BIRD HABITAT RELATIONSHIPS IN NATURAL AND MANAGED FORESTS IN THE WEST CASCADES OF OREGON[1]

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Abstract. Ecologists have advocated retaining various densities of canopy trees in harvest units in Pacific Northwest forests. In contrast to clear-cutting, this practice may better emulate the patterns of disturbance and structural complexity typical of natural forests in the region. Several ecological attributes, including vertebrate habitat diversity, are thought to be associated with stands of complex structure. The goal of this study was to determine bird abundance in canopy retention sites relative to other common stand types in the Pacific Northwest and to develop habitat functions for extrapolating bird abundance across current and future landscapes.

We used data from five previous studies in the west central Cascades of Oregon to compare bird abundance and to develop habitat functions for forest birds across a wide range of natural and managed stand structures and ages. The 67 stands included clearcuts, retention sites, young closed-canopy plantations, mature stands, and old-growth stands. ANOVA revealed that 18 of the 23 species included in the analysis differed significantly in abundance among the stand types, with some species being primarily associated with each of the stand types.

The habitat variables used to build habitat functions included tree density by size class, mean tree diameter, and variation in tree diameter. Linear, polynomial, and various nonlinear regression models were evaluated for each bird species. Significant habitat functions were generated for 17 of the 23 bird species. The analyses identified four habitat-use guilds among the 17 bird species: open-canopy; open-canopy with dispersed large trees; structurally complex closed-canopy; and structurally simple closed-canopy guilds.

This study is the first in the Pacific Northwest to compare bird abundances across natural stands, traditionally managed plantations, and stands managed under ecological forestry approaches. The results suggested that canopy tree retention benefits many, but not all, of the bird species we studied, Moreover, the nonlinear responses of bird abundance revealed thresholds in tree density at which bird abundance changed dramatically. Knowledge of these thresholds allow managers to design stands for specific biodiversity objectives. The habitat functions presented here can be used to predict bird abundance based on habitat measurements derived from field data, remotely sensed data, or output from computer models of forest dynamics.

Key words: biodiversity; birds; conservation biology; ecological forestry; forest management; habitat; nonlinear regression; Pacific Northwest.

INTRODUCTION

A key challenge in sustaining biodiversity is to understand the effects of human activities on species distributions and to use this knowledge to predict likely patterns of biodiversity under future change scenarios (Lubchenco et al. 1991). A prevalent trajectory of change in many human-dominated landscapes is the conversion of natural forests to managed plantations (Lansky 1992), with an attendant loss of native species (Harris 1984, Hansen et al. 1991). Consequently, forest managers are now developing and implementing new strategies to sustain biodiversity, ecological productivity, and other objectives (Kessler et al. 1992). This trend has generated considerable debate on the economic, social, and ecological consequences of these new strategies.

A centerpiece of this "ecological forestry" in the Pacific Northwest (PNW) of the United States is the retention of variable densities of live trees in harvest units. In contrast to clear-cutting, live tree retention is

done to maintain canopy complexity over the full rotation cycle (Franklin 1989, Gillis 1990). The rationale for this practice derives from patterns of disturbance and succession in natural PNW forests. The variable disturbance regimes, large tree sizes, and "legacies" of structures surviving disturbances result in natural forests of all ages having high variability in tree size and canopy layering (Hansen et al. 1991, Spies and Franklin 1991). This structural complexity influences several ecological attributes (Franklin et al. 1981). Canopy complexity in managed forests is hypothesized to promote: habitat diversity for forest organisms; nutrient cycling; beneficial predator–prey relationships among forest invertebrates; refugia and inocula for nonvagile mycorrhizal-forming fungal species and invertebrates; and dispersal opportunities for species that avoid forest openings (Franklin 1992, Swanson and Franklin 1992).

Initial studies of breeding birds in the PNW forest found that the abundances of several species varied with canopy tree density in recent harvest units. Some species, such as Steller's Jay (scientific names of birds are in Table 2), were more abundant in units with canopy tree retention, whereas other species (e.g., Lazuli Bunting), were most abundant in clearcuts (Vega 1993, Hansen and Hounihan 1995). Bird diversity and abundance increased significantly with canopy tree retention level in higher elevation sites (Hansen and Hounihan 1995), but did not differ significantly between clearcuts and retention sites at lower elevations (Vega 1993). Each of these studies examined a limited number of sites for only one breeding season. Hence, there is a need to quantify the relationships between canopy tree retention and avian communities over a greater range of locations and years, and to compare these results with those from other prevalent stand types in the PNW.

Quantitative data on habitat use can be used to extrapolate bird abundance across current or likely future landscapes as a function of habitat patterns (Pulliam et al. 1992, Hansen et al. 1993). Habitat has long been used as a predictor of animal abundance. Several classic studies documented fundamental relationships between organisms and habitat structure (MacArthur and MacArthur 1961, Shugart and James 1973, Anderson and Shugart 1974). James (1971) suggested that habitat attributes can be visualized as axes defining the habitat niche space where organism fitness is positive. Several subsequent studies described bird habitat niches in terms of vegetation structure and composition (reviews: Cody 1985, Verner et al. 1986). Such habitat models have had mixed success in explaining variation in bird abundance in calibrated data sets and in predicting animal distribution in independent data sets (e.g., Anderson et al. 1983, Capen et al. 1986). The strength of association among species abundance and habitat attributes can be strongly influenced by the types of habitat attributes considered, and by the spatial and temporal scales over which they are measured

(Neilson et al. 1992). Animal habitat relationships also may be clouded by demographic factors, interspecific interactions, and historical events (Van Horne 1983, Pulliam 1988). In spite of these limitations, habitat approaches for the conservation and management of biodiversity are attractive because of the ease with which habitat can be measured (either in the field or remotely). Detailed demographic data, in contrast, are expensive to collect and are available for relatively few species. Thus, approaches based on habitat seem to be the best alternative for the management of multi-species communities (Hansen et al. 1993). Moreover, field validation of the habitat functions can be used to quantify how well the functions predict animal presence or abundance in independent habitat samples.

