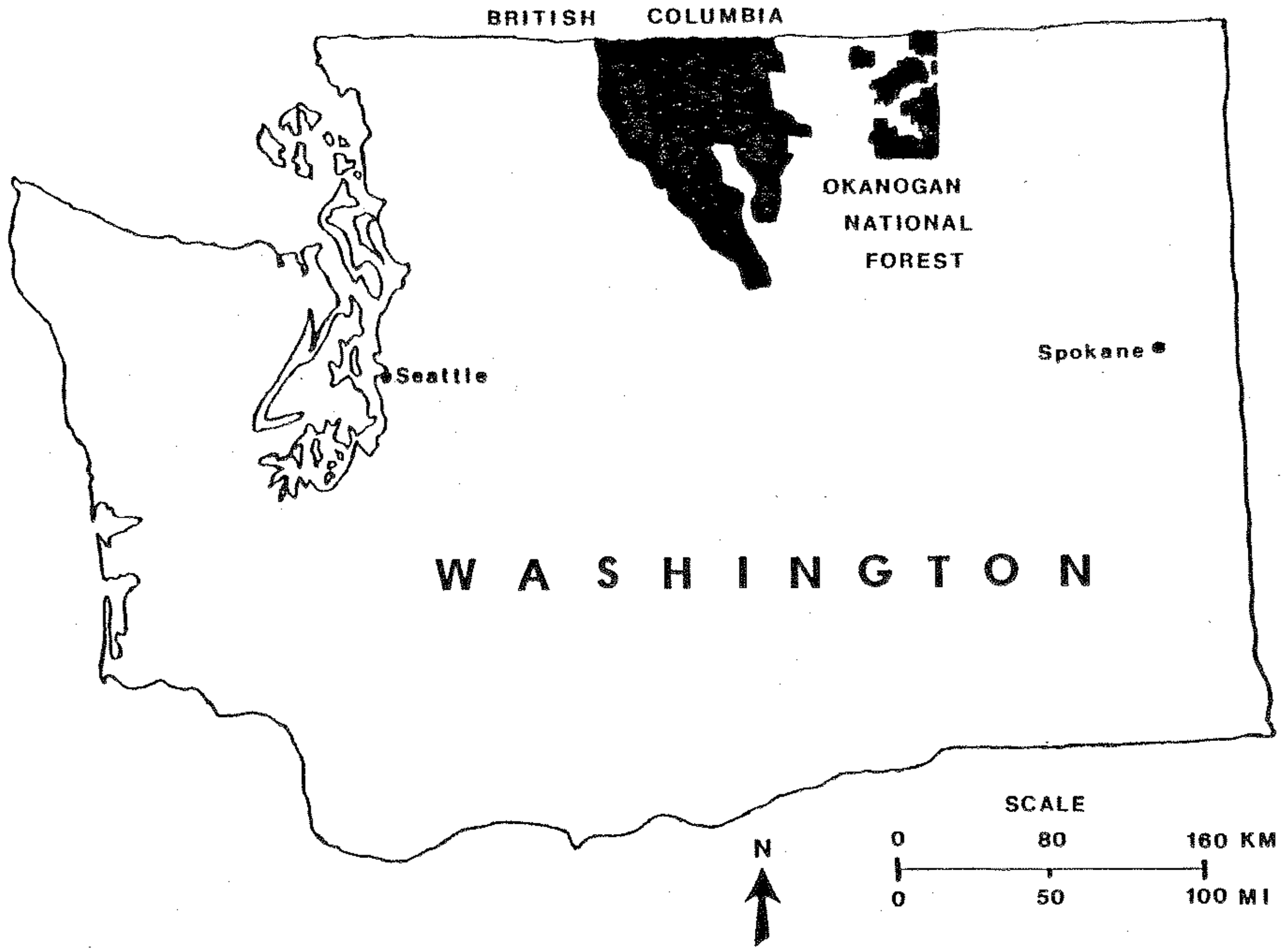
(5) Suggest guidelines for cavity-nesting bird habitat management in the ONF.

STUDY AREA

The ONF is located in north central Washington (Fig. 1) and occupies approximately 680,000 ha in Okanogan, Skagit, Whatcom, and Chelan counties. Administered lands extend from the Canadian border south to the Methow/Chelan Divide, and from the North Cascades National Park east to the Okanogan and Ferry County line.

Most of the ONF lies within the Okanogan Highlands Province (Franklin and Dyrness 1973), which consists of several upland areas characterized by moderate slopes and broad, rounded summits. Except for major, north-south river valleys, elevations within the province average over 1200 m. Widely scattered peaks range up to 2200 m. The western portion of the ONF lies within the North Cascades Province, and includes both eastern and western slopes along the Cascade Crest. In contrast to the Okanogan Highlands, the topography of this area is characterized by irregular ridges and peaks ranging from 1800-2600 m, steep slopes, and deep, U-shaped valleys.

Both dry continental and moist maritime climate types occur on the ONF (Williams and Lillybridge 1983). Precipitation patterns are primarily influenced by the Cascade Range, which intercepts westerly Pacific weather systems and creates a rainshadow over eastern areas of the forest. Average annual precipitation varies from 25 cm at lowest elevations to between 150-300 cm along Cascade slopes. In the Okanogan

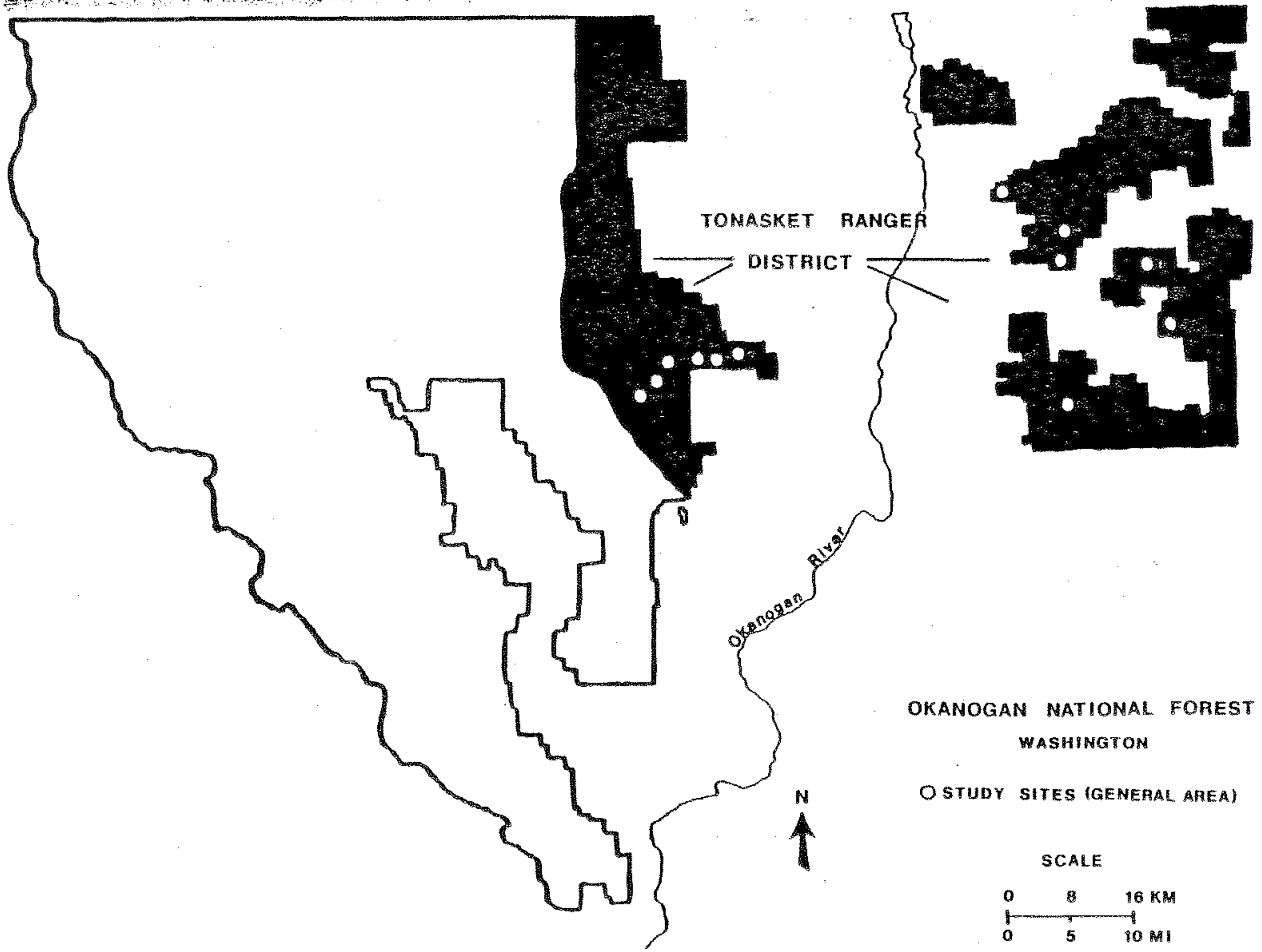

BRITISH COLUMBIA
OKANOGAN NATIONAL FOREST
Seattle
Spokane
WASHINGTON
N
SCALE
0
80
160 KM
0
50
100 MI

Highlands, annual precipitation averages from 50-75 cm. Most precipitation occurs between November and April and falls as snow (Donaldson and Ruscha 1975).

Approximately 40% of the ONF is classified as commercial forest land available for silvicultural management (ONF Draft EIS 1982). The remaining lands are designated incapable of timber production (48%) or are reserved as wilderness and research natural areas (12%). Commercial forest lands support mostly mixed coniferous stands of Douglas-fir (Pseudotsuga menziesii), western larch (Larix occidentalis), and ponderosa pine (Pinus ponderosa); subalpine fir (Abies lasiocarpa) and Engelmann spruce (Picea engelmannii) occur primarily at higher elevations. Lodgepole pine (Pinus contorta) stands occupy about 25% of commercial forest lands. The most common deciduous tree species are aspen (Populus tremuloides) and willow (Salix sp.). Wildfire, both high intensity and more frequent but lower intensity surface fire, has influenced stand structure and composition over most of the forest.

The forest types found on the ONF are most similar to those within the northern Rocky Mountain region, however characteristics of moist Pacific coastal types mix with continental Rocky Mountain elements throughout the forest, particularly along eastern slopes of the Cascade Range (Franklin and Dyrness 1973). A more detailed description of ONF vegetation patterns and associations is found in Williams and Lillybridge (1983).

All field work was conducted on the Tonasket Ranger District (RD), which occupies lands to the east and west of the Okanogan Valley (Fig. 2). The western area was officially the Conconully RD prior to consolidation in 1982.


TONASKET RANGER
DISTRICT
Okanogan River
N
OKANOGAN NATIONAL FOREST
WASHINGTON
○ STUDY SITES (GENERAL AREA)
SCALE
0 8 16 KM
0 5 10 MI

METHODS

Study Sites. Twelve sites (Fig. 2) were established for study of cavity-nesting bird abundance and habitat use. I studied six sites on the east side of the Tonasket RD in spring and summer of 1983; west side sites were studied during the same period in 1984.

Site selection was coordinated with ONF biologists and timber staff, and sites were chosen to represent (1)areas classified as commercial forest lands, (2)managed and unmanaged conditions, (3)dominant mixed coniferous wet (CDS9) and dry (CDG1) ecoclasses within the ONF land inventory system (Hall 1979, ONF 1980) where most commercial timber harvesting occurs, (4)stand structural characteristics resulting from major logging methods used in the ONF (partial and shelterwood cuts), (5)areas where snag densities may have been affected by different policies concerning snag retention, and (6)relatively uniform areas at least 40 ha in size. Aerial photographs, information concerning stand history, and on-site reconnaissance were used to identify potential areas.

Classification of study sites according to the above criteria is presented in Table 1. All sites were approximately 60-85 ha, and average elevations ranged from 1000-1500 m. Douglas-fir and western larch were the dominant tree species on each site, but proportions of other coniferous species differed in wet and dry productive ecoclasses.

Table 1. Classification of study sites, Tonasket RD, 1983-84.

Ecoclass/Location	Unmanaged	Managed: Partial cut	Managed: Shelterwood cut
Wet productive			
East side	Roggow[a]	Turner[c]	Bailey[d]
West side	Muck[b]	Strip[e]	Spike[f]
Dry productive			
East side	Burge[a]	Strike[d]	Frost[d]
West side	Oriole[b]	Rainy[e]	McCay[f]

a)Unlogged, snag cutting prohibited after 1977.
b)Unlogged, snag cutting permitted.
c)Most snags felled during logging entries, snag cutting prohibited after 1977.
d)Snags retained during logging entry, snag cutting prohibited after 1977.
e)Most snags felled during logging entries, snag cutting permitted.
f)Most snags felled during all but the most recent logging entry, snag cutting permitted.

Dry productive types contained a higher component of ponderosa pine, and lower proportions of subalpine fir, Engelmann spruce, and lodgepole pine, than wet productive types. Replicate sites within a defined category (e.g. managed, dry productive, partial cut) were similar in general vegetation structure and composition, but most replicate managed sites differed in the number of logging entries and management direction concerning snag retention.

A policy prohibiting snag cutting, both during timber harvesting and for firewood, was implemented on the east side of the Tonasket RD in 1977. First, single logging entries occurred on the Strike, Frost, and Bailey sites while this policy was in effect, and snags were retained. The Turner site was partially logged prior to 1977, and low large snag abundance in this area indicated most snags were felled during timber harvesting.

West side managed sites represented areas where timber harvesting had occurred two to four times, and most snags were routinely felled. During the most recent logging entry on the McCay and Spike sites, snags were retained; however, few large snags still existed in these areas because of previous logging activities. Snag cutting for firewood has always been permitted on the west side of the district.

Avian Populations. Avian populations were censused in all study sites using the Point Count method. Details of this technique are described in Ralph and Scott (1981) and Verner (1984). The general array of point count stations was according to that suggested by Reynolds et al. (1980). Twelve sampling points (stations) were systematically located at 200 m intervals along transects established in each site. All stations were at least 200 m from the next nearest station, and 100 m from roads and edges of adjacent habitat.

Four censuses were conducted in each site from 24 May to 15 July during 1983 and 1984. Censuses occurred between 0530 and 1000 hrs, and the starting point alternated between opposite ends of the transect on each visit. Detections of cavity- and noncavity-nesting species were recorded during an 8 min count period at each station. All counts were preceded by a 1 min pause time beginning upon arrival at the station. Simultaneous observations of conspecifics, and location and flight direction of wide-ranging species (e.g. woodpeckers), were regularly noted to minimize duplicate counts of one bird.

Nest Site Characteristics. I searched for active cavity nests in all study sites during May, June, and July. Searches were conducted after Point Count censuses and during at least one additional visit, usually in early morning. Total search time was standardized as closely as possible among sites. Occasionally I followed birds beyond site boundaries if they were observed on the site but appeared to be nesting in an adjacent area.

A potential nest was defined as active if I observed adults entering the cavity to incubate eggs or feed young, or heard sounds of young calling from the nest. Measurements of each active nest were obtained after the young had fledged.

Characteristics recorded for each nest tree included: tree species, condition (live or dead), height, and diameter at breast height (dbh); top condition (intact of broken); percent remaining bark, limbs >1 m, twigs, and needles; number of nest holes; and surface evidence of heartwood decay and fire. Decay evidence was classified as (0)absent, (1)conk (fungal fruiting body) present, (2)decay in exposed heartwood, (3)ant dust or deep pileated woodpecker feeding holes at base, (4)parts of the main stem dead and decay visible in cracks, or (5)knots swollen (McClelland 1977). Active nest hole height, orientation, and relation to canopy were also recorded. Most nest trees were photographed.

I sampled habitat surrounding the nest (nest stand) in 0.04-ha and 0.4-ha circular plots, both centered at the nest tree. Within each 0.04-ha plot I recorded canopy cover, maximum and minimum canopy height (measured using a clinometer), ground cover life forms, slope, aspect, and number of live stems by size classes (>4-8, >8-15, >15-23, >23-38, >38-53, >53-69, >69-84, >84-102, and >102 cm dbh) (James and Shugart 1970, Noon 1981), as well as numbers of stubs (dead stems >15 cm dbh, ≤6 m and >1 m tall) and stumps (>15 cm dbh, ≤1 m tall). Snags (dead stems >15 cm dbh, >6 m tall), defective live trees (>15 cm dbh with dead or broken tops), and down logs were recorded in the 0.4-ha plot. Snags and defective live trees were assigned to the same seven size classes >15 cm dbh as live stems, and all characteristics described for nest trees were measured. Logs >1.5 m in length were grouped into four decay (Maser et al. 1979) and diameter categories: (1)Class 1-2 (hard), ≥30 cm (2)Class 1-2 (hard), 15-29 cm (3)Class 3-4 (soft), ≥30 cm and (4)Class 3-4 (soft), 15-29 cm.

Study Site Habitat Sampling. I sampled habitat characteristics of study sites in 0.04-ha and 0.4-ha plots centered at the 12 Point Count stations systematically located along transects in each area. All methods and measurements were the same as those described for plots surrounding nests.

