Nesting Habitat and Abundance of Snag-Dependent Birds in the Southern Washington Cascade Range

Richard W. Lundquist and Jina M. Mariani

Authors

RICHARD W. LUNDQUIST is a wildlife biologist, Raedeke Associates, Seattle, Washington 98115. JINA M. MARIANI is a wildlife biologist, USDA Forest Service, Deer Lodge National Forest, Butte, Montana 59703.

Abstract

We examined abundance patterns and nesting-habitat use of eight cavity-nesting bird species and the brown creeper, by using point-count data collected during the breeding seasons of 1984 and 1985 and nesting data collected from 1983 to 1986 in the southern Washington Cascade Range. Naturally regenerated Douglas-fir/western hemlock forest stands were sampled, representing one of three general age-classes: young (55-80 years), mature (95-190 years), and old-growth (210-730 years). Stands within the old-growth age-class also represented a variety of moisture conditions.

Woodpeckers showed no clear and consistent abundance patterns among forest age- and moisture-classes. Vaux's swifts were consistently more abundant in old-growth stands (all moisture-classes) in both 1984 and 1985. During both 1984 and 1985, chestnut-backed chickadees were most abundant in wet old-growth stands, red-breasted nuthatches were most abundant in dry old-growth stands, and brown creepers were most abundant in mesic old-growth stands. In general, counts of most of the bird species we studied were lowest and most variable in young and mature stands.

We found few consistent bird-habitat correlations, Numbers of both chestnut-backed chickadees and Vaux's swifts correlated most strongly with density of live trees >lOO cm in diameter at breast height (d.b.h.), and swift counts correlated with density of snags >50 cm d.b.h. Except for swifts, relative abundances of snag-dependent bird species were not well-predicted by densities of snags, perhaps because all forest stands sampled were naturally regenerated and contained numerous snags.

Except for chestnut-backed chickadees, few nests of any cavity-nesting species were found in young stands. Most of the chickadee nests found in young stands, however, were in old remnant snags, not in trees produced in the current stands. Cavity nesters disproportionally selected large, hard snags for nesting. In particular, selection of hard snags by hairy woodpeckers in this study area contrasted with findings of other studies in the Pacific Northwest, on which current management guidelines have been based. Woodpeckers and creepers used western white pine snags disproportionately, but chickadees and nuthatches nested primarily in Douglas-fir and western hemlock. Disproportionate use of certain tree species for nesting was probably closely related to their decay characteristics. Sample plots centered on nest trees of all species contained higher densities of large, hard snags than randomly sampled vegetation plots. Management recommendations for Douglas-fir forests of the Washington Cascades include retention of tall, hard snags ≥ 76 cm d.b.h. for all species. White pine snags are particularly important for woodpeckers and creepers, and Douglas-fir and western hemlook snags should be retained for chickadees and nuthatches. In designing snag-retention areas, managers should provide adequate snag distribution over large areas, live-tree replacement, and patches of older stands.

Introduction

Two of the goals of the Old-Growth Forest Wildlife Habitat Program were to identify species that may depend on or find optimum habitat in old-growth forests and to determine features of these stands that distinguish them as better habitat-particularly species that depend on elements lacking in managed forests. Snags are often removed, either because of safety or fire hazard, or because they are commercially useful (Lowery and others 1977, Snellgrove 1977, Snellgrove and Fahey 1977, USDA Forest Service 1976).

Several studies have shown the importance of snags to many wildlife species, especially birds, for nesting, feeding, shelter, communication, and resting (Balda 1975, Conner and others 1975, Haapanen 1965, Marcot 1983, McClelland 1977, Raphael and White 1984). Although cavity-nesting birds and snags have been studied in various locations in the Pacific Northwest (Bull 1980, Cline and others 1980, Madsen 1985, Mannan and others 1980, Zamowitz and Manuwal 1985), to date no study has examined habitat preferences in the productive Douglas-fir/western hemlock forests of the Washington Cascade Range. Because use of nesting and foraging habitat by cavity-nesting birds in these forests may differ from that in other regions of North America or other forest types in the Pacific Northwest, forest managers need specific local information to provide adequate habitat for these species in light of conflicting values placed on snags. In response to this need, we began our study in 1983. Our objectives were to compare relative abundance estimates of snag-dependent bird species across an array of Douglas-fir forest stands of different age- and moisture-classes; to examine the relation between bird abundance estimates and densities of live trees and snags in these stands; to characterize nesting sites of bird species in various stand age-classes and to evaluate use of forest habitat elements for nesting in relation to their availability; and to discuss management considerations for cavity- and bark-nesting birds in the Southern Washington Cascades Province.

Methods

Study Area

This study was done in the Southern Washington Cascades Province (Franklin and Dyrness 1973) west of the Cascade Crest in the Gifford Pinchot National Forest and in Mount Rainier National Park. Forty-eight forest stands represented young (55-80 years old, n = l0), mature (95-190 years old, n = l0), and old-growth (210-730 years old, n = 28) age-classes (see frontispiece). All stands originated from natural disturbance; that is, they have undergone no silvicultural manipulation. All stands were in the Western Hemlock Zone (Franklin and Dyrness 1973); because of limited availability of sufficiently large stands, particularly low-elevation old growth, eight stands (six old-growth, one mature, one young) were above 1000-m elevation at the upper end of the Western Hemlock Zone, where the transition to the Pacific Silver Fir Zone begins. Stands ranged from 404- to 1218-m elevation.

During spring and summer of 1986, cavity-nesting birds were studied on a subset of 17 stands in the Packwood and Randle Ranger Districts of the Gifford Pinchot National Forest and in the southern part of Mount Rainier National Park. Six stands were young, five were mature, and seven were old-growth.

The general study area is dominated by a maritime climate (Brubaker, this volume) characterized by cool, wet winters and warm, dry summers. Most precipitation occurs between October and April, but annual and monthly precipitation can vary greatly among years.

Vegetation Sampling

Vegetation and habitat characteristics were measured in nested circular plots (0.05 and 0.2 ha) centered on each of 12 bird count stations systematically located in each stand. We tallied live trees by species and diameter at breast height (d.b.h.) (l- to 10-, 11- to 50-, and >50-cm classes in the 0.05-ha plot plus a >lOO-cm class in the 0.2-ha plot). We counted snags by species, diameter-class (l0-19 cm in the small plot and 20-49 and 250 cm in the large plot), and decay-classes (1 to 4, from hardest to most decayed, modified from Cline and others 1980). Sampling criteria conformed with standard protocols established for other studies.

To obtain more detailed information on snag attributes and densities, snags (standing dead trees 210 cm in d.b.h. and 22 m tall) were also characterized, measured, and tallied in a 30-m-wide belt transect consisting of 11 l00-m-long segments along lines between bird counting stations in each stand. All snags 250 cm in d.b.h. and the first five snags in each of two smaller d.b.h.-classes (l0-19 cm and 20-49 cm) counted within each segment were characterized by species, diameter (cm), height (m), decay-class, number of limbs, bark remaining (percent), top condition (intact or broken), needle presence, presence and number of excavated cavities, and presence of woodpecker feeding sign. All subsequent snags in the two smaller diameter-classes in each segment were then tallied by decay- and height-class (2-5 m, >5 m).

Bird Abundance Counts

Bird populations were sampled on all stands during the spring breeding seasons of 1984 and 1985 by the point-count method. Verner (1985) and selected references in Ralph and Scott (1981) describe the technique in more detail. For a more detailed description of the sampling design and constraints, see Carey and Spies (this volume). In the southern Washington Cascades, each stand contained 12 count points systematically located 150 m apart and at least 75 m from roads or edges of adjacent habitat.

Each stand was visited six times between 25 April and 12 July 1984, and between 30 April and 28 June 1985. During each visit, detections of all bird species were recorded during 8-minute periods at each counting station after a l-minute pause on arrival at the station. To the extent possible, observers avoided double-counting of individual birds from multiple stations during each visit to a stand, particularly with wide-ranging species such as woodpeckers.

Observers were trained and tested in bird identification (both aural and visual cues) and distance estimation for 1 week beginning each sampling season to improve consistency among observers (Kepler and Scott 1981). Stands were assigned so that at least two observers visited each stand alternately during a given season (and across seasons) where possible. Limited time and resources and long distances between groups of stands prevented us from attaining a more optimal stand assignment as a way of limiting observer bias and variability. Fifteen observers assisted in the bird counts, of which three participated both years.

Nest- and Cavity-Tree Searches

In 1983-85, nests were most often discovered during routine bird counts. Stands were also searched after morning counts or on days when weather prohibited counting. In 1985, we devoted additional days exclusively to nest searches on a subset of stands.

In 1986, one observer systematically searched a subset of stands for nests between 22 May and 3 July. Each stand was visited twice: searches began in the early morning and continued until the entire stand was covered, usually by mid-afternoon. Only one stand was visited per day. Two field assistants briefly helped search two stands in each forest age-class. Search time was standardized as much as possible on all sites during all years. Because some areas were sampled more years than others (for example, Wind River pilot studies), however, total search time differed among stands that were not included in the 1985 and 1986 searches.

We confirmed activity at potential nest or roost trees following the criteria of McClelland (1977) except that for purposes of analysis, we treated active roost and active nest sites together as active trees. Where no adult was observed entering a cavity, the tree was termed simply a “cavity tree.” We classified inactive cavities into the following categories based on general cavity size and shape (dimensions compiled from Bent 1964): pileated woodpecker (7.6-11 cm, oval); northern flicker (6.9-7.5 cm, round); unidentified small woodpecker, representing both hairy woodpeckers and red-breasted sapsuckers (3.8-5.1 cm, round); and unidentified nonwoodpeckers, representing chestnut-backed chickadees and red-breasted nuthatches (12.5 cm, irregularly shaped).

Characteristics recorded for each nest and cavity tree included the following: tree species, status (live or dead and top condition, after McClelland 1977), decay-class (after Cline and others 1980), diameter-class, and height (m); percentage of bark remaining; number of limbs >l m long remaining; origin of tree (current or previous forest stand) and presence of fire scar; and surface evidence of heartwood decay. Decay evidence was classified as in McClelland (1977). Additional nest characteristics included height of active nest above ground (m) and evidence of use by birds (either direct or indirect).

We sampled vegetation characteristics surrounding each nest and cavity tree in concentric 0.05-ha and 0.2-ha circular plots, centered on the nest tree, in a manner identical to that used for vegetation plots surrounding the bird-count stations.

Data Analysis

We used simple counts to analyze point-count bird abundance data. Raphael (1987a) showed that simple counts can provide as good an estimate of relative abundance as more complex techniques (Burnham and others 1980, 1981; Emlen 1971,1984; Reynolds and others 1980), when analyses are limited to within-species trends across similar (forested) habitats. Thus, for our analyses, we assumed equal detectability of each bird species among forest age- and moisture-classes.