In this paper, we integrate data from five previous studies in the west-central Cascades of Oregon to quantify bird abundance across broad gradients in forest age and management history. The first objective is to compare the abundance of individual bird species among five stand types: recent clearcuts, canopy-retention units, closed-canopy plantations, mature stands, and old-growth stands. The consequences of these patterns of habitat use for bird survival and reproduction are not examined in this study (see Vega 1993 and Hansen et al. 1994 for initial work). The second objective is to develop statistical functions relating bird abundance to stand-level habitat characteristics. We use a parsimonious set of habitat variables (tree density by diameter class) that are both associated with bird abundance and available from each of the studies. Standing dead trees, coarse woody debris, shrubs, and other habitat factors are not included. Our focus is on bird species whose nesting and foraging activities are primarily influenced by the structure of live trees. These habitat functions will be useful for predicting bird abundance across current and possible future landscapes in the area.

METHODS

Data sources

Previous studies in the PNW found that bird abundance varies with stand age, stand history, and geographic location, among other factors (Marcot 1984, Ruggiero et al. 1991). Consequently, we sought data sets on bird habitat relationships that covered a wide range of natural and managed stand types and ages, but were located within one physiognomic province. We selected five studies conducted in the Western Cascades and High Cascades Provinces (as defined by Franklin and Dyrness 1973). Attributes of the studies and locations of the study sites are presented in Table 1 and Fig. 1.

Gilbert and Allwine (1991) sampled breeding birds in 52 natural young (35–79 yr), mature (80–200 yr), and old-growth (>200 yr) stands during 1984 and 1985 as part of the USDA Forest Service Old-Growth Wild-

TABLE 1.   Attributes of stands from five Oregon Cascades studies used in this analysis. Stand types are described in the text.

Attributes	High Cascades*	Snag†	Energy‡	Young Plantation§	OGWHS‖
Year sampled	1991	1991	1992	1992	1984
Elevation range (m)	731–1189	427–854	366–946	427–903	520–1073
Stand size (ha)	9–82	13–30	11–32	18–40	>20
		NUMBER OF STANDS (BY TYPE)			
Clearcut	4		4		
Retention	8	10	4		
Closed-canopy plantation				12	4
Commercial thin	4				
Natural young					3
Natural mature			4		7
Old growth					9
Total stands	16	10	12	12	19

* Hansen and Hounihan (1994).
† W. McComb et al. (*unpublished data*).
‡ Vega (1993).
§ W. McComb et al. (*unpublished data*).
‖ Gilbert and Allwine (1991).

life Habitat Study (OGWHS) (Ruggiero et al. 1991). Four managed mature stands also were sampled in 1984. The young and mature stands were primarily mesic in soil moisture, while the old-growth stands were selected to include dry, mesic, and wet sites. Vegetation attributes of these stands were quantified by Spies and Franklin (1991). We used data from 1984 for

the 19 stands sampled in the west-central Oregon Coast Range (Fig. 1).

The High Cascades study (Hansen and Hounihan 1995), conducted in 1991, examined bird response to the retention of canopy trees in harvest units. Included were 16 stands representing a gradient of densities of trees >10 cm diameter at breast height (dbh). Hereafter,
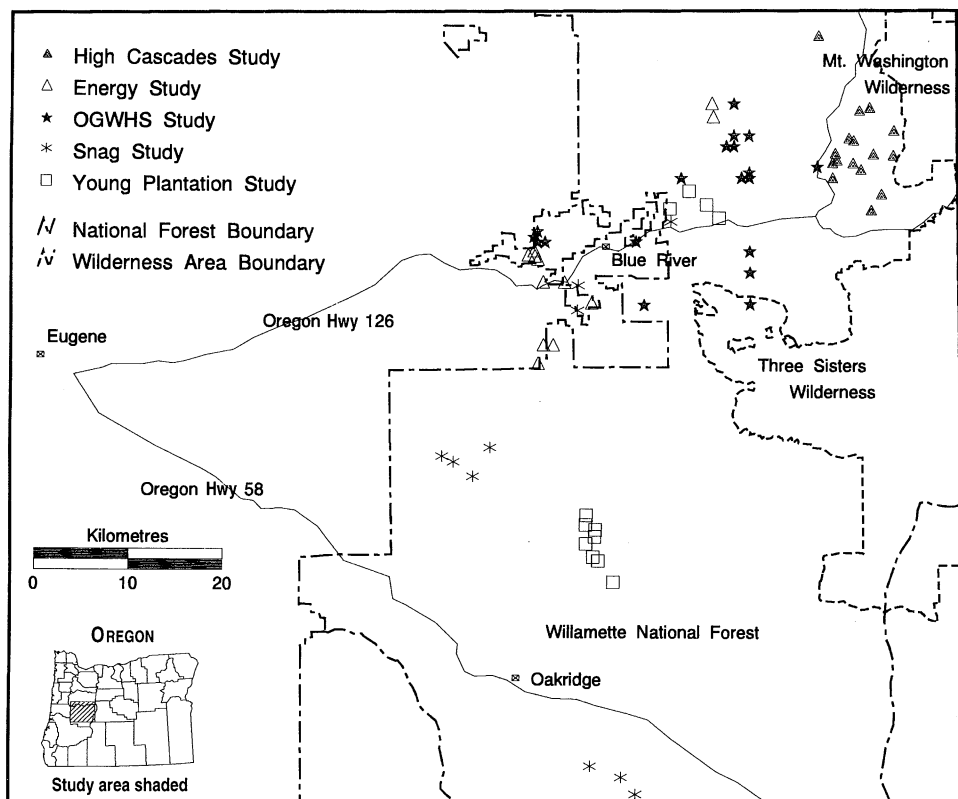

FIG. 1.   Locations of stands examined in the five Oregon Cascades studies analyzed.

"tree density" refers to trees >10 cm dbh. The stands included clearcuts (0 trees/ha), "retention" units (clearcuts where 2–14 trees/ha were retained), shelterwoods (10–33 trees/ha), and commercial thins where ≈87 trees/ha were retained. The clearcut, retention, and shelterwood sites had been harvested 2–6 yr earlier. The commercial thins were ≈80–100 yr old and had been thinned 6–12 yr prior to the study. These stands were located primarily at higher elevations in the Willamette National Forest on the fringe between the Western Cascades and High Cascades provinces.