Foraging Evidence. I inspected snags, defective live trees, stubs, and logs measured on study site habitat samples for evidence of foraging use by cavity-nesting birds. Evidence was limited to outward sign such as chipped bark, drilled holes, or excavations into sapwood and heartwood, and did not reflect foraging use by bark-gleaning birds. I classified foraging evidence on snags, defective trees, and stubs as (0)absent, (1)few in number, unidentified, (2)numerous, unidentified, (3)pileated woodpecker excavations, (4)pileated and unidentified, (5)sapsucker sapwells, (6)sapsucker and unidentified, and (7)pileated, sapsucker, and unidentified. Deep, vertical, rectangular-shaped holes, usually located at the base of the tree bole, were identified as pileated woodpecker excavations (McClelland 1977:213). I recognized sapsucker sapwells as regular horizontal or vertical rows of either round or square-shaped holes. Presence of feeding evidence on logs was tallied by decay/diameter class.

Data Analysis. Principal components analysis was used to examine variation in nest site characteristics among six cavity-nesting species. Two analyses on separate sets of nest tree and nest stand variables were performed using the SPSS program FACTOR without rotation (Nie et al. 1975). Principal component axes accounting for at least 10% of the total sample variance were interpreted by the relative sizes of correlations between axes and original variables. Descriptions of the use of principal components analysis as a data reduction and ordination technique for describing habitat relationships among breeding bird species are found in James (1971), Whitmore (1977), Conner and Adkisson (1976), and Rottenberry and Wiens (1981).

I used a series of two-group discriminant function analyses (SPSS, Klecka 1975, Hull and Nie 1981) to compare (1)nest stand habitat structure with samples representing general vegetation structure of study sites, (2)characteristics of snags and defective live trees containing confirmed nests with sampled snags and defective live trees lacking nest holes, and (3)snags and defective live trees with and without foraging evidence. Previous cavity-nesting bird studies using a similar approach include Conner and Adkisson (1977), Bull (1980), Harris (1982), and Raphael and White (1984).

Stepwise discriminant analyses were performed using Wilks´ method, and the single function derived for each analysis was evaluated by the significance of the chi-square statistic based on Wilks´ lambda (Klecka 1975). Discriminant functions were interpreted according to the magnitude of pooled within-groups correlations between the discriminant score and original variables (structure matrix) (Hull and Nie 1981:299, Marascuillo and Levin 1982, Raphael and White 1984). I used classification techniques (Klecka 1975) to assess whether a disciminant function effectively defined group differences; classification was based on the same data set used to compute the discriminant function. The proportion of cases correctly classified according to actual group membership indicated the success of between-group discrimination.

I illustrated preferences for categorical habitat characteristics (e.g. tree diameter class) with an index representing the difference between the proportion used and proportion available within each catefory (Strauss 1979). Values of this preference index range from -1.0 to 1.0; a value of 0 indicates a category is used in equal proportion to availability. I used a binomial test (Zar 1974, Raphael and White 1984) to analyze the significance of non-zero values, and controlled the familywise error rate at <.05 for all comparisons (Bonferonni method, Marascuillo and Levin 1982). Binomial tests were performed only if the results of a chi-square test including all categories was significant.

Point Count census data were analyzed using detection rates, calculated as the average number of birds recorded per 8 min count period (Marcot 1983). A single census included 12 count periods, and four censuses were conducted per study site. Detection rates for each species were determined separately by census and averaged. For the purposes of this study, detection rates provided a useful relative abundance index for comparing study sites and examining habitat relationships.

Differences in cavity-nesting bird abundance and snag densities among sites were tested using oneway analysis of variance (ANOVA) and multiple range tests; both detection rates and snag densities used in these analyses were transformed using $\log_e (X+1)$. I used correlation analysis to compare relationships between bird abundance and study site habitat characteristics.

Live tree density and basal area variables entered in all analyses were calculated using trees >8 cm dbh. Defective live trees were not included in total live tree density and basal area values.

RESULTS

I observed 17 cavity-nesting bird species in the Tonasket RD during the 1983 and 1984 breeding seasons, and found 176 active cavity nests of 15 species (Table 2). Most nests (n=135) were located within the study sites (77%), where systematic searches were conducted, and the remaining nests (n=41) were found in areas outside site boundaries.

The nest site results I report here are based on analyses of the 89 nests of primary cavity-nesting (excavator) species found in study sites (Table 2). This approach was taken because (1)these species initially select nest site characteristics and create holes subsequently used by secondary cavity-nesters (nonexcavators), and (2)direct comparisons could be made between nest site and study site habitat characteristics. Off-site nest characteristics of excavator species are presented in Appendix I.

Bird census results include both excavator and nonexcavator species observed in study sites during Point Count censuses.

Table 2. Cavity-nesting bird species observed on study sites during the 1983-84 breeding seasons, number of active cavity nests found on and off study sites for each species, and common name codes used in this study. Scientific names follow American Ornithologists' Union (1982).

Classification/Species	Bird species code	Active nests on sites	Active nests off sites
Primary cavity-nesting species[a]			
Yellow-bellied sapsucker[b] (*Sphyrapicus varius*)	YBSA	0	4
Williamson's sapsucker (*Sphyrapicus thyroides*)	WISA	20	12
Hairy woodpecker (*Picoides villosus*)	HAWO	5	4
Three-toed woodpecker (*Picoides tridactylus*)	TTWO	1	0
Black-backed woodpecker (*Picoides arcticus*)	BBWO	1	0
Northern flicker (*Colaptes auratus*)	NOFL	16	7
Pileated woodpecker (*Dryocopus pileatus*)	PIWO	6	4
Red-breasted nuthatch (*Sitta canadensis*)	RBNU	35	1
White-breasted nuthatch (*Sitta carolinensis*)	WBNU	5	0
Secondary cavity-nesting species[c]			
American kestrel (*Falco sparverius*)	AMKE	4	1
Flammulated owl (*Otus flammeolus*)	FLOW	0	0
Northern saw-whet owl (*Aegolius acadicus*)	SAOW	1	0
Black-capped chickadee (*Parus atricapillus*)	BCCH	1	0
Mountain chickadee (*Parus gambeli*)	MOCH	33	7
Boreal chickadee (*Parus hudsonicus*)	BOCH	0	0
Brown creeper (*Certhia americana*)	BRCR	7	0
Mountain bluebird (*Sialia mexicana*)	MOBL	0	1
Total primary cavity-nesters		89	32
Total secondary cavity-nesters		46	9
Total cavity nests		135	41

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a)Excavators: species that excavate their own nest cavities. RBNU, WBNU and NOFL occasionally use existing holes.

b)Red-naped sapsucker (*S. varius nuchalis*)

c)Nonexcavators: species that nest in existing cavities. MOCH and BCCH occasionally excavate their own nest cavities.

Nest Tree Characteristics

Condition. I found 76% of the excavator nests in dead trees (snags and stubs), 15% in defective live trees, and 9% in intact live trees (Table 3). The majority of nests of all species, except the Williamson's sapsucker, were in dead trees. Snags contained the highest proportion of all nests, and defective live trees held more nests than either stubs or intact live trees.

A general comparison of the relative proportion of tree conditions used for nesting with proportions available indicated that snags and defective live trees were preferred nest sites. Only 5% of trees (>15 cm dbh) in all conditions counted on habitat sample plots were snags, but 69% of all nest trees were snags. Similarly, proportions of defective live trees available and used for nesting were 1% and 15%, respectively.

Tree Species. Nests were located in five species of trees (Table 4). The highest proportions of all nests were in ponderosa pine (46%), western larch (32%), and Douglas-fir (21%). Most nests of individual bird species were found either primarily or exclusively in ponderosa pine and western larch. Only the northern flicker and red-breasted nuthatch nested in Douglas-fir. Of the remaining five tree species that occurred on study sites (pooled in the "other" category), only aspen (n=3) and willow (n=1) were used for nesting, which comprised 1% of all nests.

Table 3. Numbers of excavator nests in different tree conditions.

Bird species	Dead tree Snag	Dead tree Stub	Defective live tree	Live tree	Sample size
WISA	7	0	10	3	20
HAWO	2	1	0	2	5
TTWO	0	0	0	1	1
BBWO	1	0	0	0	1
NOFL	13	2	0	1	16
PIWO	6	0	0	0	6
RBNU	29	3	3	0	35
WBNU	3	1	0	1	5
Total	61	7	13	8	89

Table 4. Numbers of excavator nests and percentages of all nests in different tree species by tree condition. See Table 2 for bird species codes.

	WISA	HAWO	TTWO	BBWO	NOFL	PIWO	RBNU	WBNU	All nests	Percent Used	Percent Available	Preference Index[a]
Tree Species/Condition												
Western larch												
Dead	1	0	0	0	3	3	7	0	14	21	32	-0.11
Defective live	10	0	0	0	0	0	2	0	13	92	44	0.48*
Live	3	0	0	0	0	0	0	1	4	50	14	0.36*
All conditions	14	0	0	0	3	3	9	1	30	32	15	0.17*
Ponderosa pine												
Dead	6	3	0	1	8	3	12	4	37	54	6	0.48*
Defective live	0	0	0	0	0	0	0	0	0	0	5	-0.05
Live	0	1	0	0	0	0	0	0	1	12	5	0.07
All conditions	6	4	0	1	8	3	12	4	38	46	5	0.41*
Douglas-fir												
Dead	0	0	0	0	4	0	12	0	16	23	56	-0.33*
Defective live	0	0	0	0	0	0	1	0	1	8	43	-0.35*
Live	0	0	0	0	0	0	0	0	0	0	73	-0.73*
All conditions	0	0	0	0	4	0	13	0	17	21	71	-0.50*
Other species[b]												
Dead	0	0	0	0	0	0	1[c]	0	1	2	6	-0.04
Defective live	0	0	0	0	0	0	0	0	0	0	8	-0.08
Live	0	1[d]	1[d]	0	1[d]	0	0	0	3	38	9	0.29*
All conditions	0	1	1	0	1	0	1	0	4	1	9	-0.08*
Sample size	20	5	1	1	16	6	35	5	89			

a) (Percent used - Percent available) + 100 (Strauss 1979).
b) Includes Engelmann spruce, subalpine fir, lodgepole pine, aspen and willow.
c) Willow.
d) Aspen.
* Use significantly differs from availability (p <.05, binomial test).

Tree conditions used for nesting differed among tree species (Table 4). Over 90% of all nests in ponderosa pine and Douglas-fir were in dead trees, but 57% of the nests in western larch were in defective and intact live trees. All aspen nest trees were alive.

To determine whether observed patterns of tree species and condition use for nesting differed from general forest composition, I used preference indices (Strauss 1979) to compare the proportion used with the proportion available for each tree species within four condition categories. If nest site selection was random, expected use would not significantly differ from availability.

Ponderosa pine and western larch were selected in greater proportion than either occurred on study sites, if all tree conditions were included (Table 4), however dead ponderosa pine were highly preferred and dead larch were used in proportion to availability. Both defective and intact live larch were selected in much higher proportion than they occurred. Douglas-fir was the most abundant tree species on all study sites, but was used significantly less than expected in each condition. The "other" tree species were also used less than expected in all conditions except live, which was due to the inclusion of aspen in this group.

Diameter and Height. The mean diameter (dbh) of all excavator nest trees (n=89) was 65.2 cm, and mean height and nest hole height were 23.4 m and 13.7 m, respectively (Table 5). In multiple range comparisons among six species, I found that differences in mean tree

Table 5. Mean nest tree diameter, height and nest hole height for excavator species on study sites. See Table 2 for bird species codes.

	Nest tree dbh(cm)		Nest tree height(m)		Nest hole height(m)	
Bird Species	Mean	SD	Mean	SD	Mean	SD
PIWO	84.2 B[a]	17.5	36.7 B	9.1	16.1 A	3.4
NOFL	70.4 B	27.2	20.8 A	11.9	14.3 A	9.7
WISA	69.6 AB	22.0	27.8 AB	8.6	15.6 A	6.3
RBNU	63.5 AB	30.4	21.4 A	12.2	13.2 A	8.2
WBNU	54.3 A	20.1	19.9 A	13.7	11.8 A	13.7
HAWO	44.2 A	19.4	16.6 A	12.3	10.3 A	8.3
TTWO[b]	31.7	-	25.6	-	3.7	-
BBWO[b]	29.0	-	19.2	-	1.4	-
All species	65.2	27.1	23.4	11.8	13.7	8.3

a)Within each column, mean values with the same letter are not significantly different (p >.05, Duncan's multiple range test).
b)Not included in multiple range tests due to sample of only 1 nest.

diameter varied less than mean height. The mean diameter for each species, except the hairy woodpecker, was >53 cm while mean tree height ranged from 16.6 m to 36.7 m. Although the hole height of all nests ranged from 1.1 m to 41.5 m, no interspecific differences were found in mean nest hole height.

I examined potential tree size preferences by comparing the proportions of all active nest and available trees (dead and defective live only) in four diameter and five height classes (Table 6). Larger diameter trees (>53 cm dbh) were preferred, and trees in smaller diameter classes were used less than expected. Tree height preferences followed a similar pattern, with trees in the tallest height class (>24 m) used in greater proportion than availability, and trees $\leq$6 m less frequently than expected. Intermediate heights were selected in approximate proportion to availability.

Decay. I evaluated the decay condition of nest trees using external physical tree characteristics that depict deterioration over time, and outward evidence of heartwood decay (conk presence, swollen knots, etc.). As a live tree declines in vigor, and after it dies, both external and internal structural characteristics change in gradual stages. Generally needles, twigs, and smaller branches fall during initial stages of deterioration, and larger limbs, the top, and bark are lost in later stages (Scott 1978, Thomas et al. 1979, Cline et al. 1980). Dead and and broken branch stubs and tops created by this deterioration process provide entrance points for fungal decay

Table 6. Proportions of all active nest and available trees (dead and defective live only) in various diameter and height classes.

	Nesting Use (U)	Availability (A)	Preference Index[a]
Diameter Class(cm)			
>15 - 23	5	33	-0.28*
>23 - 38	14	29	-0.15*
>38 - 53	15	20	-0.05
>53	67	18	0.49*
Height Class(m)			
≤ 6	9	33	-0.24*
> 6 - 12	15	11	0.04
>12 - 18	12	12	0.00
>18 - 24	15	19	-0.04
>24	49	24	0.25*

a) (U - A) ÷ 100 (Strauss 1979).

* Use significantly differs from availability (p <.05, binomial test).

organisms that germinate and extend hyphae through exposed dead wood connected with the heartwood; these hyphae cannot directly penetrate bark or living sapwood (Boyce 1961). These decay organisms may also attack the heartwood through wounds caused by fire, mechanical damage, lightning, animals, or insects such as bark beetles (Scolytidae) and woodborers (Cerambycidae, Buprestidae).

I defined six decay stages using external physical tree characteristics (Table 7) based upon those described by Raphael and White (1984); similar decay stages were also defined by Cline et al. (1980). Live nest trees with intact live tops were excluded from the classification, and all stubs were included in decay stage 6. Decay stages 2-4 represented hard snags, stages 5-6 were soft snags, and stage 1 included defective live trees.

I found the largest proportion of all nests (47%) in soft snags, and a fairly high proportion (25%) in decay stage 4, which were harder snags. A comparison of the percentages of trees used and available in different decay stages (Table 7) indicated that a significantly higher proportion of snags in stage 5 were used for nesting than expected, stages 1-4 were used in approximate proportion to availability, and stage 6 was used significantly less than expected. A larger number of nests were located in broken top than intact top trees in most decay stages, and generally broken tops were highly preferred. Broken tops comprised only 30% of available trees in all decay stages, but 74% of all nest trees had broken tops.

Decay stage use varied among individual bird species. The highest

Table 7. Percentages of active nest and available trees in different decay stages, and numbers of nest trees with intact or broken tops.

Decay Stage	Decay Stage Characteristics Tree Condition[a]	Needles	Twigs	Branches	Top Condition[b] Intact[c]	Broken	Percent Use (U)	Percent Available (A)	Preference Index[e]
1	live	present	present	most present	4	9	16	11	0.05
2	dead	present	present	most present	1	0	1	1	0.00
3	dead	absent	present	most present	5	4	11	19	-0.08
4	dead	absent	absent	many present	8	12	25	16	0.09
5	dead	absent	absent	few present	3	18	26	13	0.13*
6	dead	absent	absent	none present	0	17	21	39[d]	-0.18*
					21	60			

a)Live trees with live intact tops excluded.
b)Numbers of nests in each top condition.
c)Dead intact top.
d)All stubs classified in this decay stage.
e) $(U - A) \div 100$ (Strauss 1979).
* Use significantly differs from availability ($p < .05$, binomial test).

proportions of Williamson's sapsucker nest trees were in decay stage 1 (59%) and stages 3 and 4 (24%). Pileated woodpecker nest trees were exclusively in stages 4 and 5, and those of the white-breasted nuthatch were primarily in stages 3 and 4. The majority of hairy woodpecker, red-breasted nuthatch, and northern flicker nests were in soft snags (stages 5 and 6). The latter two species also located a smaller proportion of nests in hard snags. Those of the red-breasted nuthatch were excavated in knotholes, exisitng foraging excavations that had penetrated the sapwood, or in softer portions of the bole, whereas those of the northern flicker were in old pileated woodpecker nest holes.