Because all stands received equal sampling effort in both years, we report number of detections recorded during count periods per visit (total count at each stand divided by six visits) for each species and year. For wide-ranging and less frequently encountered species such as woodpeckers, we departed from the standard protocol by including detections beyond the 75-m limit. For the smaller woodpeckers, detection distances did not exceed 150 m, and for the larger species, none exceeded 250 m. In addition, Vaux’s swifts were typically detected while foraging on the wing in or near the forest canopy. As a result, we included all detections of swifts that were apparently using the stand, even though no distance estimate could be made because of their movements.

Differences in bird species' abundances among forest age- and moisture-classes were tested by a series of one-way analyses of variance (ANOVA) and multiple range tests (Zar 1984). ANOVA is generally robust to small departures from normality and to moderate heterogeneity of variances when sample sizes are nearly equal (Sokal and Rohlf 1981). We log-transformed bird counts [$\log_{10}(x+1)$] before analysis to meet the underlying assumptions of normality and equality of variances more closely. The log transformation, as opposed to others, best approximated normality and made the means independent of variances. Based on Bartlett's test (Sokal and Rohlf 1981) on the log-transformed data, sample variances were sufficiently homogeneous ($P > 0.05$).

We should caution, however, that the inferential statistical procedures performed on our data should be viewed as exploratory, rather than as conclusive demonstrations of statistical significance. Although the study stands represent a wide range of geographic and environmental conditions in the region, they do not represent a random sample. Moreover, bird count stations were not sampled randomly. Therefore, conclusions on abundance patterns or relation to habitat should be viewed with caution.

We examined associations between counts of each bird species and habitat variables in two different but related ways. First, we computed Spearman rank correlation coefficients (SPSS, Inc. 1986) to look for significant correlations between tree and snag densities and counts of each bird species. For this analysis, we first summarized vegetation data into the seven most commonly occurring tree species (or groupings), with the four d.b.h. classes of live trees and two decay-classes (hard = classes 1 and 2, and soft = classes 3 and 4) of snags.

This large set of variables was reduced to 22 (appendix table 7) by examining highly significant correlations among vegetation variables. Any pairs of variables with correlations >0.50 (explaining >25 percent of each other's variances) were either combined into one, or the more ecologically interpretable variable was retained, whichever was appropriate. Thus, variables such as all live trees >100 cm d.b.h. or live western hemlock ≤ 50 cm d.b.h. were created.

In computing a large number of correlations, some may appear statistically significant (that is, $P < 0.05$) because of random sampling error. We therefore focused on correlations with the same sign (positive or negative) in both years, and emphasized those that were significant at $P < 0.01$. We considered conflicting results, such as correlations that were positive one year and negative the next, as possible evidence of Type I error (Marcot 1984, Meslow and Keith 1971). Even correlations that are consistently significant demonstrate numerical association only, not necessarily some biologically meaningful cause.

Second, we further investigated associations between bird-abundance counts and tree and snag densities by means of stepwise multiple linear regression (Kleinbaum and Kupper 1978, using SPSS, Inc. 1986). This approach generated equations explaining each bird species' abundance from vegetation variables and was used for descriptive, rather than predictive, purposes. The stepwise procedure evaluates each variable to be entered while controlling for variables already in the equation. Because of low sample size ($n = 48$ stands) and some remaining intercorrelations, we generated a new, smaller set of uncorrelated vegetation variables using factor analysis (Afifi and Clark 1984). The initial factors, each of which is a linear combination of all (22) original variables and explains a known amount of the total variance in vegetation data, were extracted by principal components analysis with the Varimax rotation to ease interpretation. We interpreted the factors with a minimum eigenvalue of 1.0 (Battacharyya 1981) by examining the relative sizes of correlations ("loadings") between the factors and original variables.

Bird counts and vegetation variables were first log-transformed for regression analyses to meet underlying distributional assumptions more closely. We regressed transformed counts of each bird species on vegetation factor scores separately for 1984 and 1985 data. Because of the number of equations generated and time limitations, we were unable to search for better fits with polynomial and interaction terms, which may explain some species distributions more fully (Meents and others 1983). We evaluated the accuracy of each regression equation by the adjusted coefficient of determination (adjusted R^2), an unbiased measure of the percentage of total variation in bird abundance explained by the equation (Sokal and Rolff 1981: 661; Zar 1984: 336) and by the standard error of estimate for the equation [(MSE), Kim and Kohout 1975: 331; Draper and Smith 1981: 20,34].

We also explored among-species variation in nest-tree characteristics by means of principal components analysis without rotation. Seven of the 11 nest-tree variables used in the analysis were entered as dichotomous variables, coded as 0 if the attribute was absent and 1 if it was present. These included top condition (broken, intact), tree condition (alive, dead), fire evidence (absent, present), and four tree species variables: Douglas-fir, western hemlock, western white pine, and other. A variable describing number of limbs (>1 m long) present was coded into intervals of 10 branches: 1 to 10 (coded 1), 11 to 20 (coded 2), and so on, or 0 if absent. We entered the other variables-tree diameter, tree height, and percentage of bark remaining (arcsine-transformed)-as continuous variables.

As with the regression analyses above and in other studies (Conner and Adkisson 1977, James 1971, Rotenberry and Wiens 1981, Whitmore 1977), principal components analysis is often used as a data reduction and ordination technique to describe habitat relationships among breeding bird species. For this analysis, however, it was used only as a first-order exploratory tool to identify attributes that accounted for much of the variation in nest trees.

For all nests except those of brown creepers, we used two-group linear discriminant function analysis (Lachenbruch 1975), using SPSSX (SPSS, Inc. 1986) to compare nest-site vegetation structure with samples representing general stand vegetation structure. We selected stand vegetation plots (those centered at bird-counting stations not containing nest trees) randomly from those stands where nests were found in two ways, and a separate analysis was done for each of them. The first sample was stratified so that the number of "random" plots equaled the number of nest-site vegetation plots in each forest age-class. This gave each age-class the same weight in both groups (nest site and random) and equalized the sample size of each group in the data set. The second sample was stratified to equalize the groups by stand to correct for disproportionately large numbers of nest plots on any given stand.

We included 15 variables in the analysis: percentage cover by logs (decay-class 1); percentage cover by deciduous shrubs or trees 0-2 m and 2-15 m tall; total canopy cover (>15 m tall) (all percentage-cover variables recorded on an octal scale); average height of dominant canopy trees (in 8-m intervals); total density of live trees 1 to 10 cm, 11 to 50 cm, 51 to 100 cm, and >100 cm in d.b.h.; total density of hard snags 10 to 19 cm, 20 to 49 cm, and ≥ 50 cm in d.b.h.; total density of soft snags 20 to 49 cm and ≥ 50 cm in d.b.h.; and density of stumps and stubs (snags <5 m tall and 210 cm in d.b.h.). All variables for the analysis were log-transformed. We recorded nest-site vegetation data for 58 of the active nests and for 23 of the trees with inactive cavities ("random" search data) for a total sample size of 81.

We performed the stepwise discriminant analyses using Wilks' method, and the single function derived was evaluated by the significance of the chi-square statistic based on Wilks' lambda (SPSS, Inc. 1986). We interpreted the discriminant function by examining the magnitude of the pooled within-group correlations between the discriminant score and the original variables (structure matrix) (Hull and Nie 1981, Raphael and White 1984, Williams 1981). We used classification techniques (SPSS, Inc. 1986) based on the same data set used to derive the discriminant function to assess the ability of the function to separate the groups effectively. The proportion of cases correctly classified according to actual group membership indicated the success of the between-groups separation. Further discussions of the theory and application of discriminant analysis can be found in Williams (1981, 1983) and Afifi and Clark (1984).

Where sample sizes permitted, we compared use of snag diameter-class, species, and condition for nesting with availability in the forest by means of log-likelihood G-tests, which are analogous to, and often preferred over, chi-square analysis (Sokal and Rohlf 1981: 704; Zar 1984: 52-53). We used Williams' (1976) correction to the G-statistic to obtain a better approximation to the chi-square distribution, even with only one degree of freedom. This correction appears to be superior to the Yates correction for continuity in such cases (Sokal and Rohlf 1981).

Because of small sample sizes for any one bird species, some pooling was necessary. Also, our samples were not large enough to analyze data comprehensively in multiway contingency tables and to search for interaction among the dimensions. Thus, we analyzed each tree attribute (diameter, species, decay-class) separately. Expected frequencies were calculated from the appropriate snag-density distributions on the stands from which the data came. Because the distribution of snags differed between forest age-classes, we evaluated the use of trees by nesting birds separately in each forest age-class, where possible. For most of the tests, however, small samples forced us to pool young with mature stands (hereafter termed "second growth"). Because live trees with nests or cavities constituted only a small fraction of the total, they were excluded from the tests.

Results

Bird Abundance Among Stand Types

Total counts of the four woodpecker species were generally too low and variable to detect significant differences among the five stand types in either 1984 or 1985 (table 1). All four were detected in all age- and moisture-classes, but not in all stands. Hairy woodpeckers were the most frequently detected, and red-breasted sapsuckers were relatively rare. Except for sapsuckers, total counts of woodpeckers were lowest in mature stands. Counts in old-growth stands varied substantially with moisture-class. Hairy woodpeckers were slightly more common in wet old-growth stands in both years; no consistent pattern was found among old-growth moisture classes between years for northern flickers or pileated woodpeckers.

The four nonwoodpecker species treated here were encountered more frequently than woodpeckers. Mean counts of these species were slightly lower in 1984, but the general

Table 1—Mean number[a] of snag-dependent bird species detected per census, based on point counts in the southern Washington Cascades, spring 1984 and 1985

		Forest type					
Species	Year	Young	Mature	Wet old-growth	Mesic old-growth	Dry old-growth	F[b]
Pileated woodpecker	1984	0.35	0.12	0.42	0.28	0.12	0.17
	1985	.30	.18	.15	.30	.20	.69
Northern flicker	1984	.22	.15	.13	.20	.52	1.43
	1985	.32	.08	.55	.42	.37	2.20
Hairy woodpecker	1984	.60	.37	1.07	.55	.57	2.01
	1985	.52	.65	1.32	.92	.65	1.78
Red-breasted sapsucker	1984	.08	.18	.07	.07	.07	.43
	1985	.05	.22	.17	.28	.07	.58
Chestnut-backed chickadee	1984	3.85	3.33	5.60	4.77	3.97	1.54
	1985	3.57 A[c]	3.85 A	9.77 B	5.58 A	4.15 A	6.35***
Red-breasted nuthatch	1984	3.62 AB	2.15 A	2.10 A	4.18 AB	5.03 B	2.72*
	1985	4.38	4.00	4.07	5.10	6.55	1.10
Brown creeper	1984	1.00 A	2.50 B	2.00 B	2.90 B	2.10 B	3.26*
	1985	2.40 AB	3.40 BC	1.80 A	4.70 C	2.30 AB	4.78*
Vaux's swift	1984	.17 A	.13 A	2.60 B	1.15 B	1.17 B	6.41***
	1985	.28 A	.58 A	2.65 B	2.42 B	2.70 B	11.68***

[a] Calculated as the mean number of birds detected per visit; all stands were visited 6 times each year, and each visit included 12 count periods (8-minute per count period).