In 1991, W. McComb et al. (*unpublished data*) did a related study (Snag) of breeding bird response to snag densities in harvest units. Although the sites were selected to represent a gradient of snag densities, they also differed in density of live trees. Included in our analysis are the 10 stands (3–56 trees/ha) they sampled across the Willamette National Forest.

The Energy study (Vega 1993), conducted in 1992, had a block design with three treatments (clearcut, retention of 4–13 trees/ha, and natural mature stands) and four replicates. The clearcut and retention sites had been harvested 2–6 yr prior to they study. The stands were located within the Blue River District of the Willamette National Forest and on adjacent private and Bureau of Land Management lands.

The final Young Plantation study (W. McComb et al., *unpublished data*) was designed as an experimental manipulation of thinning density in managed plantations 30–50 yr old. The data used here were collected in 1992 prior to the planned manipulation in the stands from the Oak Ridge and McKenzie Ranger Districts of the Willamette National Forest. Vegetation data were derived from stand examinations conducted by the USDA Forest Service.

Description of study area

The Western Cascades Province includes the topographically complex west slope of the Cascades Mountain in Oregon (Franklin and Dyrness 1973). The landforms were created by volcanic activity during the Oligocene and Miocene epochs. The present climate is wet (annual precipitation 150–300 cm) and mild (8°–9°C mean annual temperature), with most precipitation during winter and spring. The Province is within the Western Hemlock Vegetation Zone with dominant tree species including western hemlock (*Tsuga heterphylla*), Douglas-fir (*Pseudotsuga menziesii*), and western redcedar (*Thuja plicata*). Most of the stands used in this study lie within this zone.

Immediately to the east lies the High Cascades Province (Franklin and Dyrness 1973), a high-elevation plateau of volcanic origin (late Pliocene and Pleisotcene epochs) that straddles the Cascade crest. This province is cooler and wetter than the Western Cascades Province. A snow pack persists over much of the winter and spring. Ten of the stands used in this study lie between the Western Hemlock and Silver Fir Zones

(Franklin and Dyrness 1973). Dominant trees are Douglas-fir, western hemlock, grand fir (*Abies grandis*), noble fir (*A. procera*), and silver fir (*A. amabilis*).

The Willamette National Forest covers much of the west-central Oregon Cascades. Private timber companies also have major holdings here. Natural forests in the Willamette have been highly fragmented by clearcutting under a staggered-setting harvest design which is designed to distribute harvest units across the landscape (Spies et al. 1994). In recent years, new silvicultural designs have been implemented by the National Forest to include various levels of canopy trees, snags, and coarse woody debris retained following harvest (Swanson and Franklin 1992). Most of the private lands have been clear-cut and converted to short rotation plantations.

Bird and habitat sampling

The abundance of breeding birds was sampled in each study using the Variable Circular-Plot method (Reynolds et al. 1980). Plot centers were either 100 or 150 m apart (depending on the study) and ≥75 m from stand edges. Five to six plots were located in each stand, except for the OGWHS study, where 12 plots were sampled in each stand. The bird censuses began each day at first light and continued for ≈4 h. Observers walked to a plot center, waited 2 min, then recorded all birds seen or heard during an 8-min period. Bird species and distance from plot center were recorded. Observers rotated among plots and study sites to minimize bias. Each plot was censused 4–6 times during May and June of the years studied. The common names, scientific names, and codes for the bird species included in the analyses are in Table 2.

Habitat measurements were centered on the bird census plots. The variables measured and sampling methods differed among some of the studies. The methods used in the High Cascades, Snag, and Energy studies are described in Hansen and Hounihan (1995); Gilbert and Allwine (1991) and Spies and Franklin (1991) provide details on the OGWHS methods. Habitat data for the Young Plantation study were acquired from USDA Forest Service stand examinations; these were average tree density by size class for the bird census plots and several other sampling points within each stand. The only habitat data available for all five studies were tree densities across four size classes. Other important habitat data on shrubs, coarse woody debris, canopy cover, etc., were not available for all the studies and could not be used in the analyses. The four variables describing tree density by diameter class (dbh) were: TOT2 (10–30 cm); TOT3 (30–50 cm); TOT4 (50–90 cm); and TOT5 (>90 cm).

Data analyses

Only birds registered within 50 m of plot centers were included in the analyses. This prevented overlap in the areas covered from adjacent plots. Analysis of

TABLE 2.   Bird species detected in >14 of the 67 stands and considered in the analyses.

Species code	Common name	Latin name	No. of stands
AMRO	American Robin	*Turdus migratorius*	25
BGWA	Black-throated Gray Warbler	*Dendroica nigrescens*	15
BHGR	Black-headed Grosbeak	*Pheucticus melanocephalus*	16
BRCR	Brown Creeper	*Certhia americana*	28
CBCH	Chestnut-backed Chickadee	*Parus rufescens*	39
DEJU	Dark-eyed Junco	*Junco hyemalis*	61
GCKI	Golden-crowned Kinglet	*Regulus satrapa*	28
HAFL	Hammond's Flycatcher	*Empidonax hammondii*	32
HAWO	Hairy Woodpecker	*Picoides villosus*	17
HETH	Hermit Thrush	*Catharus guttatus*	15
HTWA	Hermit/Townsend's Warbler*	*Dendroica occidentalis* and *D. townsendi*	46
MGWA	MacGillivray's Warbler	*Oporornis tolmiei*	25
PSFL	Pacific-slope Flycatcher	*Empidonax difficilis*	33
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	19
RUHU	Rufous Hummingbird	*Selasphorus rufus*	21
SOSP	Song Sparrow	*Melospiza melodia*	15
STJA	Steller's Jay	*Cyanocitta stelleri*	28
SWTH	Swainson's Thrush	*Catharus ustulatus*	21
WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*	17
WEBL	Western Bluebird	*Sialia mexicana*	16
WETA	Western Tanager	*Piranga ludoviciana*	20
WIWA	Wilson's Warbler	*Wilsonia pusilla*	15
WIWR	Winter Wren	*Troglodytes troglodytes*	39

* These two species overlap and hybridize in the study area and are difficult to distinguish by song. Consequently, they were lumped in this study.

bird detection distance indicated that songs of the bird species examined in this study can be detected within 50 m (Vega 1993); thus we calculated the relative abundance of each species as the number of individuals registered within the 50-m radius plot surrounding the plot center. The results for each species were averaged over plots within a stand and across censuses and are reported as mean number of registrations per hectare per census. Only species detected in ≥15 stands were included in the analyses.