I observed outward evidence of heartwood decay on 79% of all nest trees, and on only 26% of sampled snags and defective live trees. Conks were present on 14% and 7% of nest and available trees, respectively. Nearly all of the nest trees with conks were broken top western larch or Douglas-fir, and had fire scars. Conks of <u>Fomes laracis</u> occurred on defective live larch, usually within 1-2 m of the active nest hole, which indicated the existence of heartwood decay at the cavity location.

To determine whether the presence of heartwood decay increased from the least to the most deteriorated decay stage in both nest and available trees, I examined the proportion with decay evidence in each stage for both groups. Among available trees, the proportion with signs of heartwood decay remained consistently low (<25%) in stages 1-4, and increased only slightly in stages 5 and 6. For nest trees, however, the proportion exhibiting outward signs of heartwood decay remained consistently much higher than available trees within each stage, and approximately the same proportion had decay evidence in stage 1 as in stage 6 (>80%). These results suggest that excavators prefer trees in each decay stage with heartwood softened by decay.

Principal Components Analysis of Nest Tree Characteristics. Variation in nest tree characteristics among six primary cavity-nesting species was examined using principal components analysis. This method was a useful tool for simultaneously evaluating a set of intercorrelated nest tree measurements for each bird species, and reducing the complexity of this multimensional data set to describe among-species similarities and differences. The orthogonal components formed in the analysis are linear combinations of the original variables, and each component defines a known proportion of the total variance within the data set.

Eleven variables were included in the analysis (Table 8). Top condition, decay and fire evidence, and the three tree species were entered as dichotomous variables, which assumed the value of 0 if the characteristic was absent or 1 if present. Tree condition was coded as 0 if live or defective live, or 1 if dead. Limb presence assumed coded values of 1-4 representing 25% intervals between 1% and 100%, or 0 if absent.

Table 8. Results of the principal components analysis of 11 nest tree variables for 6 species of primary cavity-nesting birds.

	Principal Component			
	I	II	III	IV
Total variance accounted for(%)	28.2	18.6	16.1	10.9
Cumulative total variance(%)	28.2	46.8	62.9	73.8
Correlations of components to original variables				
Height(m)	0.85	0.29	0.00	0.12
Diameter(cm)	0.58	0.37	0.33	0.41
Western larch	0.69	-0.35	0.18	-0.51
Ponderosa pine	-0.32	0.73	-0.48	0.10
Douglas-fir	-0.41	-0.38	0.50	0.53
Top condition	0.64	0.00	-0.36	0.03
Tree condition	-0.57	0.61	0.20	0.04
Fire evidence	0.45	0.22	0.36	0.36
Limb presence	0.49	-0.17	-0.59	0.43
Decay evidence	0.24	0.06	0.69	-0.09
Bark cover(%)[a]	-0.22	-0.75	-0.19	0.37

a)Arcsine transformed.

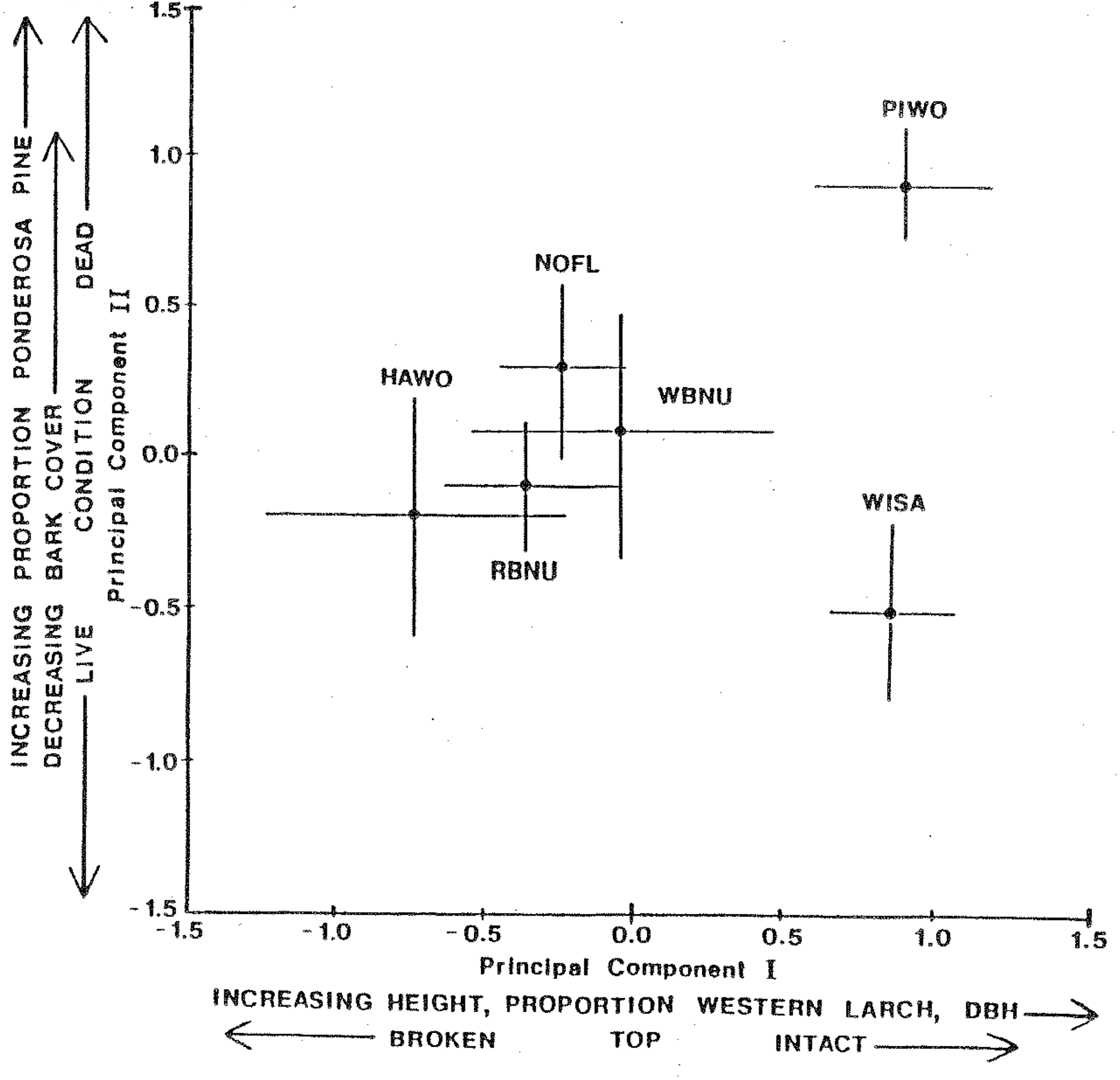
Results of the principal components analysis are summarized in Table 8. Four components, which together accounted for 73.8% of the total variance, were derived. The first component was most highly correlated with nest tree height, western larch, presence or absence of top, and diameter, and accounted for the greatest percentage (28.2%) of the total variance. High values on the first component correspond to tall, larger diameter, western larch nest trees with intact tops.

The second component accounted for an additional 18.6% of the total variance (Table 8), and was positively correlated with ponderosa pine and tree condition, and negatively correlated with the amount of bark remaining on the stem. Dead ponderosa pine nest trees with lower proportions of bark would be expected to assume high values on this component, whereas live and defective live nest trees of other tree species would have low values.

The third and fourth components accounted for 16.1% and 10.9%, respectively, of the total variance. The third component was most positively correlated with the presence or absence of decay, and negatively correlated with limb presence, with increasing values representing trees with decay and few limbs. Douglas-fir was the single variable most closely correlated with the fourth component.

Nest tree relationships among bird species can be visualized by plotting the mean values for each species on the first two principal components (Fig. 3). As can be seen along the first component axis,

Figure 3. Two-dimensional ordination of nest tree habitat relationships among 6 excavator species according to each species' mean value ± one standard error on the first and second principal component axes. See Table 2 for bird species codes.


PIWO
NOFL
HAWO
WBNU
RBNU
WISA
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
Principal Component II
INCREASING PROPORTION PONDEROSA PINE
DECREASING BARK COVER
LIVE CONDITION DEAD
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
Principal Component I
INCREASING HEIGHT, PROPORTION WESTERN LARCH, DBH
BROKEN TOP INTACT

pileated woodpecker and Williamson's sapsucker nest trees were taller and larger in diameter than those of other species, and a larger proportion were western larch with intact tops. The hairy woodpecker, which had the lowest value on this axis, nested primarily in shorter, smaller diameter, broken-topped trees and none were western larch.

Nest tree characteristics of the pileated woodpecker and Williamson's sapsucker were distinctly separated along the second component axis (Fig. 3), and each also remained separated from the other four species. All of the pileated woodpecker nest trees were dead, half were ponderosa pine, and the average amount of bark remaining on the stem was less than 20%. The majority of Williamson's sapsucker nest trees were defective live or live, few were ponderosa pine, and the average amount of bark remaining on the stem was 90%. The other 4 bird species assumed intermediate values along the second axis, and the considerable degree of overlap in variation around respective mean values indicated greater among-species similarity in nest tree characteristics defined by this axis. Dead ponderosa pine trees held a large proportion of the nests found for these species, but each bird also nested in other tree species, and located at least one nest in live or defective live trees.

<u>Discriminant Analyses of Nest and Non-Nest Trees</u>. I performed three separate two-group discriminant function analyses to examine differences between snags and defective live trees used and not used

for nesting. Active nest trees formed one group, and sampled trees without nest holes (non-nest) the second group. All analyses excluded both nest and non-nest intact live trees and stubs.

The 11 variables used in the principal components analysis comparing nest tree characteristics among bird species were also used in the discriminant analyses, and all variables except tree diameter were coded and entered in the same manner. Tree diameter was represented by the basal area factor for the tree diameter size class (e.g. size class >23-38 cm dbh = 0.07 m^2) (James and Shugart 1970) of each tree included in the analyses, since I measured the size class and not the actual dbh of sampled trees.

In the first discriminant analysis, I pooled snags and defective live trees to compare characteristics of active nest (n=74) and non-nest (n=951) trees (Table 9). Six variables significantly contributed to the discrimination between groups: tree diameter, the proportions that were ponderosa pine and Douglas-fir, top condition, decay evidence, and bark cover. All of these variables, plus fire evidence, were most highly correlated with the discriminant score. Nest trees were larger in diameter, were more likely to be ponderosa pine than Douglas-fir, more often had a broken top and outward decay and fire evidence, and had less bark than non-nest trees. The discriminant equation correctly classified 91% of all active nest and non-nest trees according to actual group membership. The classification procedure provides a measure of similarity between the two groups in the analysis (Raphael and White 1984). A higher proportion

Table 9. Results of discriminant analyses[a] comparing characteristics of (1)snags and defective live trees with active nests (n=74) vs. available non-nest snags and defective live trees (n=951), (2)snags with active nests (n=61) vs. non-nest snags (n=784), and (3)defective live trees with nests (n=13) vs. non-nest defective live trees (n=167).

	Variables entering analysis and step entered[b]			Correlations of variables with discriminant score		
Variable	Snags and defective live trees	Snags	Defective live trees	Snags and defective live trees	Snags	Defective live trees
Height(m)		7		0.17	0.09	0.28
Diameter[c]	1	2	3	0.65	0.59	0.60
Western larch			4	-0.06	-0.13	0.37
Ponderosa pine	2	1	6	0.58	0.66	-0.09
Douglas-fir	5	6		-0.18	-0.14	-0.28
Top condition	3	3	2	-0.36	-0.31	-0.36
Tree condition				-0.02	0.00	0.00
Fire evidence			5	0.27	0.18	0.29
Limb presence			7	-0.08	-0.06	-0.21
Decay evidence	4	5	1	0.48	0.38	0.77
Bark cover(%)[d]	6	4		-0.31	-0.32	-0.04

a)All analyses excluded stubs and intact live trees.

b)Variables entering the analysis significantly contributed ($p < .001$) to the discrimination between groups, given variables already entered in the equation. Variables with earliest entry step were best discriminators.

c)Variable entered for all trees was the basal area factor (m^2) for the tree diameter size class.

d)Arcsine transformed.

correctly classified indicates lower similarity, or less overlap, between groups.

The second analysis included only nest (n=61) and non-nest (n=784) snags. The same variables selected in the first analysis, with the addition of tree height (Table 9), best distinguished the characteristics of these two groups, but variables entered the equation at different steps. The proportion that were ponderosa pine was selected first, followed by tree diameter, top condition, bark cover, decay evidence, the proportion that were Douglas-fir, and tree height. In addition to the characteristics described for the first analysis, nest snags were taller than non-nest snags. The discriminant equation successfully classified 92% of all active nest and non-nest snags.

The third analysis was based on nest (n=13) and non-nest (n=167) defective live trees (Table 9). Seven variables significantly contributed to differences between groups: decay evidence, top condition, tree diameter, the proportions that were western larch and ponderosa pine, fire evidence, and limb presence. Variables identifying the discriminant function indicated that nest defective live trees more often had outward evidence of decay and fire, were larger in diameter and more likely to be western larch and have a broken top, than non-nest trees. Nest trees were also taller and had fewer limbs. The discriminant equation correctly classified 89% of all nest and non-nest trees.

Nest Stand Characteristics

Management/Productivity Site Types. The distribution of excavator nests found in wet and dry productive unmanaged, partial cut, and shelterwood cut site types is summarized in Table 10. I found a higher proportion of all nests in unmanaged sites (43%, n=38) than in partial cut (25%, n=22) or shelterwood cut sites (32%, n=29).

Nesting species composition varied among management types, but the highest number of species (n=8) nested in shelterwood sites, and an equal number (n=5) nested in unmanaged and partial cut sites (Table 10). Half of all the Williamson's sapsucker, pileated woodpecker, and red-breasted nuthatch nests were found in unmanaged sites, and most of the hairy woodpecker nests were in shelterwood sites. All white-breasted nuthatch nests were located in partial and shelterwood sites, and those of the northern flicker were almost uniformly distributed among management types. Single nests of the three-toed and black-backed woodpeckers were in shelterwood sites.

Wet or dry productivity did not appear to influence nest stand preferences. The total number of nests, as well as those of most individual species, were almost equally distributed between wet and dry productive types.

Nest Stand Structure. Similar to variables describing nest tree characteristics, variables expressing forest stand structure surrounding nest sites were highly correlated, and their simultaneous

Table 10. Numbers of excavator species nests found in wet and dry productive unmanaged, partial cut and shelterwood cut types on the Tonasket RD, 1983-84. See Table 2 for bird species codes.

	Excavator species								
	WISA	HAWO	TTWO	BBWO	NOFL	PIWO	RBNU	WBNU	All species
Management/Productivity Type									
Unmanaged									
Wet	6	0	0	0	4	1	7	0	18
Dry	4	1	0	0	2	2	11	0	20
Total	10	1	0	0	6	3	18	0	38
Partial cuts									
Wet	3	0	0	0	3	1	3	1	11
Dry	3	0	0	0	1	1	5	1	11
Total	6	0	0	0	4	2	8	2	22
Shelterwood cuts									
Wet	1	0	1	0	3	1	7	2	15
Dry	3	4	0	1	3	0	2	1	14
Total	4	4	1	1	6	1	9	3	29
Total wet productive	10	0	1	0	10	3	17	3	44
Total dry productive	10	5	0	1	6	3	18	2	45

consideration was necessary to evaluate variation among bird species. I performed a principal components analysis using eight variables describing nest stand characteristics of six excavator species.

Three principal components were derived from the analysis, which together accounted for 72% of the total variance in the data set (Table 11). The first component was most highly correlated with stand basal area, tree density, canopy cover, and the number of snags >53 cm dbh. This axis represented a gradient from an open forest condition with low numbers of small diameter trees and large snags, to dense stands dominated by larger diameter trees and snags. These stand characteristics accounted for the largest percentage (34.4%) of the total variance.

The second component was positively correlated with small and intermediate size snags (Table 11), and accounted for an additional 24% of the variance. Low to high values along this axis represent increasing numbers of snags ≤53 cm in the stand surrounding the nest tree. Canopy height was the only variable that was highly correlated with the third component, and nest trees within the tallest canopy conditions would be expected to assume high values on this axis.