[b] Based on 1-way analysis of variance among 5 groups. The significance of the test is indicated by the number of asterisks: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Counts were log-transformed for all analyses, but actual numbers are presented here for clarity.

[c] Within each row where the ANOVA was significant (indicated by asterisks), multiple range tests failed to find significant differences ($P < 0.05$) between groups of mean counts sharing the same letter (for example, "A" or "B").

patterns were similar in both years. Vaux's swift was the only cavity-nesting species with counts significantly higher in old growth (all moisture-classes) than in the other forest age-classes ($P < 0.001$) (table 1). Chestnut-backed chickadees were more common in wet old-growth stands, significantly so in 1985 ($P < 0.001$). Red-breasted nuthatches were generally more abundant in dry old-growth stands, significantly so in 1984 ($P < 0.05$). For nuthatches, however, multiple range tests failed to separate mean counts in dry old-growth stands from the other stand types, which may indicate that at least one "Type II" error was committed in the analysis; it can result from small sample sizes (causing a lack of statistical power) or highly variable counts within a given stand type (Zar 1984). On the other hand, the overall ANOVA result could have been a Type I error, but at least the trends were consistent between years.

Brown creeper counts differed significantly among the stand types in both years ($P < 0.05$). In 1984, creepers were significantly less abundant in young stands than all the other stand types. In 1985, multiple range tests failed to detect any significant differences among stand types. Although abundance patterns differed between 1984 and 1985, creeper counts were highest in mesic old-growth stands both years.

Bird Abundance in Relation to Tree and Snag Densities

Correlation analysis—Few bird-habitat correlations were consistently significant in both years. Chestnut-backed chickadee and Vaux's swift counts were most strongly (positively) correlated with density of total live trees >100 cm d.b.h. in both years (table 2). Chickadee numbers also correlated positively with live redcedars 51 to 100 cm in d.b.h. and redcedar snags >50 cm in d.b.h. Swift counts correlated positively with several other kinds of trees and snags that reached maximum densities in old-growth stands (all live *Abies* and other conifers up to 100 cm in d.b.h., live western hemlock 51 to 100 cm in d.b.h., and snags ≥50 cm in d.b.h.). Brown creeper counts correlated positively with densities of hard Douglas-fir snags >50 cm in d.b.h.

Red-breasted nuthatches correlated positively with densities of live vine maple and negatively with redcedar snags 20 to 49 and >50 cm in d.b.h. Hairy woodpecker counts correlated positively only with the density of live hemlocks 51 to 100 cm in d.b.h.; pileated woodpecker, northern flicker, and sapsucker counts did not correlate consistently with any of the vegetation variables tested.

Factor analysis of vegetation variables—Six factors were derived that had eigenvalues greater than 1.0, three of which explained at least 10 percent of the total variance (table 3).

Table 2--Spearman rank correlation coefficients between mean counts of snag-dependent birds and densities of live trees and snags

Bird species	Variable” (tree sizes in cm d.b.h.)	*Year*[a] 1984 (n = 47)	1985 (n = 46)
Pileated woodpecker	(none)		
Northern flicker	(none)		
Hairy woodpecker	Live TSHE[b]51-100	0.32*	0.34”
Red-breasted sapsucker	(none)		
Chestnut-backed chickadee	All live trees > 100	.30*	.40**
	Live THPL51-100	.30*	.40**
	Stumps and stubs	–.33*	–.35*
	THPL snags ≥50	.32*	.37*
Red-breasted nuthatch	Live ACCI 1-50	.43**	.46**
	THPL snags 20-49	–.41**	–.45**
	THPL snags ≥50	–.32*	–.40**
Vaux’s swift	AU live trees l-100	.64***	.68***
	Live PSME 1-100	–.55***	–.56***
	Live ***Abies I-100***	.39**	.41**
	Live “conifers” l-l 00	.53***	.46**
	Live TSHE 51-100	.43**	.63***
	Live THPL 51-100	.43**	.47**
	All snags IO-19	–.31*	–.37*
	Hard PSME snags ≥50	.30*	.38**
	All TSHE snags ≥50	.46**	.44**
Brown creeper	Hard PSME snags ≥50	.39**	.32*

[a] Only coefficients significant for both seasons and those significant at $P < 0.05$ are shown.

[b] Tree species codes are as follows: ACCI, vine maple; PSME, Douglas-fin TSHE, western hemlock, THPL, western redcedar; *Abies.* Pacific silver fir, grand fir. and noble fir; “conifers,” all other conifers except those above.

Table 3-Factors derived by factor analysis on 22 vegetation variables, including percentage of total variation explained, highly associated variables, and factor loadings

Factor[a]	Percentage of total variation	Cumulative percentage variation	Highly associated variables[b] (tree sizes in cm d.b.h.)	Factor loadings
1	31.7	31.7	Live PSME[c] l-100	-0.87
			All PSME snags 20-49	-.82
			All live trees >lOO	.70
			Live ***Abies* 1-100**	.64
			All snags l0-19	-.57
2	14.6	46.3	Live hardwoods 1-100	-.77
			All TSHE snags 20-49	.74
			Live TSHE 51-100	.69
			AlI Abies snags 20-49	.66
			All TSHE snags 550	.60
3	12.8	59.0	All THP20-49	.82
			Live THPL 1-50	.80
			All THPL snags ≥50	.67
			Live THPL 51-100	.64
4	7.4	66.5	All PIMO snags ≥50	.87
			All PIMO snags 20-49	.71
			Live otherconif. 1-100	.66
			Hard PSME snags ≥50	.64
5	6.2	72.7	Soft PSME snags ≥50	.87
6	5.5	78.2	Stumps and stubs	.80
			Live TSHE l-50	.67

[a] Factors listed are those extracted by principal components analysis that had eigenvalues greater than 1.0.

[b] Variables listed for each factor are those most highly associated with it (that is, with high factor loadings), as determined by the varimax rotation.

[c] Tree species codes are as follows: PIMO, western white pine; PSME. Douglas-fir, TSHE, western hemlock, THPL, western redcedar; *Abies,* Pacific silver fir, grand fir, and noble *fir;* “conifers,” all other conifers except those above.

Together they accounted for 78 percent of the total variance. Variables with high positive loadings on the first factor included densities of live trees > 100 cm in d.b.h. and live *Abies* ≤100 cm in d.b.h., both of which tend to be higher in cooler, moister old-growth stands. Variables with high negative loadings on factor 1 were those typically more abundant in younger stands: densities of live Douglas-fir ≤100 cm in d.b.h., Douglas-fir 20 to 49 cm in d.b.h., and all snags 10 to 19 cm in d.b.h. Thus, stands with high scores on the first factor tended to be older, wetter stands, and those with low scores tended to be younger stands.

The second factor (14.6 percent of the total variance) was highly positively associated with trees and snags that were most abundant in mesic old-growth conditions: densities of western hemlock snags, both 20 to 49 cm and ≥50 cm in d.b.h., live western hemlock 51 to 100 cm in d.b.h., and *Abies* snags 20 to 49 cm in d.b.h. The factor was also highly negatively associated with densities of live hardwoods 1100 cm in d.b.h. The third factor (12.8 percent of the variance) was highly positively associated with western redcedar: snags 20 to 49 cm and ≥50 cm in d.b.h. and live trees ≤50 cm and 51 to 100 cm in d.b.h.

Factors 4 (7.4 percent), 5 (6.2 percent), and 6 (5.5 percent) each accounted for much less of the total variance. Variables with high (positive) loadings on factor 4 were generally those most abundant in drier old-growth sites: western white pine snags 20 to 49 cm and ≥50 cm in d.b.h., live other conifers, including pines, ≤100 cm in d.b.h., and hard Douglas-fir snags >50 cm in d.b.h. Factor 5 was most strongly associated (positively) with soft Douglas-fir snags >50 cm in d.b.h., and factor 6 was most strongly associated with forest elements more abundant in younger stands: total stumps (natural) and stubs, as well as live western hemlock trees ≤50 cm in d.b.h.

Multiple regressions-The multiple regression equations of all bird species accounted for less than half of the observed variation in total counts (table 4). Except for Vaux’s swifts and red-breasted nuthatches, the factors entering regression equations for all bird species were not consistent between years. Two factors (1 and 5) entered the equations for swifts

Table 4—Results of stepwise multiple linear regression of mean total counts[a] of snag-dependent bird species with vegetation factors derived from factor analysis of 22 live tree and snag variables (see table 3 for lists of variables highly associated with each factor)

Year, bird species	Step	Variable	Multiple R	Adjusted R^2	SEE[b]	P
Spring 1984:						
Pileated woodpecker	1	Factor 1				
		Constant	0.29	0.06	0.28	0.048
Northern flicker	1	(Factor 6)				
	2	(Factor 1)				
		constant	.45	.17	.26	.007
Hairy woodpecker		(none entered)				
Red-breasted sapsucker	1	(Factor 3)				
		constant	.32	.08	.21	.031
Chestnut-backed chickadee	1	Factor 5				
	2	(Factor 2)				
		constant	.51	.23	.21	.001
Red-breasted nuthatch	1	(Factor 3)				
		Constant	.36	.11	.34	.012
Vaux's swift	1	Factor 1				
	2	Factor 5				
		constant	.64	.38	.39	.000
Brown creeper		(none entered)				
Spring 1985:						
Pileated woodpecker		(none entered)				
Northern flicker		(none entered)				
Hairy woodpecker	1	Factor 5				
		constant	.38	.12	.29	.010
Red-breasted sapsucker		(none entered)				
Chestnut-backed chickadee	1	Factor 1				
		constant	.54	.27	.21	.000
Red-breasted nuthatch	1	(Factor 3)				
		Constant	.41	.15	.32	.004
Vaux's swift	1	Factor 1				
	2	Factor 2				
	3	Factor 5				
	4	Factor 4				
		constant	.67	.39	.43	.000
Brown creeper		(none entered)				

[a] Bird counts and stem densities were log-transformed for the analysis. See the methods section for a description of adjusted R^2.

[b] Values given are standard error of predicted (estimated) bird counts, based on the transformed counts. SEE values were computed as: SEE = $\sqrt{[SSres/(N-k-1)]}$, where SSres = the sums of squares of residuals, N is the number of stands for a given year, and k is the number of independent variables in the equation (Kim and Kohout 1975: 331; see also Draper and Smith 1981: 20 and 34, and Marcot 1984: table 12). Small prediction errors mean the abundance of a given bird species was tightly associated with the given habitat variables, but large prediction errors suggested a loose association.

each year, with factors 2 and 4 also entering the 1985 equation. Thus, high swift counts were associated with high densities of trees and snags abundant in old-growth stands, particularly live trees >100 cm in d.b.h., soft Douglas-fir snags, and, in 1985, also with western hemlock and white pine snags and live trees. Both equations for nuthatches included only factor 3, with a negative coefficient, so nuthatch counts were typically higher in stands with a smaller component of redcedar. This analysis therefore echoed the correlation analysis for both species.