Tree density by dbh class also was averaged among plots within a stand and is expressed as trees per hectare. Three additional habitat variables were derived from the four dbh class variables. TOT2_5 is the density of trees with dbh >10 cm. DBHMEAN is the mean diameter for all trees with dbh >10 cm. This mean was calculated using the modal dbh within each size class (e.g., all trees within TOT2 were assigned a dbh of 20 cm). The modal dbh for TOT5 was assumed to be 130 cm. DBHSD is the standard deviation in dbh calculated using the modal dbh values. These variables were placed into one of two variable sets: TOT2, TOT3, TOT4, TOT5; and DBHMEAN, DBHSD, TOT2_5. In the first variable set, dbh classes were combined in habitat analyses for some species (TOT345=TOT3 +TOT4+TOT5; TOT45=TOT4+TOT5).

The bird abundance and habitat data from the five studies were merged into one data set. ANOVA and linear and nonlinear regression were used to quantify relationships between bird abundance and each of the habitat variables. These techniques assume that the residuals are independent and normally distributed with constant variance (Sabin and Stafford 1990). The data

were from nonadjacent stands assumed to be independent. Histograms of the error terms for the regressions between bird abundance and habitat variables revealed that the residuals were not normally distributed for some species. The variance of the residuals also was not constant for some species. Two stands with extremely high tree densities (both were young natural stands) were dropped from the analyses to improve the normality of the residuals. Also, log conversions [natural log(variable + 1)] of the bird abundance and/or the habitat variables were successful in correcting the deviations from normality and constant variance. An "L" at the end of a variable name denotes a log conversion (i.e., TOT2L).

We determined the relationship between bird abundance and stand type by first classifying each stand as clearcut, retention, closed-canopy plantation, natural mature, or old growth based on stand age and management history. Data from the four commercially thinned, mature stands were not included in the analysis. Differences in relative bird abundance among stand types were determined with ANOVA and multiple range tests (least significant difference test, SAS 1982). In order to reduce differences in sample sizes among stand types, we used the subset of retention sites that had 5–20 canopy trees/ha.

Regression models relating bird abundance to habitat were developed by first plotting the relative abundance of each species of bird against each individual habitat variable. Where the plots were generally linear, stepwise linear regression (holding $P = 0.05$) was used with each of the habitat variable sets to evaluate which variables contributed to significant models. Where the
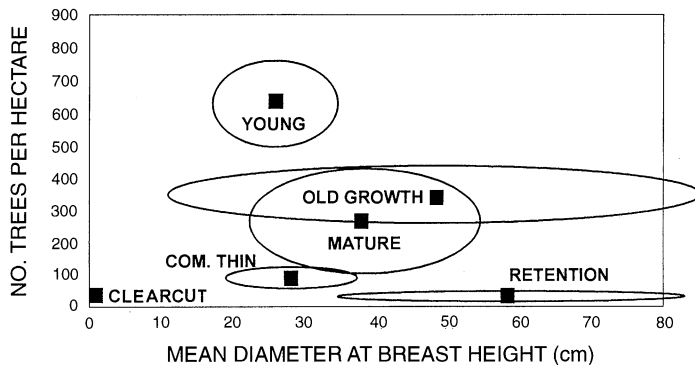
FIG. 2. Structural attributes of the stand types examined in this study. Closed squares represent means and open circles illustrate one standard deviation along each of the two axes. Young refers to closed-canopy plantation and young natural forest.

plots of bird abundance on habitat appeared nonlinear, the results of various polynomial and nonlinear functions were compared. These functions included second and third degree polynomial, Gaussian, Logistic, Lorentzian, and Extreme Value equations (TableCurve 1991). We selected "best" models and variable sets based on highest R^2 values and on the extent to which the models made sense ecologically for the bird species in question. The best models for a few species predicted nonsensical bird abundances (i.e., negative bird density) at extreme habitat values. For these species, we carefully defined the domain over which the function is realistic.

The habitat functions were tested in a simulation study (Hansen et al. 1995) that used a forest succession model to predict bird abundance in stands with different retention levels and rotation ages. The predicted abundances of most bird species appeared reasonable, based on our knowledge of their habitat associations. A few of the functions did not produce reasonable results; improved versions of these functions are reported here.

Data limitations

Data sets that are derived by merging the results of previous studies are likely to contain an unknown com-

ponent of variation due to differences among the studies. The studies we used sometimes differed in observers, geographic location of study sites, sampling effort (either number of plots within a stand or number of censuses), habitat sampling methods, and survey years. We carefully selected the studies to minimize such differences. Even so, this approach undoubtedly contributed an unknown amount of variation of the bird habitat relationships. Also, one important stand type was not included in the study: young stands (30–79 yr) with residual large trees (see *Discussion*). Finally, the differences in number of plot censused between the OGWHS and the four other studies precluded analyses of species richness and diversity across the stand types.