A two-dimensional plot of the nest stand habitat relationships among bird species is presented in Figure 4. The horizontal axis, representing the first component, separated the species into two groups. Nests of the hairy woodpecker, white-breasted nuthatch, and northern flicker were surrounded by open forest conditions characterized by few trees and large snags, and low canopy cover. In contrast,

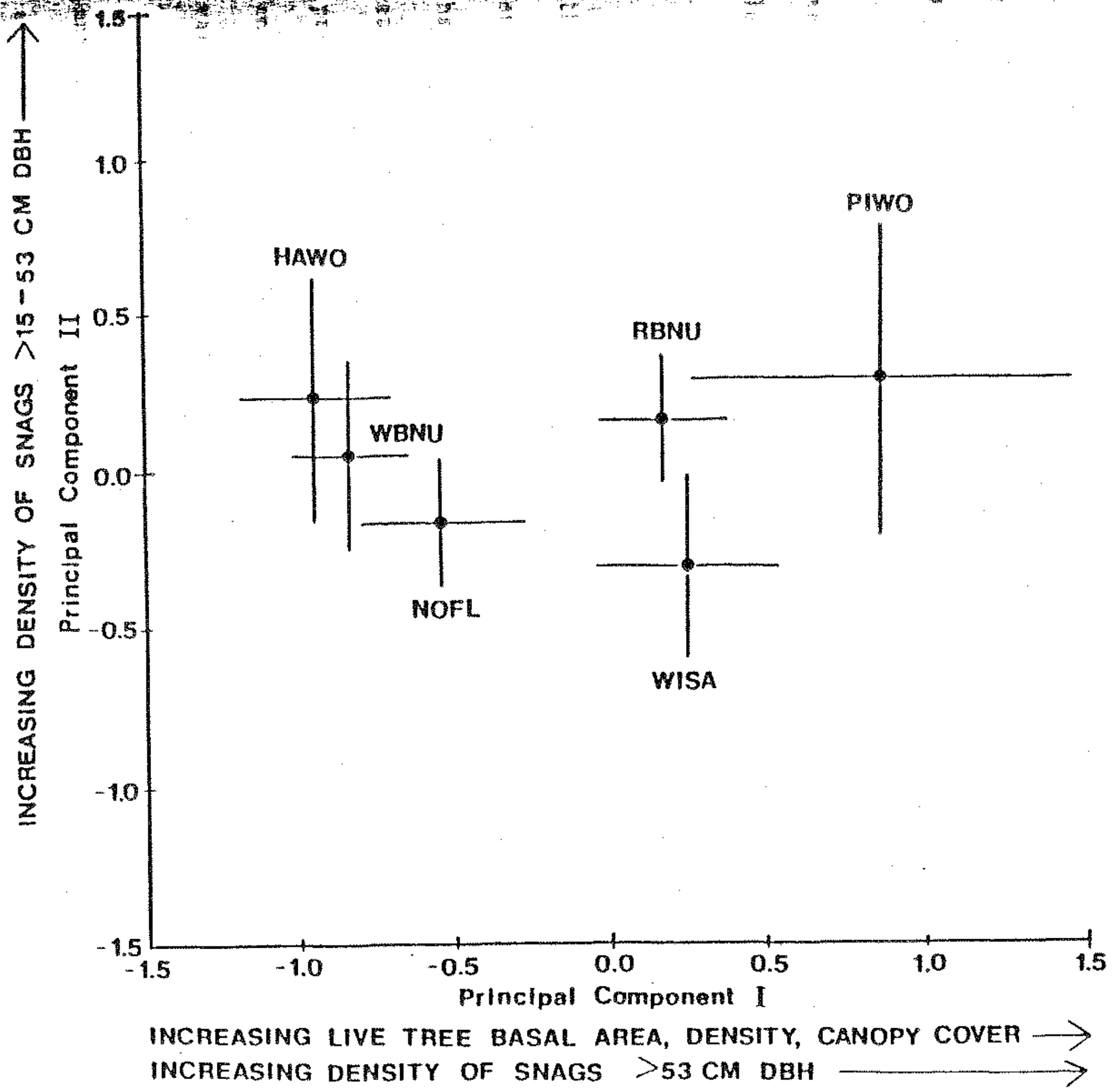
Table 11. Results of the principal components analysis of 8 nest stand structure variables for 6 species of primary cavity-nesting birds.

	Principal Component		
	I	II	III
Total variance accounted for(%)	34.4	24.0	13.6
Cumulative total variance(%)	34.4	58.4	72.0
Correlations of components to original variables			
Basal area(m^2/ha)	0.76	-0.44	0.11
Tree density(stems/ha)	0.71	-0.20	-0.54
Canopy cover(%)[a]	0.68	-0.52	-0.28
Canopy height(m)	0.40	-0.45	0.66
Snags >15-23 cm[b]/ha	0.51	0.64	-0.24
Snags >23-38 cm/ha	0.52	0.69	0.01
Snags >38-53 cm/ha	0.51	0.57	0.38
Snags >53 cm/ha	0.52	0.08	0.28

a)Arcsine transformed.

b)Diameter at breast height (dbh).

Figure 4. Two-dimensional ordination of nest stand habitat relationships among 6 excavator species according to each species' mean value ± one standard error on the first and second principal component axes. See Table 2 for bird species codes.


HAWO
WBNU
NOFL
RBNU
WISA
PIWO
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
Principal Component II
INCREASING DENSITY OF SNAGS >15 – 53 CM DBH
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
Principal Component I
INCREASING LIVE TREE BASAL AREA, DENSITY, CANOPY COVER
INCREASING DENSITY OF SNAGS >53 CM DBH

the pileated woodpecker, Williamson's sapsucker, and red-breasted nuthatch nested in denser, higher basal area stands, and nest trees were surrounded by a larger number of snags >53 cm dbh.

Bird species were not as widely separated along the vertical axis, or second principal component, indicating greater interspecific similarity in the number of small to intermediate size snags surrounding nest trees.

Mean values were arrayed similarly along the third (not pictured) and first components, but the height of trees surrounding nests varied less than tree density and basal area.

Comparisons with Study Site Stand Structure. To determine whether the stand structure surrounding nests differed from the general stand structure of study sites, I first pooled all nest stand (n=87) and habitat sample plots (n=144) separately, and performed a discriminant analysis on these two groups. The same eight variables used in the principal components analysis comparing nest stand characteristics among species (Table 11) were included in the analysis. Among these variables, the density of snags >53 cm dbh/ha best discriminated between nest and study site stands, based on its entry into the analysis at the first step and high correlation with the discriminant score. Other variables that entered the equation were canopy cover, tree density, snags >38-53 cm/ha, and canopy height. As a group, nest stands contained larger numbers of snags >53 cm dbh, and had higher tree densities and taller canopies than average stand conditions of study sites, but had lower canopy cover and fewer snags >38-53 cm dbh.

Although the discriminant function identified a significant difference between nest and study site stands, the classification results indicated a fairly high degree of similarity between the two groups. Only 64% of all plots were classified according to actual group membership, and fewer nest stand than study site plots were correctly classified.

To clarify differences between nest stands of individual bird species and study site stand structure that may have been concealed by the previous analysis, I performed separate two-group discriminant analyses comparing all nest stand plots of each species with stand sample plots of unmanaged, partial cut, and shelterwood cut sites. Results of these analyses are summarized in Tables 12, 13, and 14.

All comparisons of individual bird species nest stand plots with unmanaged site plots resulted in significant discriminant functions (Table 12). Values of discriminating variables that entered the analysis for each species, except the pileated woodpecker, were lower than those of corresponding site variables. Pileated woodpecker nest stands contained a higher mean number of trees and snags >53 cm dbh than unmanaged plots. The lower percentage of all plots correctly classified for the pileated woodpecker (87%), Williamson's sapsucker (78%), and red-breasted nuthatch (81%), indicated that nest stands of these species were more similar to unmanaged sites than those of the

Table 12. Results of 2-group discriminant function analyses comparing all nest stand plots of individual bird species vs. unmanaged site plots. Values with asterisks indicate variables that entered the discriminant equation and significantly differed between nest stand and site habitat plots. See Table 2 for bird species codes.

Variable	Unmanaged plots	PIWO	WISA	NOFL	HAWO	RBNU	WBNU
	Mean	Means for bird species nest stand plots					
Basal area(m^2/ha)	37.9	38.7	28.8***	22.3***	12.5***	27.9	13.1***
Tree density(stems/ha)	642.2	725.0***	662.5	382.8	270.0***	569.3***	320.0***
Canopy cover(%)[a]	84.0	49.0***	66.0***	33.0***	34.0***	49.0***	30.0***
Canopy height(m)	31.6	32.0	31.4	26.5	24.4	28.1	25.9
Snags >15-23 cm[b]/ha	7.8	6.7	2.8**	1.9***	5.0	5.8	4.0***
Snags >23-38 cm/ha	10.9	10.4	6.3	2.8	1.5***	6.6	2.5
Snags >38-53 cm/ha	7.8	5.4***	3.3***	2.5***	2.5***	4.5***	1.5***
Snags >53 cm/ha	7.9	12.1**	5.4***	3.9***	0.5***	5.9	1.5***
Significance of discriminant function[c]	**	***	***	***	***	***	***
Percentage of all plots correctly classified[d]		87.0	78.0	94.0	96.0	81.0	96.0

a)Arcsine transformed.
b)Diameter at breast height (dbh).
c)Based on Wilks' lambda.
d)A measure of similarity between nest stands and site plots; higher values indicate lower similarity.
** $p < .01$, *** $p < .001$.

northern flicker, hairy woodpecker, or white-breasted nuthatch which had from 94%-96% of plots correctly classified.

Snag density and tree basal area and/or density were characteristics that most consistently discriminated between nest stand and partial cut site plots (Table 13). Significant discriminant functions were derived for each species except the white-breasted nuthatch, which indicated variables in the analysis did not define differences between nest stands of this species and partial cut plots. The density of snags >53 cm dbh was the first variable to enter the analysis for the pileated woodpecker, Williamson´s sapsucker, northern flicker, and red-breasted nuthatch, and was thus the best discriminator between these nest stands and site plots. Densities of snags in all smaller size classes were also significantly higher in pileated woodpecker nest stands, but were variable in stands of other species. The general forest condition of partial cut plots was more open than nest stands of the pileated woodpecker and red-breasted nuthatch, and denser than those of the hairy woodpecker and northern flicker. The proportion of all plots correctly classified for species with significant discriminant functions ranged from 70% (most similar) for the northern flicker to 98% (least similar) for the pileated woodpecker.

In contrast to the previous analyses, basal area was the first variable to enter the discriminant equation in comparisons of pileated woodpecker, Williamson´s sapsucker, northern flicker, and red-breasted nuthatch nest stands with shelterwood cut plots (Table 14). The

Table 13. Results of 2-group discriminant function analyses comparing all nest stand plots of individual bird species vs. partial cut site plots. Values with asterisks indicate variables that entered the discriminant equation and significantly differed between nest stand and site habitat plots. See Table 2 for bird species codes.

Variable	Partial cut plots	PIWO	WISA	NOFL	HAWO	RBNU	WBNU
	Mean	Means for bird species nest stand plots					
Basal area(m^2/ha)	22.2	38.7***	28.8	22.3	12.5**	27.9***	13.1
Tree density(stems/ha)	567.2	725.0	662.5	382.8**	270.0*	569.3***	320.0
Canopy cover(%)[a]	46.0	49.0	66.0***	33.0	34.0	49.0	30.0
Canopy height(m)	26.9	32.0	31.4***	26.5	24.4	28.1	25.9
Snags >15-23 cm[b]/ha	2.6	6.7***	2.8	1.9	5.0*	5.8***	4.0
Snags >23-38 cm/ha	3.9	10.4***	6.3***	2.8**	1.5**	6.6	2.5
Snags >38-53 cm/ha	2.3	5.4***	3.3	2.5	2.5	4.5	1.5
Snags >53 cm/ha	1.2	12.1***	5.4***	3.9**	0.5	5.9***	1.5
Significance of discriminant function[c]		***	***	**	**	***	NS
Percentage of all plots correctly classified[d]		98.0	82.0	70.0	89.0	77.0	-

a)Arcsine transformed.
b)Diameter at breast height (dbh).
c)Based on Wilks' lambda.
d)A measure of similarity between nest stands and site plots; higher values indicate lower similarity.
* p <.05, ** p <.01, *** p <.001, NS=not significant.

Table 14. Results of 2-group discriminant function analyses comparing all nest stand plots of individual bird species vs. shelterwood plots. Values with asterisks indicate variables that entered the discriminant equation and significantly differed between nest stand and site habitat plots. See Table 2 for bird species codes.

	Shelterwood cut plots	PIWO	WISA	NOFL	HAWO	RBNU	WBNU
Variable	Mean	Means for bird species nest stand plots					
Basal area (m^2/ha)	10.9	38.7***	28.8***	22.3**	12.5	27.9***	13.1
Tree density(stems/ha)	249.5	725.0**	662.5***	382.8	270.0	569.3	320.0
Canopy cover(%)^a	26.0	49.0	66.0***	33.0	34.0	49.0	30.0
Canopy height(m)	22.9	32.0***	31.4	26.5	24.4	28.1	25.9
Snags >15-23 cm^b/ha	4.8	6.7	2.8	1.9**	5.0	5.8	4.0
Snags >23-38 cm/ha	3.7	10.4***	6.3***	2.8	1.5	6.6	2.5
Snags >38-53 cm/ha	1.9	5.4	3.3	2.5	2.5	4.5***	1.5
Snags >53 cm/ha	1.7	12.1***	5.4***	3.9	0.5	5.9***	1.5
Significance of discriminant function^c		***	***	**	NS	***	NS
Percentage of all plots correctly classified^d		94.0	90.0	62.0	-	80.0	-

a)Arcsine transformed.
b)Diameter at breast height (dbh).
c)Based on Wilks' lambda.
d)A measure of similarity between nest stands and site plots; higher values indicate lower similarity.
** p <.01, *** p <.001, NS=not significant.

average basal area of these nest stands was greater than that found in site plots. For all of these species except the northern flicker, the number of snags >53 cm dbh, and one of the smaller diameter classes, were also significantly higher in nest stands. Results of both discriminant function significance and classification suggested that nest stand characteristics of the hairy woodpecker, white-breasted nuthatch, and northern flicker were most similar, and those of the pileated woodpecker, Williamson's sapsucker, and red-breasted nuthatch least similar, to shelterwood sites.

Forage Site Characteristics

I observed foraging evidence on 49% of all snags, stubs, and defective live trees (n=1627) and on 13% of down logs (n=7908) occurring on study site habitat sample plots. Results of analyses for all these substrates reflect use by bird species that foraged by drilling, removing bark (scaling), or excavating into sapwood and heartwood: the pileated, hairy, three-toed and black-backed woodpeckers, northern flicker, and Williamson's and yellow-bellied sapsuckers. The northern flicker is primarily a ground forager, but also feeds on trees and logs (Bull 1980). Both of the nuthatch species are bark-gleaners.

For the following analyses, I reclassified observations of foraging evidence on snags, stubs, and defective live trees so that trees with the most extensive use could be examined. Trees with numerous holes and/or excavations (original codes 2-7) were classified as "forage trees," and those lacking or with few feeding holes (codes 0 and 1) as "non-forage" trees. The sample of available trees was the same as in previous analyses.

<u>Tree Condition</u>. Of the 426 trees with most extensive foraging evidence, 95% were dead trees (64% snags and 31% stubs) and 5% were defective live trees. Proportions of dead and defective live trees available on site sample plots were 89% and 11%, respectively. Although the relative proportional foraging use and availability of

these substrates were similar, a statistical comparison indicated that dead trees were used in significantly greater proportion to availability ($p < .05$, binomial test) and defective live trees were used less than expected ($p < .05$). Thus, of these two conditions, dead trees were preferred foraging substrates.

Tree Species. I observed foraging evidence on five species of trees (Table 15). Species with the largest proportions of all observations were western larch (45%) and Douglas-fir (44%), and fewest were on ponderosa pine (11%) and "other" tree species (1%, *Salix* sp.). Proportional feeding use and availability significantly differed for all tree species. Western larch and ponderosa pine were used in greater proportion than either occurred on study sites, while Douglas-fir and species grouped in the "other" category were used less often than expected.

Differences between tree species use and availability were also compared within three condition categories (Table 15); dead trees were divided into stubs and snags for these comparisons. Western larch snags and defective live trees, and ponderosa pine stubs, were preferred foraging substrates, while other conditions of these species were used in proportion to availability. Use of all conditions of Douglas-fir and "other" tree species was either below or the same as expected.

Table 15. Proportions of trees with foraging evidence and available by tree species and condition.

	Foraging Use (U)	Availability (A)	Preference Index[a]
Tree Species/Condition			
Western larch			
Stub	8	11	-0.03
Snag	61	45	0.16*
Defective live	74	44	0.30*
All conditions	45	34	0.11*
Ponderosa pine			
Stub	15	6	0.09*
Snag	9	6	0.03
Defective live	4	5	-0.01
All conditions	11	6	0.05*
Douglas-fir			
Stub	77	74	0.03
Snag	30	46	-0.16*
Defective live	17	43	-0.26*
All conditions	44	54	-0.10*
Other species[b]			
Stub	0	9	-0.09
Snag	0	4	-0.04
Defective live	4	8	-0.04
All conditions	1[c]	6	-0.05*

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a) (U - A) ÷ 100 (Strauss 1979).

b) Includes Engelmann spruce, subalpine fir, lodgepole pine, aspen and willow.

c) Willow.

* Use significantly differs from availability (p <.05, binomial test).

Doug fir used for foraging

Tree diameter and height. Forage tree preferences were further evaluated by comparing the proportions of forage and available trees in the same diameter and height classes used for nest trees (Table 16). Dead and defective live trees were pooled for these comparisons. Trees in the smallest diameter class (>15-23 cm dbh) were used significantly less than predicted based on availability, largest trees (>53 cm dbh) were used more than expected, and medium trees (>23-53 cm dbh) were used in the same proportion as their occurrence on study sites.