Different factors entered each equation for chestnut-backed chickadees. Factor 5, reflecting a positive association with hard Douglas-fir snags, and factor 2 (with a negative coefficient) entered the 1984 equation, but only factor 1, reflecting

Table S-Active nests and roosts of 9 snag-dependent bird species 1983-86, by forest age-class

Bird species	Forest age-class Young (n = 10)	 Mature (n= 10)	 Old-growth (n = 28)	Total
Pileated woodpecker	0		2	2
Northern flicker	1	0	2	3
Hairy woodpecker	3	1	14	18
Red-breasted sapsucker	0	2	2	4
Yellow-bellied sapsucker’	0	0	1	1
Chestnut-backed chickadee	12	3	6	21
Red-breasted nuthatch	1	3	15	19
Brown creeper	6	7	15	28
Vaux’s swift	0	0	1	1
Total	23	16	58	97

[a] This nest was pooled with those. of the red-breasted sapsucker for statistical analyses.

an association with wet old-growth conditions (particularly live trees >100 cm in d.b.h.), entered the 1985 equation. For hairy woodpeckers, northern flickers, pileated woodpeckers, and red-breasted sapsuckers, the factors entered equations for only one of the years. No factors entered creeper equations either year, although in preliminary regression runs using individual variables rather than factors, density of hard Douglas-fir snags ≥50 cm in d.b.h. (with a positive coefficient) was the only variable that entered both years’ equations (Mariani 1987).

Nest-Tree Characteristics

We found 109 active nests and roosts of 10 snag-dependent bird species in the southern Washington Cascades from 1983 to 1986. Most of these (*n* = 98) were on the study stands; the rest were in similar habitat types outside the study stand boundaries. The analyses presented here focus on 96 nests and roosts of the following eight species found on the study stands: pileated and hairy woodpeckers, northern flicker, red-breasted and yellow-bellied sapsuckers, chestnut-backed chickadee, red-breasted nuthatch, and brown creeper (table 5); the single Vaux’s swift nest was excluded from the analyses. Restricting analysis to nests found on the study stands allowed for direct comparison between nest site and study site habitat characteristics.

Most (62 percent) of the active nests and roosts of woodpeckers, nuthatches, and creepers were found in old-growth stands (table 5). In contrast, most chestnut-backed chickadee nests were found in young stands. Of the additional 127 trees with cavities of uncertain use found in 1985 and 1986, 55 percent were also in old-growth stands but because 58 percent of our study stands were old-growth, average numbers of nests found per stand were similar for all forest age-classes.

Condition-Few active or inactive nests found on the study sites were in live trees. Although we did not specifically test for use of dead versus live trees for nests or roosts, these data suggest a disproportionate selection of dead trees. Most trees (85-87 percent) on our study sites were alive, but the vast majority of nest and cavity trees were dead. Furthermore, all live trees harboring nests had dead or broken tops.

Size-The mean diameter of all active nest trees found on the study sites was 76 cm, and the mean tree height was 25 m (table 6). Nest trees ranged from 18 to 167 cm in d.b.h. and from 3 to 60 m in height. Mean nest-tree diameters for all bird species were greater than 50 cm; trees with nests of northern flickers had the largest mean nest-tree diameter, and those of brown creepers had the smallest. Flicker nest trees averaged the tallest, and chickadee nest trees the shortest. Nuthatches tended to excavate cavities closest to the top of the nest tree (averaging less than 2 m from the top), and pileated woodpeckers nested farthest from the top (averaging 21 m).

Mean diameter for trees with inactive cavities closely paralleled those of the active nest trees for the respective species (or groupings), even though sample sizes were sometimes small (pileated woodpeckers and northern flickers). In particular, the mean diameter of cavity trees used by small woodpeckers was nearly identical to that of active hairy woodpecker and red-breasted sapsucker nests. The mean diameter of nonwoodpecker cavity trees was between those of active chickadee and nuthatch nests.

On average, trees with inactive cavities were generally shorter, and except for pileated woodpeckers, inactive cavities were also located closer to the ground than active nests (that is, nest-hole height was lower), but this difference may reflect observability bias because active nests higher in trees are easier to spot than inactive ones. Trees with inactive cavities of nonwoodpeckers resembled nest trees of chickadees more closely than those of nuthatches in terms of tree height and height of the cavity above ground. Thus most inactive nonwoodpecker cavities may have been inactive chickadee nests.

The majority of nest trees of both woodpeckers and nonwoodpeckers were >50 cm in d.b.h. (fig. 1). Only two nests (brown creepers) were found in trees <20 cm in d.b.h. Log-likelihood G-tests showed that all cavity-nesting species (grouped as woodpeckers and nonwoodpeckers) used large (>50 cm in d.b.h.) snags disproportionately in all forest age-classes, no matter whether tests included all nest and cavity

Table 6—Mean and standard deviation of diameter at breast height (d.b.h.), height, nest-hole height, and diameter at the nest of all active nest trees of snag-dependent birds on study sites

		Tree d.b.h. (cm)		Tree height (m)		Nest height (m)		Diameter at nest (cm)	
Bird species	*n*	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Pileated woodpecker	2	88.0	19.8	40.0	4.2	19.0	4.2	57.5	24.7
Northern flicker	3	127.7	38.5	46.3	15.0	38.7	20.6	51.0[a]	4.2
Hairy woodpecker	18	73.9	33.4	28.6	14.4	17.7	10.4	39.6	15.0
Red-breasted sapsucker	4	76.3	4.8	22.0[a]	1.4	15.5	1.7	42.5[a]	3.5
Yellow-bellied sapsucker	1	111.0	—	38.0	—	21.0	—	65.0	—
Chestnut-backed chickadee	21	94.0	35.7	17.7	8.6	13.3	8.3	54.5	21.4
Red-breasted nuthatch	19	71.1	31.5	25.3	9.5	23.0	9.9	32.3	15.2
Brown creeper	28	58.8	33.3	25.3	12.9	9.5	5.1	44.2	31.0
All species	96	75.8	35.7	25.3[b]	12.7	16.0	10.5	43.8[c]	23.2

[a] Because of missing data, *n* = 2 for this variable.
[b] Because of missing data, *n* = 93 for this variable.
[c] Because of missing data, *n* = 92 for this variable.

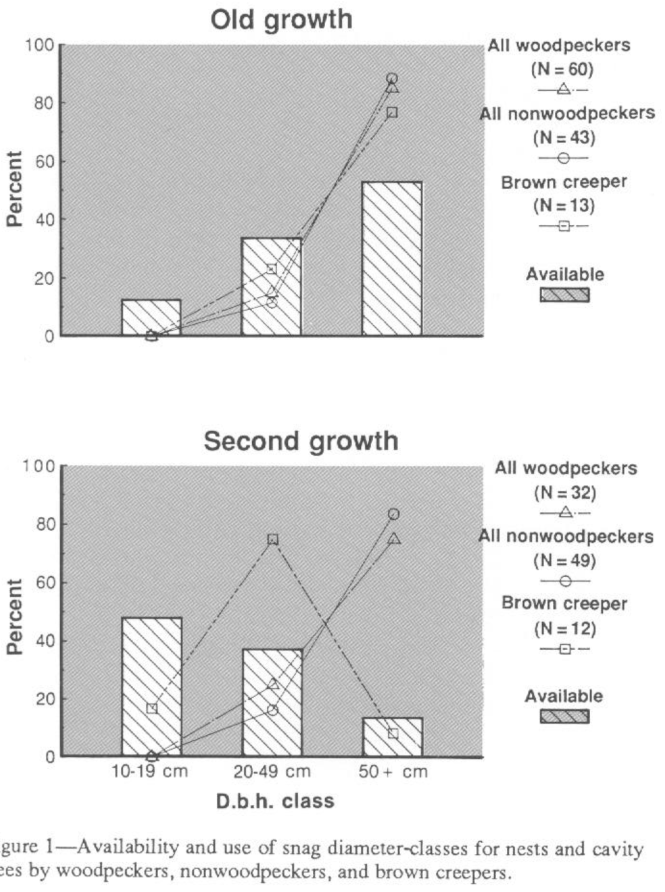

Figure 1—Availability and use of snag diameter-classes for nests and cavity trees by woodpeckers, nonwoodpeckers, and brown creepers.

trees (active and inactive) (*G*-tests, $P < 0.001$) or active trees alone ($P < 0.05$), or whether the smallest category (10-19 cm in d.b.h.) was included or not ($P < 0.05$).

Tests that examined use of snags by diameter-class by small woodpeckers (all but pileated woodpecker and northern flickers) revealed significant selection of snags (>50 cm in d.b.h. ($P < 0.005$), with one exception: active nest trees of small woodpeckers in old growth ($0.10 < P < 0.25$). Although not statistically significant, 14 of those 17 trees were >50 cm in d.b.h.

Brown creepers appeared more flexible than cavity nesters in their use of snag diameter-classes. Although creepers appeared to select large-diameter snags in old-growth stands ($P < 0.05$), no such pattern was apparent in second growth, where 20- to 49-cm-d.b.h. snags were used most often (fig. 1). The mean diameter of creeper nest trees, however, was slightly greater than 50 cm (table 6), and these analyses excluded three nests found in live trees, all >90 cm in d.b.h., two in Douglas-fir and one in a western redcedar.