RESULTS

The five major stand types sampled represented a gradient in forest structure. Total tree density (TOT2_5) was lowest in clearcuts and retention sites, intermediate in mature and old-growth stands, and highest in young stands (Fig. 2 and Table 3). There was relatively little overlap in tree density among these stand types; TOT2_5 was <60 trees/ha in clearcut and retention sites, between 60 and 560 trees/ha in mature and old-growth stands, and >450 trees/ha in young stands. Both

TABLE 3. Age and habitat attributes of the stand types sampled in this study. Tree density (mean and range) is expressed by diameter class. TOT2_5 is total density of trees with dbh >10 cm. DBHMEAN is the mean diameter of all trees >10 cm dbh, calculated modally; DBHSD is the standard deviation using modal values.

| Stand type | Age (yr) | Trees per hectare by dbh class | | | | | DBH-MEAN | DBHSD |
		TOT2 (10–30 cm)	TOT3 (30–50 cm)	TOT4 (50–90 cm)	TOT5 (>90 cm)	TOT_5		
Clearcut	2–6	0.8 0–5.3	0	0	0	0.8 0–5.3	5.0	0
Retention	2–6	2.8 0–17.0	1.7 0–6.6	5.2 0–29.6	3.2 0–44.5	13.0 1.3–56.0	58.7	24.2
Young*	30–60	435 281.6–876.0	219.7 68.0–331.0	0.15 0–2.0	0	654.9 449.5–946.9	26.9	9.3
Comm. thin	80–100†	73.6 23.8–110.1	4.5 2.0–8.0	9.3 0–37	0	87.4 57.7–115.4	28.3	9.3
Mature	80–190	110.9 35.8–275	58.4 1.3–149.0	70.8 0–175.0	2.5 0–8.0	266.8 67.7–558.0	36.7	16.9
Old growth	200–450	191 52.0–311.0	53.1 16.0–79.0	39.1 16.0–58.0	51.0 15.0–98.0	334.2 185.0–442.0	48.1	38.0

* Includes closed-canopy plantation and young natural stands.
† Commercially thinned 6–12 yr ago, now 80–100 yr of age.

TABLE 4. Results of ANOVA and multiple range tests for relative abundance of bird species across the five stand types. Numbers of stands used in the analysis are in parentheses under the stand types. Bird abundance is expressed as mean registrations per census per ha across each stand type. Data values with different superscripts within a row differ significantly ($P < 0.05$). Those with identical superscripts within a row do not differ significantly. Codes for bird species are defined in Table 2.

| | Bird abundance by stand type: | | | | | | | |
Species code	Clearcut (8)	Retention (11)	Young* (12)	Mature (11)	Old growth (9)	R^2	F	P
AMRO	0.08	0.08	0.00	0.02	0.06	.13	1.7	0.1600
BGWA	0.00[a]	0.00[a]	0.16[b]	0.02[a]	0.03[a]	.34	5.9	0.0006
BHGR	0.00	0.02	0.07	0.04	0.01	.16	2.2	0.0850
BRCR	0.00[a]	0.01[a]	0.01[a]	0.16[b]	0.23[c]	.69	25.7	0.0001
CBCH	0.00[a]	0.13[ab]	0.25[b]	0.72[c]	1.38[d]	.71	28.6	0.0001
DEJU	0.91[a]	0.65[a]	0.25[b]	0.11[b]	0.22[b]	.53	12.7	0.0001
GCKI	0.00[a]	0.01[ab]	0.47[c]	0.10[b]	0.01[ab]	.70	27.1	0.0001
HAFL	0.00[a]	0.01[a]	0.01[a]	0.53[b]	0.40[b]	.67	18.6	0.0001
HAWO	0.02[a]	0.11[b]	0.01[a]	0.02[a]	0.04[a]	.24	3.7	0.0100
HETH	0.00[a]	0.00[a]	0.22[b]	0.02[a]	0.03[a]	.49	11.0	0.0001
HTWA	0.01[a]	0.05[a]	0.96[b]	0.98[b]	1.13[b]	.65	20.9	0.0001
MGWA	0.28[a]	0.40[a]	0.03[b]	0.00[b]	0.00[b]	.41	8.2	0.0001
PSFL	0.00[a]	0.00[a]	0.27[b]	0.15[c]	0.40[b]	.62	19.2	0.0001
RBNU	0.01	0.03	0.63	0.03	0.03	.06	0.7	0.5900
RUHU	0.08[a]	0.08[a]	0.03[a]	0.00[b]	0.00[b]	.20	2.9	0.0300
SOSP	0.07	0.04	0.03	0.00	0.00	.16	2.1	0.0900
STJA	0.01[a]	0.08[bc]	0.03[ab]	0.00[a]	0.09[c]	.29	4.6	0.0030
SWTH	0.03[a]	0.00[a]	0.29[b]	0.06[a]	0.02[a]	.66	22.1	0.0001
WCSP	0.34[a]	0.09[ab]	0.00[b]	0.00[b]	0.00[b]	.23	3.4	0.0160
WEBL	0.02[a]	0.11[b]	0.00[a]	0.00[a]	0.00[a]	.38	7.0	0.0002
WETA	0.02[a]	0.08[b]	0.02[a]	0.02[a]	0.00[a]	.23	3.6	0.0100
WIWA	0.02	0.00	0.03	0.06	0.01	.10	1.2	0.3000
WIWR	0.00[a]	0.05[a]	0.60[b]	0.69[b]	0.82[b]	.67	24.2	0.0001

* Young refers to closed-canopy plantation.

DBHMEAN and DBHSD increased with stand age, except that both were relatively high in retention sites. Young stands were dominated by trees <50 cm dbh (TOT2 and TOT3), while all size classes were well represented in mature and old-growth stands. Thus, structural complexity as measured by variation in tree size was lowest in clear-cut and young stands and highest in retention, mature, and old-growth stands.

At least 64 species of birds were registered across the 67 stands. The data set we used from the OGWHS included only species that were registered in at least two stands. Thus, the total number detected across the five studies may have been slightly >64 species. Most of these were uncommon; only 23 species were sampled in ≥15 stands (Table 2). Eighteen of these species differed significantly in distribution among the stand types (Table 4). The following species were uniquely associated with particular stand types: Brown Creeper, Chestnut-backed Chickadee, and Hammond's Flycatcher (mature and old-growth); Black-throated Gray Warbler, Golden-crowned Kinglet, Hermit Thrush, and Swainson's Thrush (closed-canopy plantations); Western Bluebird and Western Tanager (retention sites). Dark-eyed Junco, MacGillivray's Warbler, and White-crowned Sparrow were more abundant in clear-cut and retention sites than in the other stand types.