Among height classes, the tallest trees (>24 m) were used for feeding in greater proportion than predicted, use of trees ≤6 m, >6-12 m, and >18-24 m was in proportion to availability, and those of intermediate height (>12-18 m) were used significantly less than expected (Table 16).

Decay. I evaluated the decay condition of forage trees in the same manner as nest trees, using 6 decay stages based on external physical tree characteristics, and outward evidence of heartwood decay. A summary of forage trees by decay stage and top condition is presented in Table 17. Decay stage 6, representing soft snags, received the highest proportion (40%) of foraging use, but use was nearly equal to availability. Only stage 3 was used in significantly higher proportion than availability, and stage 1 less than expected. In contrast to nest trees, only a slightly higher number of forage trees had broken tops than intact tops, but their proportionate use (52%) was still higher than the corresponding availability (30%) of broken top trees.

Table 16. Proportions of trees (dead and defective live) with foraging evidence and available in various diameter and height classes.

	Foraging Use (U)	Availability (A)	Preference Index[a]
Diameter Class(cm)			
>15 - 23	21	33	-0.12*
>23 - 38	28	29	-0.01
>38 - 53	19	20	-0.01
>53	33	18	0.15*
Height Class(m)			
≤ 6	31	33	-0.02
> 6 - 12	10	11	-0.01
>12 - 18	7	12	-0.05*
>18 - 24	19	19	0.00
>24	33	24	0.09*

a) (U - A) ÷ 100 (Strauss 1979).

* Use significantly differs from availability ($p < .05$, binomial test).

Table 17. Percentages of trees with foraging evidence and available trees in different decay stages, and numbers of forage trees with intact or broken tops.

	Decay Stage Characteristics				Top Condition[b]				
Decay Stage	Tree Condition[a]	Needles	Twigs	Branches	Intact[c]	Broken	Percent Use (U)	Percent Available (A)	Preference Index[e]
1	live	present	present	most present	19	4	5	11	-0.06*
2	dead	present	present	most present	1	0	1	1	0.00
3	dead	absent	present	most present	64	12	18	19	-0.01
4	dead	absent	absent	many present	91	10	24	16	0.08*
5	dead	absent	absent	few present	30	26	13	13	0.00
6	dead	absent	absent	none present	0	169	40	39[d]	0.01
					205	221			

a)Live trees with live intact tops excluded.
b)Numbers of forage trees in each top condition.
c)Dead intact top.
d)All stubs classified in this decay stage.
e)(U - A) ÷ 100 (Strauss 1979).
* Use significantly differs from availability ($p < .05$, binomial test).

I observed outward evidence of heartwood decay on 56% of snags and defective live trees with feeding sign. The majority of forage trees with decay had pileated woodpecker feeding excavations in the lower portion of the bole. Carpenter ants (Camponotus sp.) create galleries in soft or decayed heartwood within the lower bole, and are a major pileated woodpecker prey item (Bent 1939, Hoyt 1957). Forage trees had lower incidence of conks, swollen knots, and other signs of decay compared to nest trees.

Discriminant Analysis of Trees With and Without Feeding Evidence. I used discriminant analysis to determine characteristics that best distinguished forage and non-forage trees; snags and defective live trees were pooled for this comparison. Variables included in the analysis were coded and entered in the same manner as for analyses comparing nest and non-nest trees. Due to the overlap in characteristics used to identify both decay and feeding evidence (i.e. presence of pileated woodpecker excavations), decay evidence was deleted from the group of variables in this analysis.

Diameter, limb presence, and western larch were the first variables to enter the discriminant equation (Table 18), followed by tree condition, fire evidence, ponderosa pine, and bark cover. Correlations of variables with the discriminant score showed that forage trees were larger in diameter, were more often western larch and ponderosa pine than Douglas-fir, had fewer limbs, lower bark cover, and were more likely to be snags and have fire evidence.

Table 18. Results of the discriminant function analysis comparing characteristics of snags and defective live trees with (n=296) and without (n=791) foraging evidence.

Variable	Variables entering analysis and step entered[a]	Correlations of variables with discriminant score
	Snags and defective live trees	Snags and defective live trees
Height(m)		0.38
Diameter[b]	1	0.54
Western larch	3	0.52
Ponderosa pine	6	0.16
Douglas-fir		-0.48
Top condition		0.02
Tree condition	4	0.37
Fire evidence	5	0.45
Limb presence	2	-0.46
Bark cover(%)[c]	7	-0.21

a)Variables entering the analysis significantly contributed ($p < .001$) to the discrimination between groups, given variables already entered in the equation. Variables with earliest entry step were best discriminators.
b)Variable entered for all trees was the basal area factor (m^2) for the tree diameter size class.
c)Arcsine transformed.

The discriminant function correctly classified 66% of all forage and non-forage trees. This percentage was lower than that obtained in the corresponding analysis of nest and non-nest snags and defective live trees (91%), which suggested greater similarity between characteristics of forage and non-forage trees than nest and non-nest trees.

Pileated Woodpecker and Sapsucker Foraging Evidence. I observed pileated woodpecker foraging excavations on 270 (63%) of the trees with most extensive feeding evidence. The majority of pileated forage trees were dead, and a slightly higher proportion were stubs (48%) than snags (46%); only 6% were defective live trees. Ponderosa pine stubs and snags, and defective live western larch, were used in significantly greater proportion than expected ($p < .05$, binomial test), while other conditions of these two tree species and all conditions of Douglas-fir were used in approximate proportion to availability. All "other" tree species were used less than expected in all conditions.

Pileated woodpeckers preferred trees >53 cm dbh for foraging ($p < .05$, binomial test) and used all smaller diameter classes significantly less than expected ($p < .05$). In contrast to comparisons of proportional use and availability of height class and decay stage use for all trees with foraging evidence, pileateds used trees $\leq$ 6 m tall and decay stage 6 in significantly greater proportion than corresponding availability ($p < .05$), used all other height classes in the same proportion as expected ($p > .05$), and foraged on trees in decay stage 3 significantly less than expected (p <.05). Decay stage 1 was also used less than expected, and stages 2, 4 and 5 in proportion to availability. Seventy percent of the pileated forage trees had broken tops.

Only three trees with sapsucker foraging evidence were observed, and all were defective live Douglas-fir. The diameter classes of these trees were: >23-38 cm dbh, >38-53 cm dbh, and >53-69 cm dbh. Two of the trees had broken tops, and one had decay evidence (conk). Williamson's sapsuckers were frequently observed foraging on live Douglas-fir trees located in close proximity to nest trees, and were also observed sapsucking on live western larch trees on several occasions.

Down logs. Proportions of down logs with feeding evidence were compared with proportions of available logs by diameter class, decay class, and four combinations of diameter and decay characteristics (Table 19). When diameter and decay classes were considered separately, diameters $\geq$30 cm and soft logs were each used in significantly greater proportion than corresponding availability, whereas diameters 15-29 cm and hard logs were used less than expected. Among the four diameter/decay classes, soft logs in both diameter categories were used more than predicted, and the highest preference index value was for soft logs $\geq$30 cm. These results suggested that soft logs, particularly those $\geq$30 cm, were preferred feeding substrates.

Table 19. Proportions of down logs with foraging evidence and available by diameter and decay classes.

	Foraging Use (U)	Availability (A)	Preference Index[a]
Log Diameter Class[b]			
15 - 29 cm	52	70	-0.18*
⩾30 cm	48	30	0.18*
Log Decay Class			
Hard	26	59	-0.33*
Soft	74	41	0.33*
Diameter/Decay Class			
Hard 15 - 29 cm	15	45	-0.30*
Hard ⩾30 cm	10	13	-0.03
Soft 15 - 29 cm	37	26	0.11*
Soft ⩾30 cm	38	17	0.21*

a) (U - A) ÷ 100 (Strauss 1979).
b) Measured approximately 1 m from largest end.
* Use significantly differs from availability (p <.05, binomial test).

Cavity-Nesting Bird Populations

The relative abundance of cavity-nesting birds observed during Point Count censuses was compared (1)among unmanaged, partial cut, and shelterwood cut management types, (2)among sites that differed in management direction concerning snag retention, and (3)with variables describing snag density, snag size diversity, and live tree habitat characteristics on all study sites.

Bird Abundance Among Management Types. I observed a total of 15 cavity-nesting bird species in management types sampled on the east and west sides of the Tonasket RD (Table 20); nine of these species were excavators and six were nonexcavators. Species composition and the relative number of excavator and nonexcavator species varied among types, but the total number of species was similar in each type. The shelterwood cuts contained both the highest number of excavator species (n=9) and fewest nonexcavators (n=3), while partial cuts had fewest excavators (n=7) and the largest number of nonexcavators (n=6). Cavity-nesting bird species diversity (H') was slightly higher in shelterwood than partial cuts, and lowest in the unmanaged type.

Mean detection rates of excavators, nonexcavators, and all cavity-nesting birds were significantly higher in the unmanaged type than in either shelterwood or partial cuts, but rates in the two managed types did not significantly differ (Table 20). Interspecific detection rates, however, varied considerably among types.

Table 20. Mean detection rates[a] of cavity-nesting birds based on Point Count censuses conducted in unmanaged, partial cut and shelterwood cut management types in the Tonasket RD, 1983-84. For each of the 3 groups, n = the number of censuses used to calculate detection rates.

	Unmanaged (n=16)	Partial cuts (n=16)	Shelterwood cuts (n=16)	
Excavators				
Williamson's sapsucker	0.16	0.17	0.09	
Yellow-bellied sapsucker	0.03	0.00	0.02	
Hairy woodpecker	0.05	0.06	0.20	
Three-toed woodpecker	0.01	0.00	0.01	
Black-backed woodpecker	0.00	0.01	0.04	
Northern flicker	0.06	0.12	0.15	
Pileated woodpecker	0.11	0.07	0.03	
Red-breasted nuthatch	1.24	0.65	0.61	
White-breasted nuthatch	0.03	0.05	0.11	
Nonexcavators				
American kestrel	0.02	0.02	0.04	
Flammulated owl	0.00	0.02	0.00	
Black-capped chickadee	0.02	0.02	0.00	
Mountain chickadee	1.30	1.12	1.13	
Boreal chickadee	0.00	0.02	0.00	
Brown creeper	0.49	0.17	0.11	
Excavators(A)	1.69 B[b]	1.11 A	1.24 A	F[c]= 9.71***
Nonexcavators(B)	1.83 B	1.36 A	1.28 A	F = 5.03**
All cavity-nesters(A+B)	3.52 B	2.47 A	2.52 A	F = 9.00***
Number of species	12	13	12	
Bird species diversity(H')[d]	1.54	1.63	1.68	

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a)Calculated as the average number of birds detected/8 min count period; 4 censuses were conducted per study site, each including 12 count periods.

b)Within each row, mean detection rates with the same letter are not significantly different ($p > .05$, Student-Neuman-Keuls multiple range test).

c)Based on analysis of variance test among 3 groups: ** $p < .01$, *** $p < .001$. Detection rates were transformed $\ln(x+1)$ for all analyses but original values are shown for clarity.

d)Shannon's index (Shannon and Weaver 1949).

The red-breasted nuthatch was the most common excavator species in all management types, and the three-toed woodpecker was rarely observed (Table 20). The pileated woodpecker and red-breasted nuthatch were detected most frequently in unmanaged sites, while mean detection rates of the hairy and black-backed woodpeckers, northern flicker, and white-breasted nuthatch were highest in shelterwood cuts. Detection rates of the Williamson's sapsucker were similar in unmanaged and partial cut types, and lowest in shelterwood cut sites; many detections of this species in both partial and shelterwood cuts, however, were of birds that appeared or were known to be nesting in areas beyond site boundaries. Yellow-bellied sapsucker detections were exclusively in west side sites that were in close proximity to aspen stands.

The mountain chickadee was the most abundant nonexcavator species, and the brown creeper was the only other nonexcavator observed regularly in all management types (Table 20). Mean detection rates of both these species were highest in the unmanaged type. The flammulated owl was observed only on the east side of the district, and the boreal chickadee only on the west side.

Bird Abundance Among Sites Differing in Snag Management Direction.

To examine potential differences in cavity-nesting bird abundance among sites differing in management direction concerning snags, I formed four groups of sites based on the classification presented in Table 1: (1)unmanaged, with snags unaffected by logging activity (Roggow, Muck, Burge, Oriole), (2)most snags retained when sites were logged in single entries (Bailey, Strike, Frost), (3)most snags cut during initial logging entries and retained in the most recent entry (Spike, McCay), and (4)most snags cut in all logging entries (Turner, Strip, Rainy). Each site was classified only by the management direction affecting snags in relation to logging activity, regardless of the policy concerning snag removal for firewood.

Mean snag densities found in each of these four groups are presented and compared in Table 21. Unmanaged sites had significantly higher densities of snags in all diameter classes than each of the other groups. The second group, where snags were retained when logging occurred, had significantly higher densities of all snags >15 cm dbh and in the >53 cm dbh class than sites where snags were retained only in the last entry, or sites where most snags were cut in all entries; the latter two groups differed only in the density of snags >38-53 cm dbh. The most significant difference in snag densities among the four groups, indicated by the F ratio for the comparison, was in the density of snags >53 cm dbh.

Excavator, nonexcavator, and all cavity-nesting bird mean detection rates significantly differed among the four groups of sites (Table 22). Results of each multiple range test indicated that mean detection rates for unmanaged sites and sites where snags were retained when logging occurred were significantly higher than for sites where most snags were cut in early entries but retained in the last entry, or

Table 21. Mean snag densities on sites grouped by management direction concerning snags. For each group, n = the number of site sample plots used to calculate snag densities.

	Unmanaged	Managed			
	Snags unaffected by logging[a] (n=48)	Snags retained when logged (n=36)	Most snags cut first entries retained last entry (n=24)	Most snags cut all entries (n=36)	
Snag Densities(stems/ha)					
>15 cm dbh	34.4 C[b]	14.0 B	9.5 A	9.2 A	F[c]=27.1***
>15 - 23 cm dbh	7.8 B	3.6 A	5.1 A	2.9 A	F = 8.0***
>23 - 38 cm dbh	10.9 B	4.0 A	3.6 A	3.8 A	F =15.4***
>38 - 53 cm dbh	7.8 C	3.1 B	0.6 A	2.0 B	F =21.0***
>53 cm dbh	7.9 C	3.3 B	0.2 A	0.5 A	F =41.7***
>23	26.4	10.4	4.4	6.3	

a)See Table 1 for more detailed descriptions of management directions; also see text.

b)Within each row, mean snag densities with the same letter are not significantly different ($p > .05$, Duncan's multiple range test).

c)Based on analysis of variance test among 4 groups: *** $p < .001$. Snag densities were transformed $\ln(x+1)$ for all analyses, but original values are shown for clarity.

Table 22. **Cavity-nesting bird mean detection rates compared among sites grouped by management direction concerning snags.** For each of the 4 groups, n = the number of censuses used to derive detection rates.

	Unmanaged	Managed			
	Snags unaffected by logging^{a} (n=16)	Snags retained when logged (n=12)	Most snags cut first entries retained last entry (n=8)	Most snags cut all entries (n=12)	
Excavators					
Williamson's sapsucker	0.16	0.13	0.09	0.15	
Yellow-bellied sapsucker	0.03	0.00	0.03	0.00	
Hairy woodpecker	0.05	0.18	0.19	0.03	
Three-toed woodpecker	0.01	0.01	0.00	0.00	
Black-backed woodpecker	0.00	0.03	0.03	0.00	
Northern flicker	0.06	0.15	0.14	0.11	
Pileated woodpecker	0.11	0.06	0.01	0.06	
Red-breasted nuthatch	1.24	0.73	0.51	0.60	
White-breasted nuthatch	0.03	0.14	0.06	0.05	
Nonexcavators					
American kestrel	0.02	0.05	0.03	0.00	
Flammulated owl	0.00	0.02	0.00	0.00	
Black-capped chickadee	0.02	0.00	0.00	0.02	
Mountain chickadee	1.30	1.51	0.82	0.95	
Boreal chickadee	0.00	0.00	0.00	0.02	
Brown creeper	0.49	0.17	0.07	0.16	
Excavators(A)	1.69 B^{b}	1.43 B	1.06 A	1.00 A	F^{c}=11.11***
Nonexcavators(B)	1.83 B	1.75 B	0.93 A	1.15 A	F =10.70***
All cavity-nesters(A+B)	3.52 B	3.18 B	1.99 A	2.16 A	F =16.75***
Number of species	12	12	11	10	

a)See Table 1 for more detailed descriptions of management direction; also see text.

b)Within each row, mean detection rates with the same letter are not significantly different ($p > .05$, Duncan's multiple range test).

c)Based on analysis of variance test among 4 groups: *** $p < .001$. Detection rates were transformed $\ln(x+1)$ for all analyses, but original values are shown for clarity.

snags were cut in all entries. These tests also showed that detection rates did not differ between unmanaged sites and those where snags were retained when logging occurred, or between sites where snags were retained in only the most recent entry and those where most snags were cut in all entries.