Decay—The distribution of active nests among snag decay-classes differed somewhat from that of trees with inactive cavities. Of all active woodpecker nest trees, 92 percent (22 of 24) were in decay-classes 1 and 2, only 61 percent of all trees with inactive woodpecker cavities were in these classes. A similar trend held for nonwoodpecker trees: 59 percent (22 of 37) of the active trees and 36 percent (20 of 55) of the inactive trees were in decay-classes 1 and 2 (appendix table 8). This discrepancy may reflect the fact that some inactive trees had old holes with no conclusive evidence of

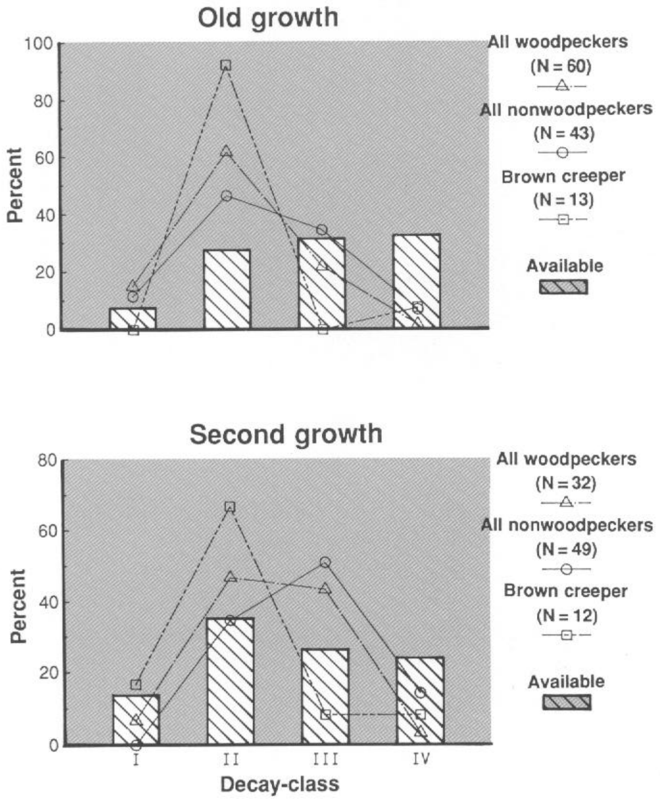

Figure 2—Availability and use of snag decay-classes for nests and cavity trees by woodpeckers, nonwoodpeckers, and brown creepers.

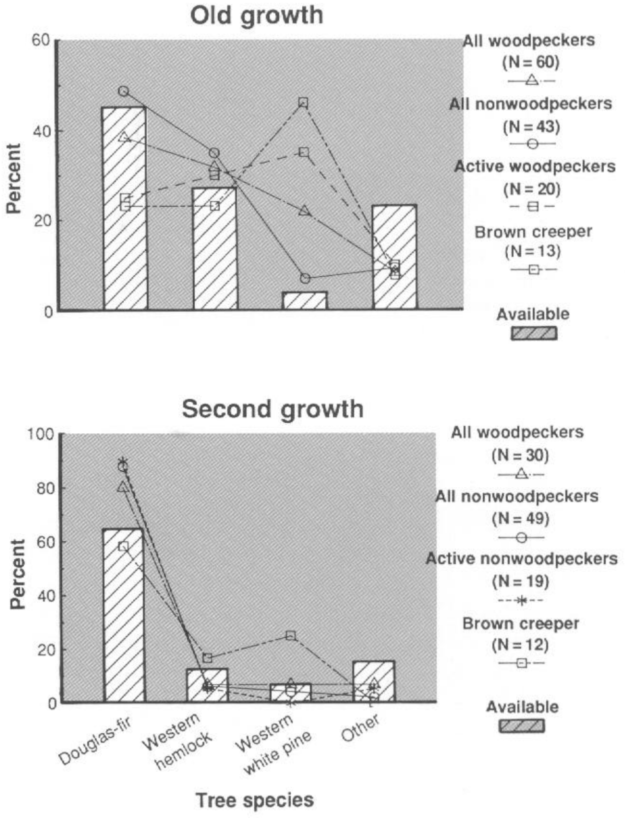

Figure 3—Availability and use of snag species for nests and cavity trees by woodpeckers, nonwoodpeckers, and brown creepers.

recent use. Because old or inactive brown creeper nests are difficult to detect, the sample includes only active creeper nest trees. The vast majority of creeper nest snags (80 percent, 20 of 25) were in decay class 2.

When use of snag decay-classes was compared to availability, small sample sizes again forced us to pool some decay-classes. Brown creepers nested in decay class 1 and 2 snags (pooled together for testing) more frequently than expected in all stand age-classes (*G*-tests, $P < 0.05$). Similarly, in old-growth stands, woodpeckers, chickadees, and nuthatches used snags in decay-classes 1 and 2 disproportionately, no matter whether we considered only active trees or included inactive trees as well ($P < 0.001$) (fig. 2).

In second-growth stands, woodpeckers used snag decay-classes 2 and 3 more frequently than expected ($P < 0.001$) (fig. 2), but the sample included both active and inactive nest trees. Active chickadee and nuthatch nests were found in snags in decay-classes 2 and 3 (pooled) more frequently than expected ($P < 0.025$), but trees with inactive cavities were found in decay-class 3 snags more than expected ($P < 0.001$) (fig. 2).

Tree species—Active nests of cavity-nesting birds were found most commonly in three tree species in the southern Washington Cascades: Douglas-fir, western hemlock, and western white pine. A wide variety of tree species held nests in old growth; most nests found in young and mature stands were in Douglas-fir.

In old growth, woodpeckers used western white pine more than expected (active nests, $P < 0.01$); active plus inactive trees, $P < 0.001$) (fig. 3A). Active nests of all woodpeckers in old growth were most commonly found in western white pine; inactive cavities were most commonly in Douglas-fir. Chickadees and nuthatches nested in western hemlock snags more frequently than expected in old growth, especially when considering only active nests, but not significantly so ($0.10 < P < 0.25$ in both tests).

In second-growth stands, woodpeckers used Douglas-fir snags slightly more than expected, but not significantly so ($0.10 < P < 0.25$) (fig. 3B). Too few active woodpecker nests were found in these stands to evaluate tree species use without including inactive trees. Nonwoodpeckers also used

Douglas-fir more than expected, but use differed from availability only when we included both active and inactive trees together ($P < 0.005$). In young stands alone, nonwoodpeckers (mostly chickadees) also nested in Douglas-fir more than expected ($P < 0.025$).

Like woodpeckers, brown creepers nested most frequently in western white pine snags in old-growth stands, and the proportional use of this species was greater than expected (based on availability) in second growth as well (fig. 3). Sample sizes were too small to test this selection in either forest age-class separately, but creepers used white pine snags significantly more than expected ($P < 0.05$) when tested over all stands combined.

Principal Components Analysis of Nest Tree Characteristics

Five principal component axes had eigenvalues greater than 1.0, four of which accounted for at least 10 percent of the total variance each. All five together accounted for 81 percent of the total variance. The first principal component (27 percent of the total variance) was most highly positively correlated with the number of limbs and most highly negatively correlated with Douglas-fir and with fire evidence. Thus, high values on this axis represented trees with more limbs (and generally less decay); low values corresponded to trees that had fire scars and were more likely to be Douglas-fir.

The second principal component, which accounted for nearly 20 percent of the total variance, was most highly positively correlated with tree height, diameter, and western white pine and most highly negatively correlated with western hemlock. Thus, nest trees with high values on this axis were taller, larger trees with intact tops likely to be western white pine, whereas trees with low values were more likely to be western hemlocks. Little additional insight was gained by interpreting the third and fourth components, each of which accounted for much less variation (13 percent and 11 percent, respectively).

A plot of mean (and standard error) principal component scores along the first two axes illustrates spatial relationships among bird species' nest-tree characteristics (fig. 4). Among the active nests, along axis 1, pileated and hairy woodpeckers, sapsuckers, red-breasted nuthatches, and brown creepers tended to nest in trees with more branches remaining than did northern flickers and chestnut-backed chickadees. The latter species tended to nest in Douglas-firs with fire evidence. The second axis further separated woodpeckers and creepers from chickadees and nuthatches. Woodpeckers and creepers tended to nest in taller, larger trees and more often in white pine. The exceptionally large standard error for sapsuckers was probably the result of a very small sample size ($n = 3$), together with a high degree of variability in nest-tree characters.

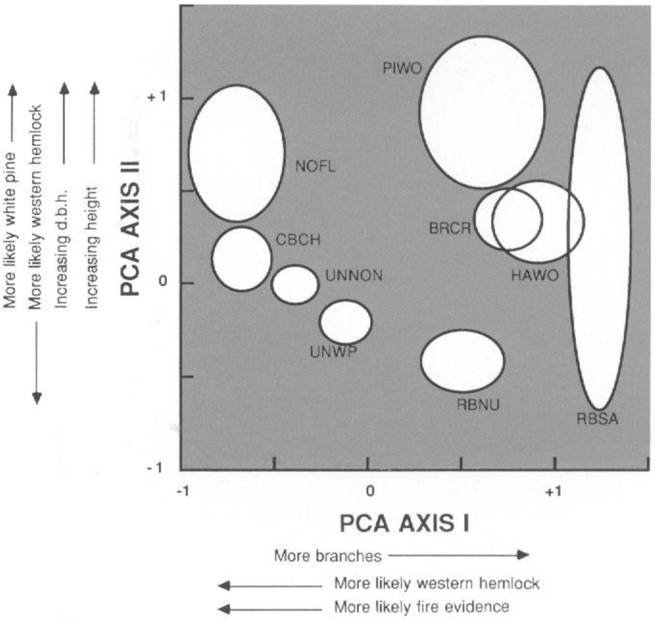

Figure 4—Principal components ordination of nest-tree characteristics of seven bird species and two categories of inactive trees on the first two principal component axes. Ellipses represent mean ± one standard error in principal component scores for each species or grouping. Codes are as follows: PIWO, pileated woodpecker; NOFL, northern flicker; HAWO, hairy woodpecker; RBSA, red-breasted and yellow-bellied sapsuckers; CBCH, chestnut-backed chickadee; RBNU, red-breasted nuthatch; UNWP and UNNON, trees with inactive cavities of woodpeckers and nonwoodpeckers, respectively.

Comparison of Nest-Site Vegetation With General Stand Characteristics

Both discriminant function analyses comparing nest-site vegetation plots with randomly sampled stand vegetation plots produced generally similar results. In both runs, higher proportions of nest sites (77-87 percent) were correctly classified by the discriminant functions than were random plots (72-74 percent).

Five variables entered discriminant equations in both runs: hard and soft snags >50 cm in d.b.h., stumps and stubs, and total canopy cover. The first variable entered, that which best distinguished nest sites from random plots, was either soft snags 20 to 49 cm in d.b.h. or hard snags >50 cm in d.b.h. Based on consistent early entry into the equations and on relatively high correlations with the canonical discriminant functions, the two latter variables, together with total density of stumps and stubs, were the most important variables discriminating nest sites from random plots. As a plot of mean and standard deviation discriminant scores for the two runs including active nest sites shows, nest sites generally had higher densities of hard snags >50 cm in d.b.h. and stumps and stubs, and lower densities of soft snags 20 to 49 cm in d.b.h., than did the random study-site samples (fig. 5).