Statistically significant habitat functions were generated for 17 of these 23 species (Table 5). Hairy Woodpecker, one of these species, was omitted from further consideration because it is strongly influenced by snag density, a variable not evaluated in this study. Five of the species not showing significant relationships (Black-throated Gray Warbler, Red-breasted Nuthatch, Rufous Hummingbird, Song Sparrow, and Wilson's Warbler) were detected in <22 stands. Each of these was most abundant in particular stand types, and larger sample sizes would likely reveal significant habitat relationships. In contrast, the density of Steller's Jay, detected in 28 stands, was highly variable within each of the stand types.

The ANOVA and regression analyses suggested four habitat-use guilds among the species: open-canopy; open-canopy with large dispersed trees; structurally complex closed-canopy; and structurally simple closed-canopy. The open-canopy guild included American Robin, Dark-eyed Junco, and White-crowned Sparrow. The abundance of these species had a negative logistic relationship with TOT2.5L (Table 5). Each of these species was most abundant in clearcuts and their densities dropped dramatically with increasing tree density. White-crowned Sparrow was not found in sites with >30 trees/ha. American Robin was generally absent from stands with >450 trees/ha (Fig. 3). Dark-eyed Junco was moderately abundant across all tree densities (Fig. 4).

Three species were primarily associated with retention stands: MacGillivray's Warbler, Western Bluebird, and Western Tanager (Figs. 5–7). Densities of these

TABLE 5. Habitat functions for the 17 species of birds showing significant habitat associations among the 67 stands sampled. LOG denotes natural log; conversions were done as LOG(response variable + 1). For all species, if $LOG(Y) < 0$ then $LOG(Y) = 0$. Codes for bird species are defined in Table 2.

Species	Function	R^2	F	P	Notes
AMRO	$LOG(Y) = 9.932/(1 + 105.720 \times EXP(.220 \times TOT2\_5L))$	.09	9.5	0.001	If $TOT2\_5L > 6.1$ then $LOG(Y) = 0$
BHGR	$LOG(Y) = .0061 + .00013 \times TOT2$	.19	15.0	0.0002	
BRCR	$LOG(Y) = .0309 + .00055 \times TOT4 + .0024 \times TOT5$	.35	17.4	0.0001	If $LOG(Y) < 0.031$ then $LOG(Y) = 0$
CBCH	$LOG(Y) = -.0499 + .0672 \times TOT3L + .0510 \times TOT4L + .0760 \times TOT5L$	.58	28.7	0.0001	
DEJU	$LOG(Y) = .5651 - .0654 \times TOT2\_5L$	.36	36.5	0.0001	
GCKI	$LOG(Y) = .3578/(1 + 6375.52 \times EXP(-.0183 \times TOT2\_5))$	.42	29.7	0.0001	
HAFL	$LOG(Y) = .0395 - .2445 \times TOT2\_5L + .1374 \times TOT2\_5L^2 - .0152 \times TOT2\_5L^3$	.45	17.4	0.0001	If $TOT2\_5L < 1$ then $LOG(Y) = 0$
HAWO	$LOG(Y) = .0183 + .2654 \times EXP((-EXP(-((TOT2\_5L - 1.438)/.3915))) - ((TOT2\_5L - 1.437)/.3915) + 1)$	.50	24.6	0.001	If $TOT2\_5L > 6.2$ then $LOG(Y) = 0$
HETH	$LOG(Y) = .2534/(1 + 934.65 \times EXP(-.0118 \times TOT2\_5))$	.47	26.2	0.0001	If $TOT2\_5 < 275$ then $LOG(Y) = 0$
HTWA	$LOG(Y) = .1306 + .0022 \times TOT3 + .0034 \times TOT4 + .0032 \times TOT5$	.54	24.4	0.0001	If $TOT2\_5 = 0$ then $LOG(Y) = 0$
MGWA	$LOG(Y) = .0149 + .3142 \times EXP(-.5 \times ((TOT2\_5L - 2.4253)/-.9752)^2)$	.35	15.3	0.001	If $TOT2\_5L > 5$ then $LOG(Y) = 0$
PSFL	$LOG(Y) = .0030 + .0003 \times TOT2 + .0005 \times TOT3 + .0007 \times TOT4 + .0037 \times TOT5$	.67	31.7	0.0001	If $TOT2\_5 < 25$ then $LOG(Y) = 0$
SWTH	$LOG(Y) = .2443/(1 + 1654.04 \times EXP(-.01635 \times TOT2\_5))$	.54	39.4	0.0001	
WCSP	$LOG(Y) = .0142/(1 - .9486 \times EXP(-.1430 \times TOT2\_5L))$	.24	15.0	0.001	If $TOT2\_5L >= 3.4$ then $LOG(Y) = 0$
WEBL	$LOG(Y) = .0102 + .1442 \times EXP(-.5 \times ((TOT2\_5L - 1.7630)/.5240)^2)$	.26	9.2	0.001	If $TOT2\_5L > 4.2$ then $LOG(Y) = 0$
WETA	$LOG(Y) = .0068 + .0680 \times TOT2\_5L - .0213 \times TOT2\_5L^2 + .0017 \times TOT2\_5L^3$	.18	4.7	0.02	If $TOT2\_5 = 0$ then $LOG(Y) = 0$ If $TOT2\_5L > 6$ then $LOG(Y) = 0$
WIWR	$LOG(Y) = .0574/(1 + 333.86 \times EXP(-1.549 \times TOT345L))$	.61	80.0	0.001	If $TOT2\_5 < 3.3$ then $LOG(Y) = 0$

birds were parabolically related with TOT2_5L within the range of 1–150 trees/ha (Table 5). The curves peaked at ≈ 4 trees/ha for Western Bluebird and at ≈ 10 trees/ha for MacGillivray's Warbler and Western Tanager.