Mean detection rates for 10 of the 15 cavity-nesting bird species were highest in unmanaged sites, sites where snags were retained when logging occurred, or in both of these groups (Table 22). Hairy and black-backed woodpeckers were observed most frequently in sites where snags were retained when logging occurred or were retained in the most recent entry.

Relationships Between Cavity-Nesting Bird Detection Rates and Habitat Variables. Mean detection rates of both excavators and nonexcavators were most strongly correlated with the density of snags >15 cm dbh/ha and snag basal area/ha (Table 23). Among the four diameter classes of snags, both groups were more highly correlated with snags >38-53 cm dbh and >53 cm dbh than smaller snags. I used partial correlation to test the relation of combined excavator and nonexcavator detection rates to total snag density (>15 cm dbh), controlling for each of the diameter classes separately. The partial correlation coefficient was low ($r = 0.51$, $p > .05$) when the effect of snags >53 cm dbh was removed statistically, but remained significant when the effect of snags >38-53 cm dbh ($r = 0.59$, $p < .05$), snags >23-38 cm dbh ($r = 0.71$, $p < .05$), or snags >15-23 cm dbh ($r = 0.89$, $p < .05$) was removed. These

Table 23. Correlations[a] of cavity-nesting bird abundance (based on mean detection rates) with habitat variables measured on 12 study sites.

Habitat variable	Excavators (A)	Nonexcavators (B)	All cavity-nesters (A+B)
Snags >15 cm dbh/ha	0.80*	0.82*	0.88*
Snags >15-23 cm dbh/ha	0.52*	0.37	0.49
Snags >23-38 cm dbh/ha	0.68*	0.69*	0.76*
Snags >38-53 cm dbh/ha	0.74*	0.75*	0.82*
Snags >53 cm dbh/ha	0.74*	0.82*	0.85*
Snag basal area(m^2/ha)	0.78*	0.87*	0.91*
Snag size diversity[b]	0.57*	0.57*	0.61*
Logs >15 cm[c]/ha	0.03	0.36	0.23
Soft logs $\geqslant$30 cm[c]/ha	-0.12	0.19	0.06
Live tree basal area(m^2/ha)	0.32	0.24	0.29
Live tree density(stems/ha)	0.20	0.19	0.21
Canopy height(m)	0.38	0.46	0.45
Canopy cover(%)[d]	0.49	0.40	0.48

a)Pearson product-moment correlation coefficients. Detection rates, snag densities, snag basal area and live tree basal area were transformed using ln(x+1).

b)Diversity (H') based on combination of 5 height classes and 4 diameter classes.

c)Diameter measured approximately 1 m from largest end.

d)Arcsine transformed.

* Significant at $p < .05$.

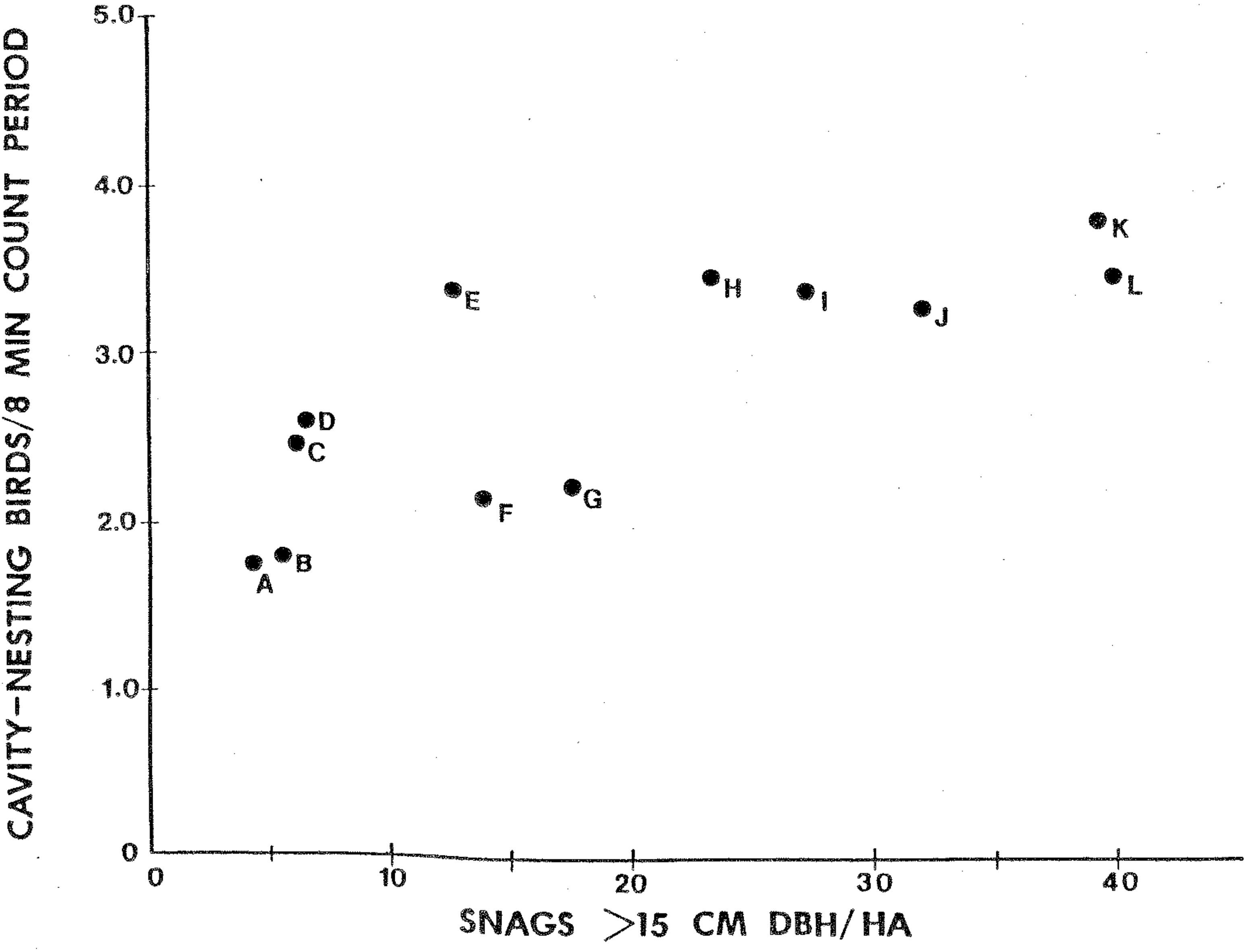
results suggest that, of the four snag diameter classes, cavity-nesting bird abundance was most closely related to the density of snags >53 cm dbh.

Both excavator and nonexcavator mean detection rates were also significantly correlated with snag size diversity (H′, calculated using a combination of four diameter and five height classes), but not with any of the log or live tree variables (Table 23).

Relationship Between Cavity-Nesting Bird Detection Rates and Snag Densities. In previous analyses I found that among sites differing in snag management direction, cavity-nesting bird detection rates were highest in the two groups of sites with greatest densities of all snags >15 cm dbh, and snags >53 cm dbh (Tables 21 and 22). Furthermore, cavity-nesting bird abundance was most closely associated with densities of snags >53 cm dbh. To clarify the relationship between bird and snag abundance, I compared cavity-nesting bird mean detection rates first with all snags >15 cm dbh (Fig. 5), and then with snags >53 cm dbh (Fig. 6), on the 12 study sites.

Mean detection rates generally increased in relation to increasing densities of snags >15 cm dbh (Fig. 5). However, the Spike (letter "F") and Turner ("G") sites had lower detection rates, but higher snag densities, than the Strike ("E"), Frost ("D"), or Rainy ("C") sites. Also, the mean detection rates on sites with >20 snags/ha ("H" - "L") were similar to that found on Strike ("E"), which had an average of 12 snags/ha.

Figure 5. Cavity-nesting bird mean detection rates in relation to densities of snags >15 cm dbh on the 12 study sites. Letters representing sites: Strip, A; McCay, B; Rainy, C; Frost, D; Strike, E; Spike, F; Turner, G; Bailey, H; Muck, I; Roggow, J; Burge, K; Oriole, L.


CAVITY-NESTING BIRDS/8 MIN COUNT PERIOD
5.0
4.0
3.0
2.0
1.0
0
0
10
20
30
40
SNAGS >15 CM DBH/HA
A
B
C
D
E
F
G
H
I
J
K
L

Detection rates in relation to densities of snags >53 cm dbh increased in a more distinct, nonlinear (convex) manner (Fig. 6) than in relation to all snags >15 cm dbh, and the sites fell into two different groups. The six sites with <1 snag >53 cm dbh/ha clearly had the lowest detection rates, and those with $\geq$3.5 snags/ha had the highest rates. The Strike ("E") site, which had fewer snags >15 cm dbh than either Spike ("F") or Turner ("G"), had a greater density of large snags which apparently contributed to the higher detection rate found in this site.

Mean detection rates did not significantly differ among the six sites with $\geq$3.5 snags >53 cm dbh/ha ($p > .05$, $F = 0.36$, ANOVA), despite the wide range in large snag density in these areas. However, the tree species composition of snags >53 cm dbh may have influenced detection rates more than the actual density of snags in this diameter class, due to excavator preferences for ponderosa pine and western larch as nest and forage sites. Roggow had the greatest density of snags >53 cm dbh, but 77% were Douglas-fir, which was a higher proportion than on any of the other sites (Table 24). Strike had the lowest density of large snags, but 93% were ponderosa pine and western larch, and only 7% were Douglas-fir. The common characteristic of all six sites, however, was that approximately three to four of the snags >53 cm dbh/ha were ponderosa pine and/or western larch.

Figure 6. Cavity-nesting bird mean detection rates in relation to densities of snags >53 cm dbh on the 12 study sites. Letters representing sites are the same as in Fig. 5: Strip, A; McCay, B; Rainy, C; Frost, D; Strike, E; Spike, F; Turner, G; Bailey, H; Muck, I; Roggow, J; Burge, K; Oriole, L.

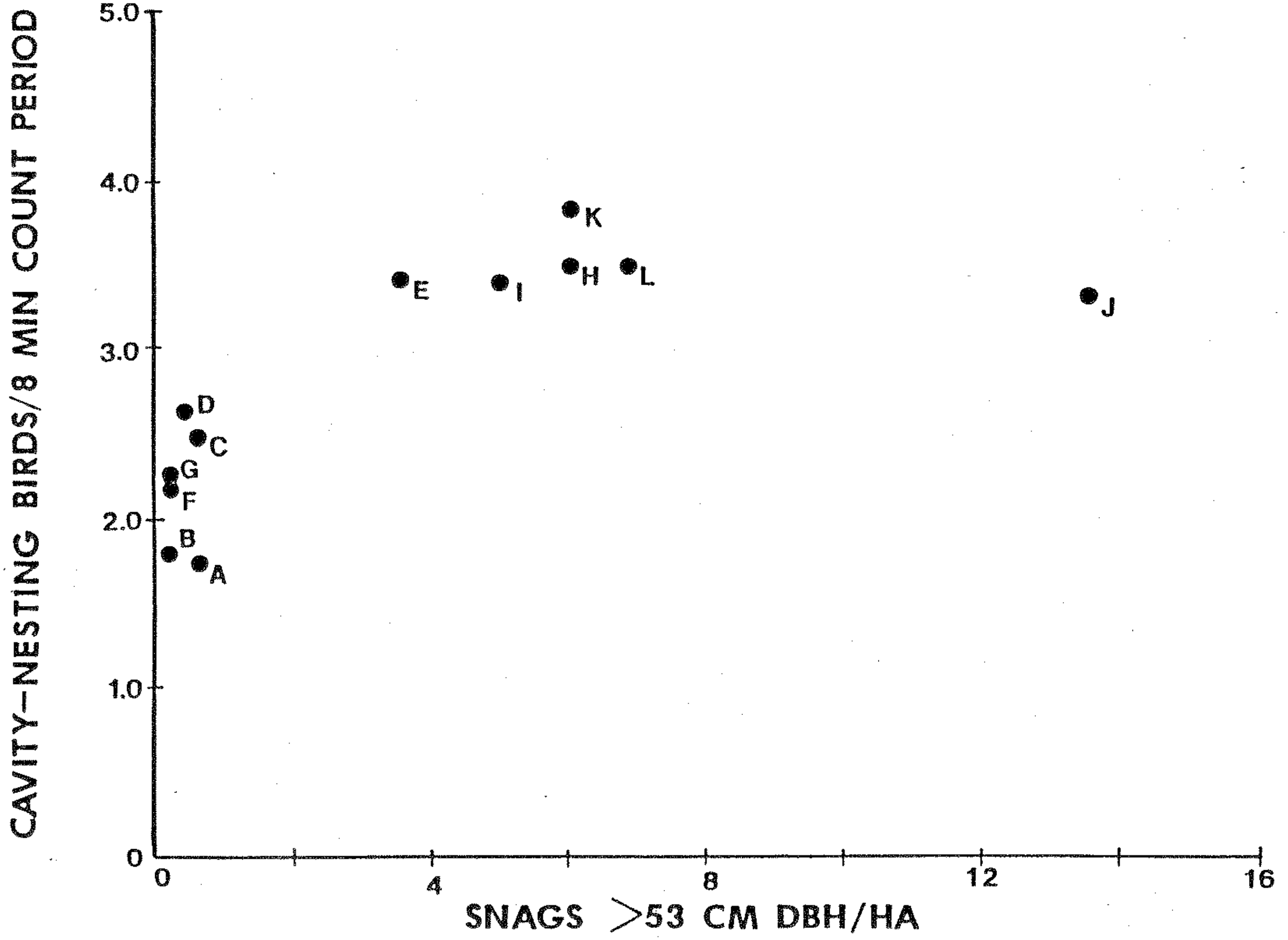

CAVITY-NESTING BIRDS/8 MIN COUNT PERIOD
5.0
4.0
3.0
2.0
1.0
0
0
4
8
12
16
SNAGS >53 CM DBH/HA
A
B
C
D
E
F
G
H
I
J
K
L

Table 24. Tree species composition of snags >53 cm dbh on study sites with the highest mean detection rates of cavity-nesting birds.

Study site	Snags >53 cm dbh (total #/ha)	Douglas fir (%)	Douglas fir (#/ha)	Western larch (%)	Western larch (#/ha)	Ponderosa pine (%)	Ponderosa pine (#/ha)
Roggow	13.5	77	10.4	23	3.1	0	0.0
Oriole	6.9	61	4.2	13	0.9	26	1.8
Burge	6.0	37	2.2	17	1.0	46	2.8
Bailey	6.0	50	3.0	46	2.8	4	0.2
Muck	5.0	25	1.2	75	3.8	0	0.0
Strike	3.5	7	0.2	43	1.5	50	1.8

DISCUSSION AND MANAGEMENT IMPLICATIONS

Nest Tree Characteristics

Diameter. Comparisons of nest and non-nest trees showed that nest trees were larger in diameter (Table 9), and that diameter was one of the most important characteristics distinguishing these two groups. Excavators preferred dead and defective live trees >53 cm dbh for nesting, and used diameters >15-38 cm dbh significantly less than expected (Table 6). The mean diameter of all excavator nest trees was 65.2 cm, and the majority of individual species nested in trees >53 cm dbh (Table 5); only the hairy, three-toed, and black-backed woodpeckers appeared to prefer smaller diameter trees.

Forest managers in the ONF currently follow snag management guidelines recommended by Thomas et al. (1979), which suggest providing snags equal to or greater than the minimum or smallest diameter that can be used by each excavator species. The minimum diameters suggested for the seven excavators occurring in the ONF are: 25.4 cm dbh for the hairy woodpecker; 30.5 cm dbh for the northern flicker, black-backed and three-toed woodpeckers, Williamson's sapsucker, and red-breasted and white-breasted nuthatches; and 50.8 cm dbh for the pileated woodpecker. My results and those of numerous recent studies conducted in other parts of the western United States, however, provide substantial evidence that most excavators nest in larger than minimum-sized trees (Appendix II, and also Mannan et al. 1980, Zarnowitz and Manuwal 1985).

The nest tree diameter must accommodate cavity dimensions required by each bird species, which vary according to species size. The average width of pileated woodpecker cavities is 20 cm (Bent 1939), and the widths of cavities created by other excavators found in this study range from 8 cm to 16 cm (Bent 1939, Raphael and White 1984). Larger diameter trees provide both additional space for cavity excavation and greater insulation around the nest, which may enhance reproductive success. Studies examining the relationship between clutch size and cavity diameter have shown that hole-nesting species produce bigger clutches in larger than smaller diameter cavities (Karlsson and Nilsson 1977, Trillmich and Hudde 1984). Thicker insulation provided by large diameter trees may protect eggs and nestlings from extreme temperatures that occur during the breeding season; in the Tonasket RD, for example, temperatures can fluctuate from below 4°C to over 30°C during May, June, and July.

Conner (1979) suggested that management strategies based on minimum tree diameters could cause a gradual decline in cavity-nesting bird populations because of reduced reproductive success, and recommended managing for mean diameters. He stressed that, since nest tree diameters are normally distributed, natural selection should favor individuals nesting in trees closest to the mean area, rather than the tails or extreme areas, of a diameter distribution curve.