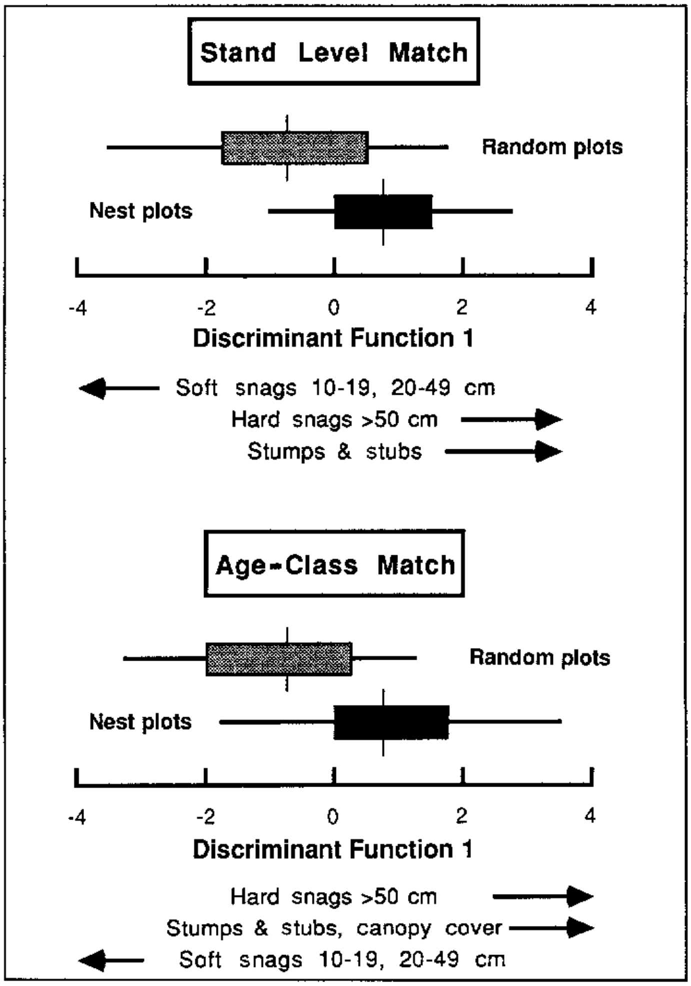

Figure 5—One-dimensional plot comparing mean (vertical bar), ± one standard error (thick horizontal bar), and range (thin horizontal bar) of discriminant scores for active nest-site vegetation plots (n = 81) and random samples (n = 81) of stand vegetation plots. All bird species' nest sites combined. Samples within each analysis were weighted equivalently at the stand level (top graph) and by age-class (bottom).

Discussion

Bird Abundance Among Stand Types

Only the Vaux's swift was significantly more abundant in old-growth stands (all moisture-classes) during both years. Although no other species showed such a strong association with old growth, mean counts of other species reached maximum abundance in one of the old-growth moisture-classes, and patterns were not always consistent between years. Few of these patterns were statistically significant, but the fact that counts of most species were often lowest or more variable in young or mature stands may suggest that these species find more consistently suitable conditions in a specific moisture-class of old growth (that is, chickadees in wet old growth, nut-hatches in dry old growth, and creepers in mesic old growth).

Merely to demonstrate significantly higher abundance in a particular habitat type does not necessarily mean that fitness, as defined by survival and reproductive success, is higher in that habitat (Van Horne 1983). The true evaluation of habitat quality can be made only by including such demographic data for comparison among sites (Wiens and Rotenberry 1981a).

In this study, gathering extensive demographic data on several bird species at once on study stands distributed over such a wide geographic range was impractical. Measures of variation in abundance, such as coefficients of variation (CV), however, may provide a way of evaluating habitat quality (Marcot 1984). This use is based on observations that in less preferred habitats, which were saturated only in high-density years, populations may fluctuate more than in preferred habitats, which were saturated except in lowest-density years (Krebs 1971; O'Connor 1981, 1986). Coefficients of variation varied greatly from year to year and from species to species, but the highest for each species were most often in mature stands. Although we did not test for statistical differences among coefficient of variation for any bird species, this comparison may suggest that mature stands were less suitable habitat than old growth for snag-dependent birds.

Several factors may have contributed to the observed lack of year-to-year consistency in bird abundance among stand types. For instance, harsh winter weather can affect populations of permanent-resident species (Gaud and others 1986, Graber and Graber 1979, Hejl and Beedy 1986, Hejl and others 1988, McClelland 1977) and may explain the generally lower mean counts we observed in 1984 than in 1985. The winter of 1983-84, although similar to long-term means, included periods of substantially higher precipitation and lower temperatures than either the next winter or those means. Several authors (Beedy 1982, Hejl and Beedy 1986, Hejl and others 1988, Raphael and White 1984) have found similar decreases in both permanent and summer resident species after harsh winters in coniferous forests in California.

In addition, observer bias or variability may have contributed to the lack of consistency in abundance patterns (or habitat associations) between years. Problems such as variation in different observers' training, experience, hearing ability, knowledge of local birds, and attentiveness can conceal patterns present in the system studied or cause spurious patterns to occur (see references in Ralph and Scott 1981). Although the effects of observer bias on our data are not known, we attempted to minimize it by conducting training sessions each season, having each stand visited by more than one observer during each year, and maintaining as much continuity of observers between years as possible.

The lack of clear, consistent abundance patterns of woodpeckers among forest age-classes may also be a problem of scale (Wiens 1981a). Woodpecker home ranges may be as large as the area encompassed by the array of count stations on each stand, and much larger for pileated woodpeckers (Bull and Meslow 1977, Mannan 1984b). Although we can assign some association or importance of one or more forest age-classes to wide-ranging species such as woodpeckers, the ability to evaluate habitat quality based solely on relative abundance patterns of these species is necessarily limited when the sampling unit (the stand) is small relative to home-range size. Evaluations of woodpecker occurrence or abundance over larger scale areas that encompass home ranges of many breeding pairs might provide better indices of habitat quality.

A related problem is that higher counts of the more wide-ranging species do not necessarily indicate the presence of nesting pairs. For example, pileated woodpecker counts were relatively high in young stands in both years. No nests or roosts of pileated woodpeckers were found in those stands during our study, but the stands had many snags with recent evidence of pileated feeding. Thus, young unmanaged stands may provide good feeding but not nesting habitat for pileated woodpeckers. This difference may be true for other woodpecker species, too, because few nest or roost trees of any woodpecker species were found in young (or mature) stands.

Other factors complicating the analysis of bird abundance patterns among the stand types are elevation and latitude. The study stands were, by design, distributed over a relatively wide geographic range and, by necessity, over a wide elevational range within this forest type in the southern Washington Cascades. Manuwal and others (1986) found that total bird abundance varied inversely with both elevation and latitude: counts were generally higher in stands lower in elevation and situated farther south in the study area, regardless of stand age. The same was true of the species we studied.

The bird count data were admittedly short term (only 2 years of data). Gaud and others (1986) argue that recommendations based on only 1 or 2 years' data may be inaccurate, and suggests a minimum of 5 years of study to adequately account for yearly fluctuations in bird abundance. The continuation of long-term monitoring on similar stands in the southern Washington Cascades will help clarify the relation of bird abundance patterns to forest stands of different age-classes.

Bird-Habitat Relationships

Relatively few correlations between cavity-nesting bird counts and snag and live-tree densities were consistent or interpretable. The significant correlations found between counts of woodpeckers or nuthatches and trees they were seldom observed using (or the negative associations) may be spurious, or the habitat variables may represent other features not sampled explicitly. The biological significance of the association between hairy woodpeckers and large, live hemlocks is not apparent, except that these trees may serve as future sources of potential nest trees (Zarnowitz and Manuwal 1985).

On the other hand, chestnut-backed chickadees, principally foliage-gleaners, correlated positively with densities of large overstory trees, which probably provide an optimum foraging environment. This correlation may be due to greater abundance of either insects or cones. Large, dominant conifers, particularly Douglas-fir, that are more exposed to the sun's rays are known to produce more cones than codominant trees (Fowells 1965). Similarly, Raphael and Barrett (1984) found that abundance of chickadees, which reached its maximum in old-growth stands in northwestern California, correlated with a principal component axis associated with higher densities of largest Douglas-fir (>90 cm in d.b.h.). In another study in California (Morrison and others 1987), chickadees were positively associated with mean canopy height, which clearly relates to the size of the largest trees.

The association of chickadees with very large western redcedars probably accounted for their greater abundance in wet old-growth stands, as densities of redcedars equaled or exceeded Douglas-firs of comparable size there. Because chickadee numbers were more consistently correlated with live trees than with snags, characteristics of foraging habitat may have been more important than nesting habitat in determining chickadee abundance, given that large, decayed snags and stubs suitable for nesting were relatively abundant in all stands.

Vaux's swifts correlated most strongly with the kinds of trees that provide suitable nesting habitat: very large live trees (mainly Douglas-fir, western hemlock, and western redcedar) and large snags (Douglas-fir and hemlock). Large, broken-topped trees (live or dead) with the trunks hollow at the top are known to harbor nests of Vaux's swifts (Baldwin and Zaczkowski 1963, Jewett and others 1953). During the 1983 pilot study, one swift nest was found in a broken-topped redcedar snag (77 cm in d.b.h., 10 m tall) in an old-growth stand. The need for large broken-topped trees probably accounts for the strong association of swifts with old growth, because these trees are most abundant there. The greater number of large, overstory trees and resulting broken, multilayered canopy in old growth, may however, also provide an optimum foraging environment for swifts, which are aerial foragers. Broken, multilayered canopies of old-growth stands may allow greater access to flying insects surrounding overstory trees than would closed, continuous canopies of younger stands.

Based on our regression analyses, abundance of cavity-nesting birds was not well predicted by live-tree and snag densities. Others (Marcot 1984, Morrison and others 1987, Raphael and Barrett 1984) have also found that habitat variables explain little of the variance in bird abundance. Morrison and others (1987) found their final regression models to predict presence or absence of bird species adequately, but the equations did not clearly track the variation in abundance between years (but see comments by Hejl and others 1988). Problems in elucidating bird-habitat relationships via correlation or regression analysis can result from a variety of factors, including, but not limited to, the following: nonlinear or nonmonotonic relationships; incomplete sampling of habitat gradients; variability in species' responses to habitat features; sampling scale; or not sampling the correct variables (Best and Stauffer 1986). Each is discussed briefly below.

The relation of bird abundance to habitat features can be linear, curvilinear, or otherwise nonmonotonic (Best and Stauffer 1986, Colwell and Futuyama 1971, Meents and others 1983). Some authors (Madsen 1985, Raphael 1980) have found the relation of cavity-nesting bird abundance to snag densities, particularly large snags, to be curvilinear. Meents and others (1983) found that although linear bird-habitat relationships were most common, polynomial variables increased the amount of variance explained by regression equations.

The lack of consistent associations between these bird species and snag densities (the kinds most often used for nesting) may also have been because all the stands were naturally regenerated and contained numerous snags or because they were all canopied stands. The lack may thus be viewed as a form of incomplete sampling of habitat gradients. Most recent studies that demonstrated stronger cavity nester and snag associations in western coniferous forests have included managed stands, where some or all snags have been removed (Balda 1975, Madsen 1985, Mannan and others 1980, Raphael and White 1984, Zamowitz and Manuwal 1985). On our study stands, snag densities may have been above a threshold (sensu Raphael 1980), so that other factors were more predictive of (and limiting to) snag-dependent bird populations. We suspect correlations would be stronger if managed stands or clearcuts lacking high densities of remnant snags were included in the analysis (Verner and Larson 1989).