The third guild was most abundant in mature and old-growth stands and was positively associated with the larger tree size classes. Brown Creeper, Chestnut-backed Chickadee, and Hammond's Flycatcher had low densities in young stands (Table 4). Most were not detected in retention stands with TOT2_5 <8 trees/ha. Brown Creeper, a bark gleaner, was linearly associated
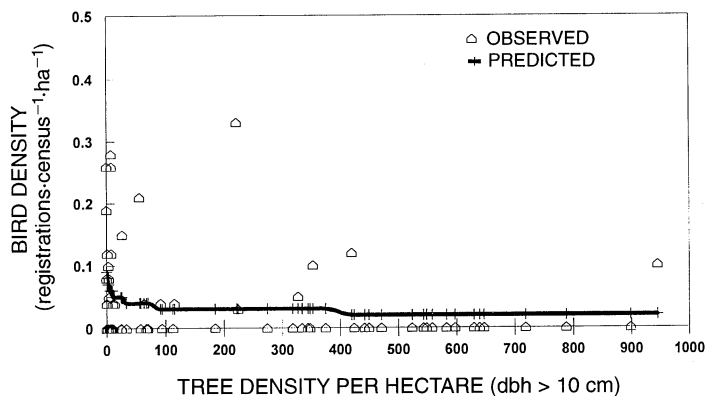
AMERICAN ROBIN

FIG. 3. Observed and predicted relationships between American Robin density and tree density (TOT2_5) across 67 stands in the central Oregon Cascades. The predicted relationship is based on the function listed for this species in Table 5.
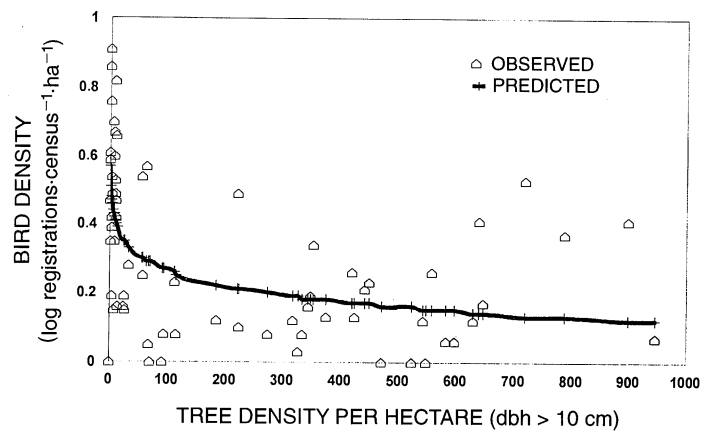
DARK-EYED JUNCO

FIG. 4. Observed and predicted relationships between Dark-eyed Junco density and tree density (TOT2_5) across 67 stands in the central Oregon Cascades. The predicted relationship is based on the function listed for this species in Table 5.

with TOT4 and TOT5 and was barely present in stands with TOT2_5 <10 trees/ha or >550 trees/ha. Chestnut-backed Chickadee was associated with TOT3L, TOT4L, and TOT5L. It was not present in stands with TOT2_5 <12 trees/ha, but was moderately dense in young stands with high tree densities. Hammond's Flycatcher density was related to TOT2_5L with a third degree polynomial function that was positive between ≈8 and 950 trees/ha. This bird was relatively sparse at tree densities <60 trees/ha and >600 trees/ha; it peaked in mature and old-growth stands where TOT2_5 was relatively low (Fig. 8). Hermit/Townsend's Warbler, Pacific-slope Flycatcher, and Winter Wren were most abundant in mature and old-growth stands, but were also relatively common in young stands. Pooled Hermit and Townsend's Warbler density was linearly related to TOT3, TOT4, and TOT5. These species were present in retention stands with low tree densities. The best model for Pacific-slope Flycatcher was linear and included all four tree size classes. This species was not detected in stands where TOT2_5 was <60 trees/ha.

Winter Wren was best described by a positive logistic model on TOT345L. The relationship reached a plateau at a level of TOT345 ≈150 trees/ha. The species was relatively abundant in all stands except those with TOT2_5 <50 trees/ha.

The final guild included birds that were linearly associated with small and intermediate sized trees and that reached peak densities in young stands. Present in this guild were Black-headed Grosbeak, Black-throated Gray Warbler, Golden-crowned Kinglet, Hermit Thrush, and Swainson's Thrush (Table 4). Black-headed Grosbeak was positively related to TOT2, but did not differ significantly among stand types in the ANOVA. Black-throated Gray Warbler was significantly more abundant in young stands in the ANOVA but did not have a significant regression model. Golden-crowned Kinglet, Hermit Thrush, and Swainson's Thrush (Fig. 9) had a positive logistic relationship with TOT2_5.

The strengths of these bird–habitat relationships generally increased with bird sample size. The bird species with the highest R^2 values (0.35–0.67) were detected
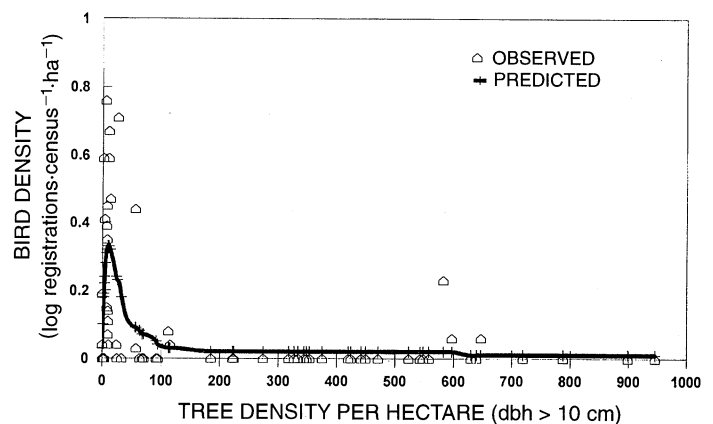
MACGILLIVRAY'S WARBLER