I suggest that forest managers in the ONF adopt Conner's (1979) approach and provide mean rather than minimum tree diameters for primary cavity-nesting species. In my study, mean diameters ranged from 44.2 cm for the hairy woodpecker to 84.2 cm for the pileated woodpecker, and the single nest trees of the three-toed and black-backed woodpeckers were 31.7 and 29.0 cm, respectively (Table 5). A higher number of trees should be in larger size classes since the mean nest tree diameter for five of the eight excavator species was >53 cm.

Height. I found greater interspecific variation in nest tree height than diameter (Table 5), and detection rates of all cavity-nesting birds were positively correlated with snag size diversity (Table 23). Raphael and White (1984) found similar relationships for cavity-nesting birds in the Sierra Nevada, and recommended management for a diversity of heights among large diameter trees to meet species' requirements. Excavators, as a group, preferred trees >24 m tall for nesting (Table 6) and used heights $\leq$ 6 m significantly less often than expected. Thus, because top breakage decreases tree heights over time, and also contributes to height diversity, management for taller trees should be emphasized.

Species, Condition, and Decay. Tree species, condition, and the presence of decay are important, related characteristics that influence a tree's suitability for nesting. Although tree species preferences vary among different forest types and geographic areas, excavators appear to consistently select combinations of species and conditions with optimum decay characteristics. The presence of heartwood decay is essential to most excavators (Shigo and Kilham 1968, Kilham 1971, Jackman 1974, Crockett and Hadow 1975, Conner et al. 1976, McClelland 1977), and a sound outer sapwood provides protection for the cavity nest. Miller et al. (1979) found that both cavity position and shape closely followed decay patterns. Excavators probably distinguish the presence of decayed or sound wood in potential nest trees by the different resonance emitted by each substrate (Conner et al. 1976).

Ponderosa pine snags and both defective and intact live western larch trees were highly preferred for nesting in the ONF (Table 4), and Douglas-fir was used significantly less than expected in all conditions relative to its abundance on study sites. Although the proportional use of dead western larch did not differ from expected use, it should be noted that larger diameter larch snags were selected for nesting in markedly higher proportion than corresponding availability; 71% of the dead larch nest trees were >70 cm dbh, but only 3% of the sampled larch snags were >70 cm. Generally I observed that smaller diameter larch snags had much lower evidence of heartwood decay, and fewer had broken tops, than those of larger diameter, and thus were probably not as suitable for nesting.

Relative to the low availability and patchy distribution of aspen on the Tonasket RD, this tree species appears to be important for nesting wherever it occurs. Nearly half of the off-site excavator nests were in live aspen (Appendix I), and most of these were in aspen stands located in close proximity to study sites. I found eight cavity nests in a 1 ha aspen stand near the Rainy site, which was equal to the number found within the entire adjacent 70 ha study area. I suspect that aspen may be particularly important in forest areas where coniferous snag densities are low.

Excavator tree species preferences in the ONF are related to the different sapwood and heartwood decay patterns in ponderosa pine, western larch, Douglas-fir, and aspen. In western larch, the thin sapwood layer remains intact for long periods around heartwood that decays very slowly (McClelland 1977), so that portions of a large larch may remain suitable for nest cavity excavation many years after the invasion of decay organisms. Unlike western larch, the sapwood of Douglas-fir decays more rapidly than the heartwood (Wright and Harvey 1967, Cline et al. 1980); by the time the heartwood becomes sufficiently soft for excavation, the sapwood may be too deteriorated to provide adequate support and protection for a nest cavity. In ponderosa pine, cavities may be excavated completely within decayed portions of the extremely thick sapwood (Miller et al. 1979), within heartwood decay columns high in broken-topped trees where sapwood is thinner (Bull 1980), or low in smaller diameter trees decayed by root rot fungi (Miller et al. 1979, Bull 1980). Live aspen is highly susceptible to heartwood decay, and like western larch, it is particularly suitable for nesting because the thin sapwood remains intact and provides a protective outer shell (Shigo and Kilham 1968, Kilham 1971).

Western larch snags and defective live trees were also highly preferred by excavator species studied by McClelland (1977) in the northern

Rocky Mountains, and Douglas-fir comprised only 3% of the 273 nest trees he found; a high proportion of aspen and ponderosa pine were also used for nesting compared to their relatively low availability. In northeastern Oregon, Bull (1980) found that western larch was the preferred live tree species, and among dead trees, ponderosa pine was preferred. Although both of these authors reported slightly different tree species use among the excavators I studied in the ONF, pileated woodpeckers preferred western larch and/or ponderosa pine snags in all three areas.

Among the six decay stages I defined, based on external characteristics depicting tree deterioration, excavator species as a group used all except stages 5 and 6 in approximately the same proportion as corresponding availability (Table 7). Stage 5 was preferred, and more deteriorated snags in stage 6 were used for nesting less than expected. Mannan et al. (1980) also found lower excavator use of trees in most deteriorated decay stages.

Decay stage use varied among individual bird species, but generally I did not find a definite relationship between the decay stages used by each species and its relative excavation ability. For example, the pileated woodpecker is the strongest excavator, but this species located nests in both hard and soft snags; the white-breasted nuthatch, a weaker excavator, used only hard snags. I think that a tree′s suitability for nesting in each decay stage can vary considerably regardless of the external physical characteristics I defined, and that two important features of trees in all stages are the top condition and the presence or absence of heartwood decay.

Forage Site Characteristics

Tree Diameter and Height. Similar to nest trees, excavators preferred diameters >53 cm and heights >24 m for foraging (Table 16), and diameter was the characteristic that best distinguished forage and non-forage trees (Table 18). The diameter and height classes of forage trees matched availability more closely than nest trees, however, indicating excavators tend to be less selective in tree sizes used for feeding than for nesting.

Raphael and White (1984) also found that diameter was the best discriminator between trees with and without foraging evidence, and reported that both live trees and snags >38-53 cm dbh were preferred. Mannan et al. (1980) found that snags >60 cm dbh showed the most foraging use. Generally larger diameter trees may be preferred because they harbor higher insect densities (Parker and Stevens 1979), and also provide greater bark surface and internal area for feeding. Particularly during fall and winter months, when food resources are more limited and many substrates become snow-covered, large snags may become the only concentrated sources of excavator insect prey that reside below the bark surface, such as bark and woodboring beetle larvae and carpenter ants. Conner (1979) observed that pileated and hairy woodpeckers shifted their foraging strategies during winter months, and used methods that penetrated trees more deeply than in other seasons. Similarly, Bull (1980) found that the northern flicker shifted from ground foraging in summer to excavating in dead wood during the fall.

Tree Species, Condition, and Decay. The discriminant analysis of forage and non-forage trees showed that, in addition to diameter, the proportions of trees that were western larch or ponderosa pine and tree condition were characteristics that distinguished these two groups (Table 18). Western larch snags and ponderosa pine stubs were preferred foraging substrates (Table 15). Defective live trees were used significantly less than expected relative to occurrence, but among those with foraging evidence, western larch were preferred. Although the same tree species were preferred for both foraging and nesting, preference index values indicated that excavators used a wider range of species as forage than as nest sites.

Proportions of forage trees in the six decay stages closely corresponded to availability (Table 17), but the actual decay stage of a tree at the time it was used is difficult to determine when only the presence of feeding evidence is recorded. For example, the most intensive feeding activity may have occurred while the tree was alive but weakened and dying, or recently after death, but feeding holes would remain visible in successive decay stages. Extensive evidence on trees in more deteriorated stages thus may reflect cumulative foraging use in earlier stages, rather than use in the current stage.

Nonetheless, a wide variety of insects, represented by many species and families, are attracted to weakened, dying, or dead trees (Furniss and Carolin 1977:38), and are found within the phloem, sapwood, or heartwood regions of the bole throughout different stages of tree deterioration (Kimmey and Furniss 1943, Wright and Harvey 1967). The specialized foraging methods and morphology of excavators may allow these birds to forage opportunistically among all decay stages. Within the first six years after tree death, Cline et al. (1980) found extensive activity of woodboring beetles within the bark, cambium and sapwood, and observed that the presence of these insects elicited woodpecker feeding. In more advanced stages of deterioration, heartwood regions softened by wood-decaying fungi are penetrated by woodboring cerambycids and buprestids, and provide suitable substrate for termite (_Zootermopsis_ spp., _Reticulitermes_ spp.) and carpenter ant colonies.

Forage trees had a lower incidence of conks, swollen knots, and other outward signs of heartwood decay compared to nest trees, and a larger proportion had intact tops. The presence of heartwood decay generally may not be as important in the suitability of trees as forage substrates due to the availability of numerous insects in outer regions of the bole. Taller trees with intact tops provide greater surface area for feeding; also, Raphael and White (1984) suggested that taller trees may reduce interspecific conflicts by allowing vertical stratification of foraging activity among excavators using similar foraging methods and portions of the tree. Stallcup (1968) concluded that one of the factors contributing to the segregation of foraging activity among sympatric species of woodpeckers and nuthatches in Colorado was the different zones of a tree used for feeding.

Down logs. Soft logs (Class 3-4) $\geq$30 cm in diameter were highly preferred for feeding, and soft logs 15-29 cm were also used in significantly greater proportion than expected (Table 19). Numerous excavator species forage on down logs during the breeding season (Raphael and White 1984:34) to satisfy a portion of their food requirements. The pileated woodpecker feeds extensively on this substrate during the spring, summer, and fall (Bull 1975, McClelland 1977, Bull 1980, Mannan 1984), and appears to particularly prefer large logs that are softened by decay and contain carpenter ant colonies. Although I did not quantify foraging behavior, I observed pileated woodpeckers excavating in Class 3-4 down logs ($\geq$30 cm dbh) on numerous occasions during my study.

Nest Stand Structure

Live tree basal area, tree density, canopy cover, and the number of snags >53 cm dbh accounted for the greatest variation in nest stand structure among excavators (Table 11, Fig. 4), and these characteristics separated the bird species into two groups. The pileated woodpecker, Williamson's sapsucker, and red-breasted nuthatch nested in denser, higher basal area stands that contained a larger number of snags >53 cm, and nest stands of these species were most similar to unmanaged site plots (Tables 12, 13 and 14). In contrast, nest trees of the hairy woodpecker, northern flicker, and white-breasted nuthatch were surrounded by open forest conditions characterized by fewer trees and large snags, and lower canopy cover; nest stands of these three species were more similar to partial and shelterwood cut than unmanaged site plots. The lower success of the discriminant analysis comparing all excavator nest stands with all study site plots, compared to those comparing individual species and management type plots, can probably be attributed to contrasting nest stand preferences of these two groups.

Pileated Woodpecker. Of all the excavator species, the pileated woodpecker appeared to have the most restrictive or narrowest preferences for certain forest structural features. Nest stands of this species had the highest live basal area and tree density, and also contained the largest numbers of snags in all diameter classes; these characteristics also consistently distinguished pileated nest stand from study site sample plots (Tables 12, 13 and 14).

Other studies of this species in western coniferous forests have reported similar results. Bull (1980) found significantly higher large tree densities and numbers of snags surrounding pileated nests than in available forest habitat, and pileateds nested in denser stands than the other species she studied. In the northern Rockies, pileated nests were located primarily in high basal area, old-growth stands, and McClelland (1979) suggested that forests with an old-growth component of western larch, ponderosa pine, or black cottonwood (_Populus trichocarpa_) seem to be essential for the long-term support of this species. Harris (1982) found that pileated woodpeckers nested in distinct, structurally similar stands typified by high densities of large trees and snags, and suggested that the presence of these characteristics, rather than the actual productivity (high or low) or age (old- or young-growth) classification, determined the suitability of pileated nesting habitat.

Among the sites I studied in the Tonasket RD, pileated woodpecker nests were found in (1)unmanaged sites dominated by old-growth characteristics including large trees, snags, and down logs, (2)managed sites where snags had been retained when logging occurred, and (3)a dense, unlogged riparian area within and extending beyond the boundaries of a partial cut site. Apparently each of these areas, in different ways, supported a suitable combination of habitat features (particularly an old-growth component) that this species requires for nesting and feeding during the breeding season.

Although I was not able to evaluate pileated woodpecker territory sizes within the design of my study, other researchers have estimated that this species uses areas approximately 130 ha (Bull and Meslow 1977) to from 200-400 ha (McClelland 1979) in size for nesting and feeding during the breeding season. Mannan (1984) found pileateds occupying areas from approximately 400-500 ha in size, primarily within older forests (70+ years of age).

Williamson´s Sapsucker and Red-breasted Nuthatch. Nest stands of the Williamson´s sapsucker and red-breasted nuthatch were similar to those of the pileated woodpecker, but these species nested in a wider range of habitat conditions. Nests located in managed stands, however, were usually located in denser patches of forest containing higher snag densities. In the northern Rockies, McClelland (1977) found only four Williamson´s sapsucker nests, but the average live basal area of nest stands was 34 m^2/ha; red-breasted nuthatch nests were found in a broad range of habitats, but the live basal area surrounding nests did not significantly differ from that of the pileated woodpecker. Raphael and White (1984) found that Williamson`s sapsucker and red-breasted nuthatch nest stands were distinguished from those of other excavators on the basis of live basal area and location in unburned forest; also, live basal area and snag densities were among characteristics that best discriminated Williamson´s sapsucker nest stands from random sample plots.

Hairy Woodpecker, Northern Flicker, and White-breasted Nuthatch. Of these three species, the northern flicker was the least selective in relation to stand structural features immediately surrounding the nest, but generally nests were located either within or close to open forest areas. Other studies have also noted the adaptiveness of this species to varied habitat conditions, and preference for nesting near or in open forest stands (Dennis 1969, Conner et al 1975, McClelland 1977, Bull 1980).

The hairy woodpecker and white-breasted nuthatch also appeared to prefer open stand conditions, and nests located in more densely forested sites were within open portions of the area. Average snag densities in most diameter classes were lower in nest stands of these species compared to other excavators, and were infrequently higher than snag densities in site sample plots (Tables 12, 13 and 14). McClelland (1977) found hairy woodpecker nests within old-growth forest as well as in or near shelterwood cuts. In northeastern Oregon, open stands with low basal areas, stem densities, and canopy cover characterized hairy woodpecker nest stands (Bull 1980), but in contrast to nest sites I observed for this species, snag densities in all diameter classes were significantly higher in nest stands than in general forest conditions.

Raphael and White (1984) described the northern flicker, hairy woodpecker, and white-breasted nuthatch as "habitat generalists" relative to other cavity-nesting species, indicating use of a wide range of forest types. These authors also found that the hairy woodpecker and northern flicker nested in open forest conditions, and densities of snags >23 cm dbh and live basal area best distinguished nest stand characteristics from those of random sample plots.

<u>Black-backed and Three-toed Woodpeckers</u>. I found too few nests to adequately characterize nest stands for either of these species in the Tonasket RD. McClelland (1977) found two black-backed and four three-toed woodpecker nests, and considered both species uncommon in areas of the northern Rockies he studied. The black-backed woodpecker nests were in a recent burn and a shelterwood cut, and those of the three-toed woodpecker were in both open and dense forest conditions. He cited evidence that both of these woodpeckers were much more common in the northern Rockies prior to 1940, when extensive fires occurred in the region, and suggested their declined abundance may be related to the lower incidence of large burns since that time. Each species appears to be attracted to areas containing high densities of dead or dying trees resulting from insect outbreaks or fire (Blackford 1955, Yeager 1955, Koplin 1969, Bock and Lynch 1970).

Bull (1980) described three-toed woodpeckers as uncommon in forests of northeastern Oregon, and found this species only in lodgepole pine stands. Black-backed woodpeckers nested primarily in open, ponderosa pine forests. In the Sierra Nevada, Raphael and White (1984) found highest proportions of black-backed woodpecker nests in burned red fir, burned red fir edge, and lodgepole pine forest types, and nest stands were characterized by low basal area and canopy cover.

Major Factors Influencing Populations of Cavity-Nesting Birds

Snag Density. Cavity-nesting bird abundance was most closely correlated with densities of snags >53 cm dbh, and mean detection rates were highest in study sites containing ≥ 3.5 snags >53 cm dbh/ha. The nonlinear relationship between detection rates and densities of snags >53 cm dbh (Fig. 6) appeared to be a function of both the abundance and tree species composition of snags in this diameter class. Detection rates did not significantly differ among study sites with from 3.5 to 13.5 large snags/ha, but the variation in snag abundance among these areas was primarily due to differences in numbers of Douglas-fir snags (Table 24). A consistent feature of snag densities in each of these sites, however, was the presence of approximately three to four ponderosa pine and/or western larch snags >53 cm dbh/ha, which were tree species preferred by excavators as nest and forage sites. These results suggest that, in the ONF, both large snag density and species composition influenced the relative abundance of cavity-nesting birds.