Even if strong relationships are found, they may change, depending on whether or not the entire habitat gradient is examined (Colwell and Futuyama 1971, Wiens and Rotenberry 1981b). For example, Best and Stauffer (1986) found that snag density could be deemed to have little influence on habitat suitability for downy woodpeckers and house wrens if samples from areas of low snag-density were not analyzed. Examination of the entire gradient revealed not only increased suitability at higher snag densities (relative to low densities), but differences between the two species' suitability indices at lower densities.

A third factor concerns the relative abundance and detectability of the bird species under study. Some species are typically encountered less frequently than others, and the less frequently a species is encountered, the more variable its observed response to habitat features (Best and Stauffer 1986). Thus, in this study, the more wide-ranging woodpeckers may have been no less responsive to variation in snag densities than, say, swifts and chickadees, but the relative infrequency with which the woodpeckers were encountered may have made count data insufficient to detect possible relationships.

For species with large home ranges relative to the sampling array on each stand, low probability of encounter relates back to a problem of scale. As discussed above, sample stands may be too small to evaluate habitat relationships of woodpeckers. In addition, habitat variables and bird counts summarized as stand means may be too coarse to account for the possibility that some species may be using only small portions of each stand. Such patterns of use may contribute to the lack of significant correlations or cause spurious ones to appear.

Abundance of cavity-using birds is not necessarily correlated with or a function of densities of snags; other, unmeasured variables may be more important. Nevertheless, our findings, as well as those of others (Balda 1975, Madsen 1985, Mannan and others 1980, Raphael and White 1984, Zamowitz and Manuwal 1985), certainly attest to the importance of snags to cavity-using birds, particularly in terms of management for these species.

Nest Tree Characteristics

Size-Although a variety of kinds of trees harbored nests, our analyses clearly revealed disproportionate use of trees with certain attributes by cavity- and bark-nesting birds. Our findings agree with other studies that have demonstrated disproportionate use of large-diameter snags as nest trees (Madsen 1985, Mannan and others 1980, Raphael and White 1984, Zamowitz and Manuwal 1985). Mean nest-tree diameters in this study were generally larger than those reported from the Olympics of Washington (Zarnowitz and Manuwal 1985), but smaller than in the Oregon Coast Range (Mannan and others 1980, Nelson 1989). Hairy woodpeckers typically nested in snags of substantially larger diameter in this study area (and the Oregon Coast Range) than reported from studies in the northern Rockies (Harris 1982, McClelland 1977) the Blue Mountains of Oregon (Bull 1980), the east slope of the Cascades in northern Washington (Madsen 1985), or the Sierras of California (Raphael and White 1984). Unfortunately, because our data and those from the Oregon Coast Range were from natural stands, many of which were old growth, we could not assess the extent to which cavity-nesting birds can successfully use smaller snags where larger ones are not available, as was shown for white-headed woodpeckers in the Sierra Nevada (Milne and Hejl 1989). Future studies must specifically address that question.

Presumably, large-diameter trees offer better thermal insulation and more room to house larger clutches, thereby enhancing reproductive success (Karlsson and Nilsson 1977). Not surprisingly, nest trees of the largest bird species-pileated woodpeckers and flickers-were typically larger (at breast height and at cavity height) than the mean for all species. The smallest bird species, however-chickadees and nuthatches-likewise nested in large-diameter trees. Creepers, which typically nest under slabs of bark, showed more plasticity in nest-tree size-selection than the cavity nesters. Other factors, such as decay state, tree species, and bark characteristics, were more important in determining the suitability of potential nest trees for this species.

Decay-The disproportionate use of hard snags by woodpeckers, most commonly hairy woodpeckers, contrasts with the findings of Mannan and others (1980) in Oregon (but see Nelson 1989), who found nests of hairies most often in decay-class 3, although their data included only seven nests. The only exception among the woodpeckers in our study was the flicker, which nested most frequently in decay-class 3 snags, most of which in young stands were in fire-scarred, remnant snags.

Because they are less well-equipped for cavity excavation, chickadees and nuthatches might be expected to nest in trees in more advanced decay stages. In second growth, this was generally true, and, as with flickers, most nests were in remnant snags. In old growth, however, their disproportionate use of all hard snags may be explained partially by the observation that nest holes were near the tops of snags (or even live trees) where the wood was most severely decayed and resembled conditions in more rotten snags. The selection of decay-class 2 snags by creepers probably relates to the greater percentage of remaining bark, as well as relative firmness of the sapwood.

Tree species-Only three tree species contained active nests: Douglas-fir, western hemlock, and western white pine. The disproportionate use of white pine by. woodpeckers and creepers is important in that it is a relatively minor, but widely distributed, forest component throughout western Washington. White pine has a patchy distribution and has declined in this century since the introduction of the fungus *(Cronartium ribicola)* that causes white pine blister rust (Allen 1959, Fowells 1965, Boyd 1980).

Our findings differ, however, from other studies of cavity-nesting birds in Douglas-fir forests in the Northwest. In Oregon, all cavity nesters apparently used Douglas-fir more than expected, based on availability (Nelson 1989). In the Olympics of Washington, woodpeckers-mostly hairy woodpeckers-appear to nest primarily in western hemlock (Zarnowitz and Manuwal 1985). Thus, even within the Western Hemlock Zone in the Northwest, woodpeckers use tree species to different degrees in different areas.

Chickadees and nuthatches, nesting primarily in Douglas-fir and hemlock, were apparently less selective than woodpeckers as to nest-tree species. This analysis was complicated, however, by the fact that most of the nuthatch nests were found in old growth (in hemlocks), whereas most chickadee nests were found in young stands (in Douglas-firs). It is not clear why most chickadee nests were found in younger stands, given that chickadees were more abundant in old growth, except that nests may have been easier to see in young stands.

Selection of tree species by primary excavators probably relates to relative decay characteristics of trees, as well as the sizes of each tree species available (Conner and others 1976, Jackson 1977, McClelland 1977). The progression and rate of decay of snags results from the interaction of biotic and abiotic factors over time and varies with size and age of the tree at death, species, and geographic location (Kimney and Fumiss 1943). Because Douglas-fir snags decay more slowly than most other species (Buchanan and Englerth 1940, Cline and others 1980), and because decay usually proceeds from outside inward (Kimney and Fumiss 1943, Wright and Harvey 1967), this species is especially suitable for nests of the weaker excavators, chickadees, nuthatches, and flickers. These traits also underscore the importance of large, remnant Douglas-fir snags as the most suitable nest sites for chickadees in young stands, both in this area and in the Oregon Coast Range (Mannan and others 1980). Without these large, remnant snags, abundance of breeding chickadees probably would have been lower in young stands.

Western hemlock, a common snag species on the study stands, is much less durable than Douglas-fir and often harbors fungal heart rot while it is still living (Buchanan and Englerth 1940, Engelhardt 1957). The importance of fungal heart rot to woodpecker nesting is well known (Conner and others 1976, Jackson 1977, Kilham 1971, McClelland 1977, Shigo and Kilham 1968). The susceptibility of hemlocks to heart rot fungi probably makes them attractive to hairy woodpeckers and sapsuckers. Because hemlock snags remain standing a relatively short time, cavity nesters would have to use this species while the trees were still alive or within the first several years after death. These attributes undoubtedly contributed to the frequent use of hard hemlock snags, as well as occasional live trees, by cavity nesters.

Western white pine, compared to its relative rarity ($\leq$ 5 percent of available snags), was the species most frequently used by woodpeckers for nesting. Although reasons for its decline are relatively well known, information relating to decay rates of dead trees is nearly lacking. The common infections of this species by fungal heart rots (Fowells 1965), its apparent resistance to uprooting (Cline and others 1980), and the durability of sapwood and major limbs (pers. obs.) probably account for the suitability of western white pine as woodpecker nest sites. McClelland (1977) and Madsen (1985) similarly attributed woodpecker selection of western larch in Montana and northcentral Washington, respectively, to decay of the heartwood in combination with relatively sound sapwood. The rarity of large white pine snags only underscores their importance to woodpeckers in this portion of the Washington Cascades.

Nest tree surroundings--Our finding that nest sites of cavity-nesting birds contained higher densities of large, hard snags-the kinds in which they typically nested-agrees with other studies that have reported nests of excavators in dense patches of snags (Bull 1980, Harris 1982, Madsen 1985, Raphael and White 1984). We do not know whether this observation implies selection of dense patches of snags by the birds, or whether it is simply an artifact of the patchy way in which trees are killed by insects or disease. Also, we do not interpret this observation to mean that isolated snags do not have value as nesting habitat. In fact, some nest trees that were used in successive years were not located within a group of snags.

Conclusions anld Magnagement Considerations

In recent years, much attention has focused on the specific problem of providing adequate numbers of suitable snags through time and space in intensively managed forests (Davis and others 1983; Neitro and others 1985; Thomas and others 1976, 1979). Our purpose here is not to rework these guidelines, but only to refine or augment them with information specific to Douglas-fir/western hemlock forests of the Washington Cascades.

Nest Sites

We concur with Evans and Conner (1979a), Raphael and White (1984), and Madsen (1985), among others, who argue for the use of mean nest-tree diameters as a guideline for snag management. Managing for minimum diameters of trees known to be used could cause a gradual decline in cavity-nesting bird populations (Conner 1979a). We therefore recommend managing for snags of at least 76 cm in d.b.h., the mean d.b.h. of all active nests, where possible in this area. This diameter is notably larger than those recommended by Thomas and others (1979) for the Blue Mountains or Neitro and others (1985) for westside forests, particularly for hairy woodpeckers and sapsuckers. Woodpeckers appear to nest in larger trees in Douglas-fir forests (Mannan and others 1980, Nelson 1989, this study, Zarnowitz and Manuwal 1985) than in eastside forests, though sample sizes are relatively small from most study areas. Snags no less than 50 cm in d.b.h. should be given top priority in managing for cavity- and bark-nesting birds because this broad size-class was used disproportionately for nesting by all bird species we studied. Emphasis should be placed on the largest snags available in a given area, because larger snags remain standing longer, retain bark longer, and support a larger variety of wildlife (Cline and others 1980, Conner 1979a, Evans and Conner 1979).

Managers **must** also consider the decay state of snags. Our study suggests that most woodpeckers (particularly hairy woodpeckers) prefer hard snags for nesting; softer snags were generally avoided. Neitro and others (1985: 144), however, assumed that hairy woodpeckers used primarily decay stages 4 and 5, in contrast to red-breasted sapsuckers, which used stages 2 and 3. Our results and those of Mannan and others (1980) and Nelson (1989) do not agree. The number of hard snags required for the most common woodpecker species in the western Cascades would be vastly underestimated if the guidelines of Neitro and others (1985: 145, table 9) are followed. On the other hand, weaker excavators, such as flickers, chickadees, and nuthatches, were more likely to nest in soft snags, as might be expected, but depending on the forest age-class and the characteristics of available snags, even these species nested frequently in harder snags and defective live trees.