Many other researchers have also found positive relationships between breeding cavity-nesting bird abundance and snag densities, diameters, and/or species composition (Haapanen 1965, Balda 1975, Mannan et al. 1980, Balda et al. 1983, Brush et al. 1983, Zarnowitz and Manuwal 1985). Raphael and White (1984:50) illustrated a nonlinear relationship between bird and large snag (>38 cm dbh) densities that was very similar to the one I found in the ONF, showing that cavity-nesting bird density increased rapidly up to three snags >38 cm dbh/ha, then increased very little up to a maximum at 7.5 snags/ha.

Although studies conducted during the breeding season suggest that certain features of snag physiognomy may determine a maximum density of cavity-nesting birds, many complex factors such as food availabilty, territorial behavior, interspecific competition for nest sites, and weather may also influence the population dynamics of these species (McClelland 1977, Short 1979, Raphael and White 1984). For example, effects of severe weather on insect abundance and bird mortality, and the availability of roost holes and denser forest stands for thermal protection during this season, may be particularly limiting for resident cavity-nesting birds (Haapanen 1965, McClelland 1977, Graber and Graber 1979, Raphael and White 1984). Based on variation found in cavity-nesting bird density in relation to weather variables, and the role of winter carrying capacity in a hypothetical model, Raphael and White (1984) emphasized the importance of future research that examines winter habitat requirements. These authors (1984:60) also suggested that "the management of cavity-nesting birds should focus on winter rather than breeding habitat, at least where winters are harsh."

<u>Management Type and Snag Retention Policies</u>. Both excavators and nonexcavators were more abundant in the unmanaged type than in partial or shelterwood cut types, but detection rates in the two managed types did not differ. When sites were grouped and compared by management direction concerning snag retention, however, it was apparent that

differences in snag densities, particularly those >53 cm dbh, influenced cavity-nesting bird abundance more than managed or unmanaged status.

In managed sites where a large number of snags >53 cm dbh were retained during a first, single logging entry, bird abundance did not differ from that found in unmanaged sites. Also, both cavity-nesting bird detection rates and densities of snags >53 cm dbh in these two groups were significantly higher than in sites where snags were retained in the most recent logging entry, and sites where most snags were cut in all entries (Table 21, Table 22). Detection rates in the latter two groups presumably did not differ because of the similar, low abundance of snags >53 cm dbh in these sites resulting from routine snag-felling in successive logging entries; also, large snag recruitment through natural mortality was probably limited by the removal of large live and defective live trees during timber harvesting.

Snag retention policies concerning firewood cutting may also have influenced differences in snag densities among managed sites, but direct comparisons between sites on the east side of the Tonasket RD where snag cutting for firewood was prohibited after 1977, and west side sites where snag removal was permitted, were not possible due to differences in the timing and number of logging entries in sites on respective sides of the district.

Three of the four east side managed sites were logged for the first time after 1977, and snags were retained; opportunities for firewood cutting in these areas prior to logging were limited by road access, and snag densities were not affected by routine felling during previous logging activity. It is likely, however, that the policy prohibiting snag cutting for firewood in these sites furthered the protection of retained snags after logging occurred. In contrast, snag densities in west side sites were influenced by combined effects of logging activity and firewood cutting both before and after 1977.

Thus, in areas where timber harvesting has not previously occurred, it is possible to retain adequate large snag densities to support an abundance of cavity-nesting birds similar to that found in unmanaged areas. Also, restriction of snag cutting for firewood may play an important role in protecting retained snags. In managed sites where large snag densities have been reduced by combined effects of routine felling and removal for firewood, measures to increase numbers of large snags should be emphasized in addition to retention of existing snags.

Attempts to retain snags in areas where timber harvesting occurs represent a very positive trend in forest management. Recent studies that document a greater abundance of cavity-nesting birds in logged areas where snags were retained include those by Dickson et al. (1983), Marcot (1983), and Scott and Oldemeyer (1983).

Snag Density. Numerous authors (e.g. Bull 1978, Evans and Conner 1979, Thomas et al. 1979, Raphael and White 1984) have calculated the number (Y) of standing snags required to provide habitat for excavators using components of the formula:

$$(Y) = (A) \times (B) \times (C)$$

where (A) = the maximum excavator species density, (B) = the number of snags used annually for nesting and roosting by each pair, and (C) = a snag reserve to allow for a margin of available snags that may be unsuitable for cavity excavation. The ONF currently uses values suggested by Thomas et al. (1979) in this formula.

Thomas et al. (1979) calculated factor (A) using minimum excavator territory sizes reported in the literature. Raphael and White (1984) strongly discouraged calculation of maximum density (A) on the basis of minimum territory size, and recommended using census records published in American Birds to determine maximum densities for each excavator species. These authors pointed out the lack of data demonstrating a minimum territory size defended by any excavator, and also discussed the considerable variation in territory sizes reported for individual species. I suspect, however, that excavator density estimates based on census results may have similar inherent weaknesses as those based on minimum territory size.

Census techniques used to obtain bird density estimates, including the spot-map method (International Bird Census Committee 1970) which is used to derive densities published in American Birds, are beset by numerous problems that limit confidence in the accuracy of resulting values (well-summarized by Verner 1981 and 1984). Particular problems associated with the spot-map method as a source of reliable excavator density estimates are (1)the use of plot sizes that are small, and frequently less than 10 ha (Verner 1984), relative to the large territories and ranges of most excavator species, (2)the considerable variation and bias in density estimates introduced by the routine procedure of extrapolating densities found on small plots to a standard of 40 ha (Engstrom and James 1981, James and Wamer 1982), and (3)the difficulty in determining whether maximum densities obtained on certain plots were related to plot size, sampling intensity, habitat features, or many other factors that can influence census results (Verner 1984). Similar to estimates of minimum territory size, these problems can contribute to either a considerable over- or under-estimation of maximum population densities.

Despite the potential limitations associated with estimation of maximum excavator densities using minimum territory size or published census results, both methods represent useful attempts to form management guidelines based on the best available information. Until additional studies are designed and conducted specifically to assess questions concerning excavator territory sizes and maximum densities, or researchers and managers can mutually agree upon the relative merits of one approach over the other, either method appears to be a reasonable management alternative. Furthermore, snag densities could be provided to support a varied percentage of theoretical maximum population potential for individual species in different forest habitats (Raphael and White 1984), rather than a uniform 40%-60% for all excavators (Thomas et al. 1979).

Recommended values for (B) in the formula, the number of snags used for nesting and roosting by each pair, vary from one to four (Evans and Conner 1979, Thomas et al. 1979). Until further data are available concerning roost tree requirements for fledged young and predator avoidance, and for winter habitat needs of resident species, these values should be regarded as minimums.

To calculate the margin of available snags that may be unsuitable for cavity excavation (C) for the ONF, I used classification results from the two-group discriminant analysis comparing snags with active nests and non-nest snags (Table 9) and from an additional, identical discriminant analysis I performed comparing active nest snags and sampled snags containing nest holes (n=118). The classification results from these analyses provided separate percentages of non-nest snags and sampled snags with nest holes that were classified as nest snags, indicating they were suitable for nesting based on characteristics of variables included in the analyses. I evaluated the suitability of sampled snags with nest holes because this group may have included (1)old nest trees whose characteristics (e.g. deterioration) had changed since the time of use, or (2)snags with partially excavated, unused cavities.

Based on the results of the two discriminant classification procedures, I found that one out of every eight sampled snags (including non-nest snags and those with nest holes) was suitable for nesting. Thus, for the ONF, the value of the snag reserve (C) could be set at eight.

Snag Recruitment. Although snag retention on commercial forest lands represents an important management tool for maintaining snag habitat for cavity-nesting birds, methods for the enhancement and replacement of existing snag densities are also necessary. Sources of snag attrition that have contributed to and still create snag deficiencies in many areas include routine snag-felling, timber stand improvement and thinning practices, prescribed burning, compliance with safety standards for the protection of forest workers and visitors, and firewood cutting. Furthermore, in logged sites where snags have been retained, increased susceptibility to windthrow can cause considerable snag losses (Styskel 1983). Snags also fall naturally over time. In unmanaged stands, the number of trees dying usually exceeds the number of snags falling, and snags are continually produced; in managed stands, however, where live tree densities are substantially reduced by timber harvesting, natural tree mortality is generally too low to provide sufficient snag numbers to meet cavity-nesting bird requirements (Bull et al. 1980, Ffolliott 1983).

Management techniques for snag recruitment include (1)allocating specific numbers of live trees that will be left to die over the length of a particular planning interval or silvicultural rotation (Bull et al. 1980, Cimon 1983), (2)topping live trees with explosives (Bull et al. 1981), and (3)inoculating live trees with heartwood decaying fungi (Conner et al. 1983). The objective of the first method is to increase the number of live trees left during timber harvesting so that desired snag densities and diameters are provided through natural mortality. Techniques (2) and (3) enhance the potential nest site suitability of recruited trees while they are alive and after death, since excavator species prefer both live trees and snags with broken tops and heartwood decay. The economic implications of these techniques must also be considered, as each method entails costs that must be deducted from total timber yield revenues (Bull et al. 1980, Ffolliott 1983).

Opportunities for snag recruitment exist in either even-aged or uneven-aged silvicultural systems (Bull et al. 1980, Raphael and White 1984). Live tree allocations in both systems should be distributed and located in a manner that best satisfies cavity-nesting bird habitat requirements and also minimizes conflicts with timber management activities. Leaving trees in dispersed clumps or patches (McClelland 1977, Thomas et al. 1979, Raphael and White 1984), rather than as evenly distributed, individual trees, is one way of meeting both objectives.

Many excavator species appear to prefer nest locations within patches of snags. For example, Raphael and White (1984) found that the average number of snags >38 cm dbh surrounding excavator nests was four times higher than on random plots, and snag density variables also significantly discriminated nest site characteristics of most individual excavator species from those of random plots. Average snag densities surrounding nests of nearly all excavator species studied by Bull (1980) were also higher than in general forest conditions. In my study, the number of snags >53 cm dbh was significantly higher in excavator nest stands than in site sample plots, and snag densities in nest stands of the pileated woodpecker, Williamson's sapsucker, and red-breasted nuthatch were consistently higher than in plots representing snag densities in managed stands (Tables 13 and 14). Thus, a clumped dispersion of live trees allocated to become snags appears to be the best approach for meeting nest habitat needs of most excavator species. Clump dispersion within each planning area should be based on estimated excavator territory sizes so that the potential use of snags by individual species is not limited by territoral behavior.

From the standpoint of timber management planning, clumps of live trees for snag recruitment could be identified and recorded more effectively than scattered individual trees. Initially, optimal areas for clump location could be delineated that avoid potential log landings, existing or proposed roads, and other areas where snags would conflict with safety standards and timber harvesting activities.

During timber sale layout, patches of live trees meeting snag recruitment specifications could be recorded and mapped for future reference in subsequent silvicultural operations, such as timber stand improvement, prescribed burning, and additional logging entries. Rates of tree mortality, use of allocated trees by cavity-nesting birds, and patterns of snag fall over time, particularly relative to stand conditions, could be monitored more efficiently, which would provide valuable information concerning the success of snag recruitment guidelines. Moreover, Styskel (1983) suggested clumping as a technique for minimizing timber yield reductions associated with snag recruitment.

Tree species and diameter specifications of snag recruitment allocations should be guided primarily by excavator species nest tree preferences. In the ONF, retention of ponderosa pine and western larch (especially those with with broken or dead tops), and trees >53 cm dbh, should be emphasized. Lengthened silvicultural rotations probably will be necessary, either in patches of trees allocated for snag recruitment or entire units of managed stands, to produce snags >53 cm dbh.

Firewood Cutting. For many years, public firewood cutting was encouraged on national forest lands to reduce levels of unsalvaged dead standing and down wood, and few restrictions were imposed on its removal. During the past decade, however, the lower cost of collecting and burning wood for home heating, compared to the rising costs of fossil fuels and electricity, has contributed to a significant increase in private and commercial firewood cutting on forest lands (Raphael and White 1978, Davis 1983, Baker 1983). Expanded road systems have made more areas accessible to woodcutters, and permit systems and fees have become necessary to administer the intensified firewood demand and harvesting activity. Furthermore, the recognized conflicts between uncontrolled snag removal for firewood, and management efforts to retain and replace snag for wildlife habitat, are a source of increasing concern (Scott et al. 1980, Goodwin and Balda 1983, Styskel 1983).

In the ONF, snag deficiencies in several forest areas have been attributed to intensive firewood gathering (ONF Draft EIS 1982:59), and policies prohibiting snag cutting in these areas have represented an attempt to conserve and enhance snag abundance. At the same time, however, resource managers face considerable public pressure to maximize firewood, and especially snag, availability.

The existing firewood permit system can be used to exert greater control over snag removal in the ONF, and as a tool for furthering snag habitat management objectives. Legally enforceable permit provisions should restrict the snag diameters and species that can be cut, and specify areas where snag cutting is prohibited (such as those where snag recruitment and/or retention is critical). Active enforcement of these provisions is essential. Furthermore, cutting of downed wood should be emphasized, and materials explaining the objectives of permit provisions, as well as the importance of maintaining snags for wildlife habitat, should accompany each permit.

Monitoring programs. The National Forest Management Act (16 U.S.C. 1600) regulations for forest planning (36 CFR 219) require that each National Forest develop a program for monitoring population trends of management indicator species, and determining potential relationships between population changes and habitat effects of management activities. The monitoring process provides an essential framework for collection of long-term data needed to evaluate and revise the many guidelines, policies, and models designed to integrate wildlife habitat and timber management (Carey 1983, Marcot et al. 1983, Salwasser et al. 1983, Verner 1983).

In the ONF, excavator species have been identified as indicators for dead and defective tree habitat (ONF Final Plan, in prep.). Forest resource managers, to date, have indicated a strong commitment to improving snag management, through both adoption of specific policies and support of this study. A carefully designed monitoring program, which measures both excavator population trends and habitat availability, will be essential for interpreting the effectiveness of existing and future guidelines.

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APPENDIX I. Characteristics of excavator nest trees found in locations outside study site boundaries (off-site) in the Tonasket RD, 1983-84.

Table Ia. Mean nest tree diameter, height and nest hole height for excavator species off-site nest trees. See Table 2 for bird species codes.

	Nest tree dbh(cm)		Nest tree height(m)		Nest hole height(m)		
Bird Species	Mean	SD	Mean	SD	Mean	SD	Sample size
PIWO	86.3	30.1	27.0	3.7	11.6	3.8	4
WISA	75.6	26.9	33.1	9.2	20.8	9.2	12
NOFL	53.2	27.0	21.6	9.7	14.2	11.0	7
YBSA	34.5	5.2	27.2	3.5	11.4	6.6	4
RBNU	31.0	-	27.7	-	19.6	-	1
HAWO	30.1	1.8	23.2	3.2	9.8	5.4	4
All species	59.8	30.1	27.7	8.6	15.6	9.1	32

Table Ib. Numbers of excavator species off-site nest trees by tree species and condition.

	WISA	YBSA	HAWO	NOFL	PIWO	RBNU	All nests
Tree Species/Condition							
Western larch							
Snag	0	0	0	0	0	0	0
Defective live	7	0	0	0	0	0	7
Live	4	0	0	0	0	0	4
All conditions	11	0	0	0	0	0	11
Ponderosa pine							
Snag	0	0	0	2	3	0	5
Defective live	0	0	0	0	0	0	0
Live	0	0	0	0	0	0	0
All conditions	0	0	0	2	3	0	5
Douglas-fir							
Snag	0	0	0	1	0	0	1
Defective live	0	0	0	0	0	0	0
Live	0	0	0	0	0	0	0
All conditions	0	0	0	1	0	0	1
Aspen							
Snag	0	0	0	0	0	0	0
Defective live	1	0	0	1	0	0	2
Live	0	4	4	3	1	1	13
All conditions	1	4	4	4	1	1	15
All tree species							
Snag	0	0	0	3	3	0	6
Defective live	8	0	0	1	0	0	9
Live	4	4	4	3	1	1	17
Sample size	12	4	4	7	4	1	32

APPENDIX II. Mean nest tree diameter (dbh,cm), height (ht,m), and nest hole height (nhh,m) for 8 primary cavity-nesting bird species reported by other studies conducted in western coniferous forests of the United States, and this study. See Table 2 for bird species codes.

	McClelland (1977)			Bull (1980)			Harris (1982)			Raphael and White (1984)			This study (1985)		
Bird Species	Dbh	Ht	Nhh	Dbh	Ht	Nhh	Dbh	Ht	Nhh	Dbh	Ht	Nhh	Dbh	Ht	Nhh
PIWO	83[a]	29	17	76	28	15	67	24	18	-	-	-	84	37	16
NOFL	54	16	12	56	15	8	71	15	-	61	13	8	70	21	14
WISA	67	30	19	70	24	15	-	-	-	82	20	11	70	28	16
RBNU	53	20	16	-	-	-	40	15	-	70	15	9	64	21	13
WBNU	-	-	-	-	-	-	-	-	-	64	10	6	54	20	12
HAWO	37	22	11	42	15	8	40	6	-	44	14	5	44	17	10
TTWO	24	13	4	26	23	7	-	-	-	-	-	-	32	26	4
BBWO	25	21	2	37	19	5	-	-	-	45	17	3	29	19	1

a)All mean values rounded to the nearest cm or m.