The species of snag is also important. Given the species' relative rarity in the forest, large, hard western white pine snags should be retained wherever they occur in areas managed for woodpeckers. Retaining white pine snags for woodpeckers will benefit brown creepers as well. Chickadees and nuthatches, on the other hand, nested primarily in Douglas-fir and hemlock snags and were seldom found nesting in white pine. Obviously, comprehensive management schemes designed to provide for all cavity-nesting bird species must consider the needs of each species in the community. Meeting the snag requirements of one species will not necessarily meet the needs of other species (Mannan and others 1984).

Besides nesting in different types of snags than woodpeckers do, chickadees and nuthatches were not found to nest in old woodpecker holes, except in two instances. Although some birds may have fashioned their cavities from old woodpecker feeding holes or "false-start" cavities, most chickadee and nuthatch nests appeared to be solely the work of the nesting pair. These species chose trees of suitable species, size, and decay states and nested in locations appropriate to their abilities to excavate their own cavities. Suitable snags were sufficiently abundant in most of these natural stands to provide sites for nest cavities. Perhaps the presumed energetic efficiency of using old woodpecker holes was partially offset by possible fouling of holes caused by previous use or risk of predation in larger holes, thus making them less attractive or more harmful than newly excavated holes (Short 1979).

Conceivably, as snags--especially large ones-become scarcer in managed forests, noticeable changes in patterns of nest-site use from increased competition, because of lower snag availability, could occur. Possible changes include: smaller average diameter of nest trees (Milne and Hejl 1989); use of the smallest diameter portion of trunks (or limbs) capable of supporting nest-cavity dimensions (Short 1979); greater use of old woodpecker cavities by chickadees and nuthatches as more easily excavated sites became scarcer; greater use of defective live trees; or greater interference competition (Miller 1967) among bird species, which would effectively reduce the number of available (that is, unoccupied) snags. Pressures caused by the reduction of the snag resource, if sufficiently severe, could lower reproductive success of cavity-nesting birds or cause population declines outside of unmanaged areas or old-growth reserves. The list of possible changes could serve as hypotheses to test in examining responses of cavity nesters to changes in the snag resource under different management schemes.

Another important consideration is that, in the younger stands, very few nests were found in trees that arose from the current stands. The only species found nesting commonly in young stands, chestnut-backed chickadees, used remnant snags primarily. Thus, even under natural conditions, stands less than 80 years old have limited numbers of suitable nest trees for most cavity nesters. Stands initiated after clearcutting, with few, if any, remnant snags, would likewise contain few suitable nest trees. Given the target rotation ages of managed forests, roughly comparable to the young stands we studied, recommendations for retention of old growth where possible, strips of trees and snags along riparian corridors, patches of snags (and live trees) in clearcuts, as well as areas of longer rotations (Neitro and others 1985) become critical for maintaining populations of cavity-nesting birds. Modem silvicultural techniques have enabled foresters to produce larger trees that can serve as potential nest trees in shorter periods. Younger, faster-growing trees, however, tend to decay more rapidly after death than do older, slower-growing trees (Kimney and Furniss 1943), so the number of snags provided may have to be adjusted.

Foraging Sites

In managing for cavity- and bark-nesting birds, characteristics of foraging habitats should not be overlooked (Conner 1980). Birds may focus foraging activities on different species and sizes of trees from those used for nesting, and foraging activities may change seasonally (Conner 1981, Lundquist and Manuwal 1990). For example, in our study area, creepers, chickadees, hairy woodpeckers, and nuthatches foraged on large-diameter (>50 cm), live Douglas-fir more than expected based on availability, and chickadees appeared to shift to western hemlock in the winter (Lundquist and Manuwal 1990). Retention of large live trees, either in old growth or longer rotation patches, could also benefit species such as Vaux's swifts indirectly by serving as future sources of large snags (Mannan and Meslow 1984).

Implementing Snag Management

Harvest of old-growth forests, and shorter rotations, resulting in the prevalence of relatively young second-growth forests, will make the success of snag-management policies even more crucial for snag-dependent wildlife in the future. The Pacific Northwest Region (USDA Forest Service 1985) recommends managing dead and defective live trees to maintain viable populations of cavity-dependent wildlife at 40 percent of their population capacities on commercial forest lands. This policy was intended to set minimum standards and a baseline for managing Northwest forests. Although significant progress has been made in establishing and carrying out management programs in the last decade, Bull and ‘others (1986b) report considerable inconsistency in the numbers of snags being maintained on National Forest Districts. Nearly one-third-of the Districts surveyed reported fewer snags than necessary to maintain cavity-nesting bird populations (as defined by Thomas and others 1979). Similarly, Morrison and others (1986) concluded that although current guidelines for maintaining large snags in the Tahoe National Forest in California were appropriate, they were not being implemented effectively.

Recommendations that may help-attain snag-management goals in balance with human needs include retaining more snags than the minimum required to support targeted cavity-nesting bird populations. This recommendation allows for unforeseen losses, such as to windthrow or firewood cutters or uncertainties regarding natural fall rates of snags. It will also allow for removing trees that may pose safety threats while still maintaining enough trees for wildlife. Neitro and others (1985) discussed in detail innovative ways of selecting suitable types of snags compatible with logging safety regulations. In view of possible increases in demand for fuelwood (Force 1986), management plans should include ways to minimize impacts on snags provided for wildlife, such as restricting access to critical areas or limiting the size of snags cut. Producing large snags at high cost-either as direct or “opportunity” costs-and then leaving them unprotected from fuelwood cutters makes no sense, particularly where the number of snags is below stated goals (Bull and others 1986b, Morrison and others 1986).

Spatial distribution of snags is also important in designing management plans. Although our study and others (Bull 1980, Raphael and White 1984) have found cavity nesters in relatively dense patches of snags, lone snags may also provide suitable nest sites. Priority should be given to suitable snags (appropriate size, decay stage, and species) whether they occur in clumps or singly, to allow for adequate distribution over a large area. Adequate cover can be provided around lone snags in the form of live trees, which are also a source of future snags. Such flexibility in management will help prevent suitable snags of several cutting units from being crowded too close together to be usable.

Monitoring is essential to assess snag numbers and losses, their use by wildlife, and the implementation and effectiveness of snag-management programs. Given that the complete ecological and economic role of snags and cavity-dependent wildlife is not fully understood at present, management schemes must be carefully designed and flexible enough so that future management options are not lost. As new information and understanding are gained, programs can be modified as required to ensure the continued health of avian communities in managed forests.

Acknowledgments

This research was done in partial fulfillment of the requirements for the degree of Master of Science at the University of Washington for each of the authors. We gratefully acknowledge the advice and support of the members of our graduate committees: D.A. Manuwal, A.B. Carey, and C.D. Oliver (Lundquist); and D.A. Manuwal, S.D. West, and K.J. Raedeke (Mariani). We express our appreciation to M.Q. Affolter, B. Booth, J.B. Buchanan, C.B. Chappell, M. Emers, K.W. Hegstad, A. Hetherington, M.H. Huff, A.B. Humphrey, D.A. Leversee, D.A. Manuwal, K. Newgard, B.R. North, M.J. Reed, B.A. Schrader, L.W. Willimont, and K. Ziegler for assistance with the field work. B.G. Marcot, R.L. Hutto, K.G. Smith, and J. Verner provided valuable comments on earlier drafts of the manuscript. We thank USDA Forest Service personnel at the Gifford Pinchot National Forest and at Mount Rainier National Park for their assistance. Computer funds were made available through the Academic Computer Center at the University of Washington. We gratefully acknowledge the support of L.F. Ruggiero, A.B. Carey, F.B. Samson, and K.B. Aubry, USDA Forest Service, Olympia. This study was funded by USDA Forest Service contracts PNW-83-219 and PNW-86-244.

This paper is contribution 114 of the Wildlife Habitat Relationships in Western Washington and Oregon Research Project, Pacific Northwest Research Station, USDA Forest Service. **0**

Appendix

Table 7-Stern count[a] variables and codes used in bird and vegetation correlation and regression analyses

Code	Description
Coarse variables:	
LT4	Live trees >100 cm d.b.h.
TSTP	Stumps and stubs (snags <5 m tall, >l0 cm d.b.h.)
SS	All small snags l0-19 cm d.b.h.
Species-specific variables:	
DFD13	Live Douglas-fir l-100 cm d.b.h.
WHD12	Live western hemlock l-50 cm d.b.h.
WHD3	Live western hemlock 51-100 cm d.b.h.
RCD12	Live western redcedar l-50 cm d.b.h.
RCD3	Live western redcedar 51 - 100 cm d.b.h.
ABD13	Live *Abies* spp. l-100 cm d.b.h.
CPD13	Live other conifers l-100 cm d.b.h.
VMD12	Live vine maple l-50 cm d.b.h.
HDD13	Live other hardwood spp. l-100 cm d.b.h.
DFS34	All Douglas-fir snags 20-49 cm d.b.h.
DFS5	Hard Douglas-fir snags (DC I-II) ≥ 50 cm d.b.h.
DFS6	Soft Douglas-fir snags (DC III-V) ≥ 50 cm d.b.h.
WHS34	All western hemlock snags 20-49 cm d.b.h.
WHS56	All western hemlock snags ≥ 50 cm d.b.h.
RCS34	All western redcedar snags 20-49 cm d.b.h.
RCS56	All western redcedar snags ≥ 50 cm d.b.h.
ABS34	All *Abies* spp. snags 20-49 cm d.b.h.
WPS34	All western white pine snags 20-49 cm d.b.h.
WPS56	All western white pine snags ≥ 50 cm d.b.h.

[a] All stem counts were converted to densities (number per hectare).

Table 8-Comparison of active nest trees and trees with inactive cavities of woodpeckers and nonwoodpeckers among decay classes by forest age-class

Hole-nester group/ tree-use status	Decay-class				Total
	I	II	III	Iv	
Woodpeckers/active					
Old-growth	7	12	1	0	20
Mature	0	0	1	0	3[a]
Young	1	2	0	0	3
Total	8	14	2	0	26
Woodpeckers/inactive					
Old-growth	2	25	12	1	40
Mature	1	7	4	0	12
Young	0	5	8	1	14
Total	3	37	24	2	66
Nonwoodpeckers/active					
Old-growth	4	10	4	0	18
Mature	0	5	1	0	6
Young	0	3	7	3	13
Total	4	18	12	3	37
Nonwoodpeckers/inactive					
Old-growth	1	10	11	3	25
Mature	0	6	4	1	11
Young	0	3	13	3	19
Total	1	19	28	7	55

[a] Includes two sapsucker nest snags with missing data.

Continue