FIG. 5. Observed and predicted relationships between MacGillivray's Warbler density and tree density (TOT2_5) across 67 stands in the central Oregon Cascades. The predicted relationship is based on the function listed for this species in Table 5.
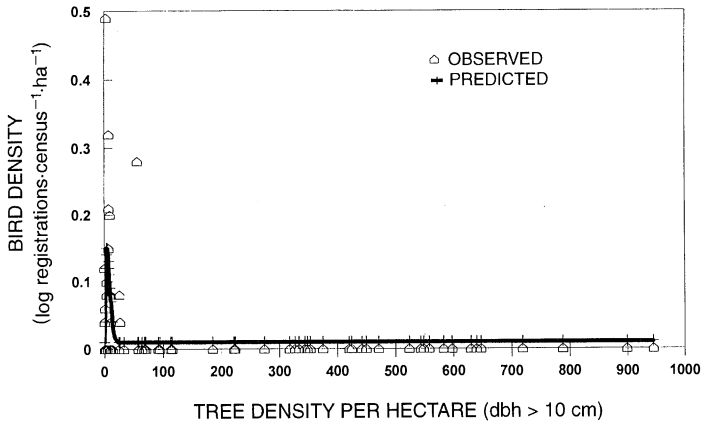
WESTERN BLUEBIRD

FIG. 6. Observed and predicted relationships between Western Bluebird density and tree density (TOT2_5) across 67 stands in the central Oregon Cascades. The predicted relationship is based on the function listed for this species in Table 5.

in ≥25 stands (Tables 2 and 4). Hermit Thrush and Swainson's Thrush were exceptions; they had R^2 values of 0.47 and 0.54 but were detected in only 15 and 21 stands, respectively.

DISCUSSION

Limitations of the study design

Our goal was to determine bird abundance in canopy retention sites relative to other common stand types in the PNW and to develop habitat functions for extrapolating bird abundance across current and future landscapes. Data from a single, large, well-designed study were not available, so we used the results of five previous studies that were similar in methods, sampling intensity, and geographic location. In spite of careful selection, differences among the studies probably contributed an unknown amount of variation to our results. Differences in sampling years may be especially important. It is our experience that bird abundances can differ substantially between years due to weather and other factors. Data from each of the studies were from a single breeding season, and the year differed among

studies. Most of the mature and old-growth stands used in this study were censused in 1984 (OGWHS), while the other stand types were sampled in 1991 and 1992. We have no means of determining if breeding bird densities were especially high or low during any of these years.

The studies also differed in observers. All the observers underwent careful training, however, and it is not likely that there were major differences in the abilities of the observers to detect the more abundant bird species analyzed in this study. A third difference among studies was in sampling effort. The OGWHS used about twice as many census plots per stand as the other studies. This undoubtedly allowed more of the rare birds to be detected, but probably did not influence detection rates for the more abundant species considered in our analyses. Finally, the stands sampled in each study may have been biased in geomorphic or landscape context. We did select studies that were similar in elevation range and geographic location, but no attempt was made to control for aspect or landscape patterning of the neighborhood.
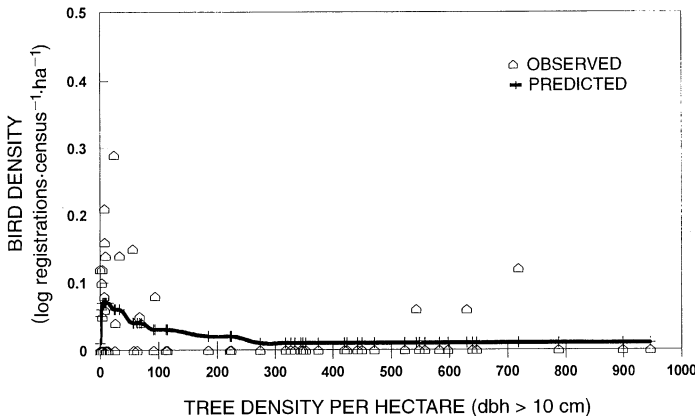
WESTERN TANAGER

FIG. 7. Observed and predicted relationships between Western Tanager density and tree density (TOT2_5) across 67 stands in the central Oregon Cascades. The predicted relationship is based on the function listed for this species in Table 5.
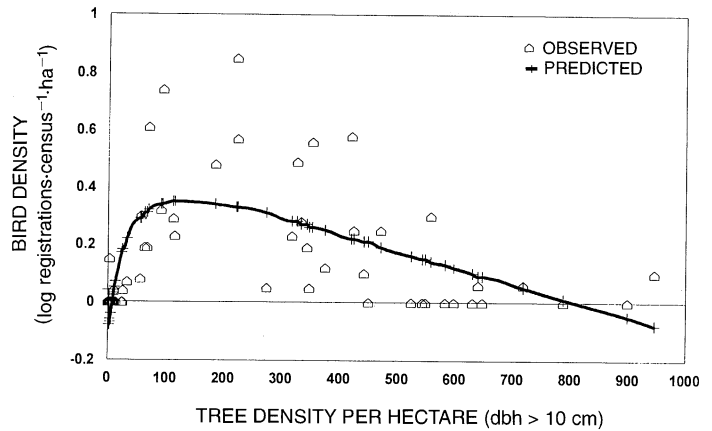
HAMMOND'S FLYCATCHER

FIG. 8. Observed and predicted relationships between Hammond's Flycatcher density and tree density (TOT2_5) across 67 stands in the central Oregon Cascades. The predicted relationship is based on the function listed for this species in Table 5.

In spite of these potential sources of variation, the abundances of most bird species across stand types were surprisingly consistent with previous studies. In total, we feel the approach was reasonably successful and allowed, for the first time in the region, an examination of a large number of canopy tree retention sites relative to other stand types and the generation of bird habitat functions across this range of natural and managed stand types.

Stand types and regression variables

The value of retaining canopy trees in harvest units can best be evaluated by drawing comparisons with other common stand types. Natural forests in the PNW are dominated by structurally complex young (30–80-yr-old), mature (80–200-yr-old), and old-growth (>200-yr-old) stands (Spies and Franklin 1991). The latter two stand types were well represented in our study. Bird habitat studies have not yet been done in natural, structurally complex young stands in the PNW, and thus, could not be considered here. Clear-cutting has been the favored timber harvest system in the PNW

since modern logging began in the 1950s. The oldest of these stands have now achieved canopy closure. This paper is the first to compare bird abundance in these structurally simple stands with that in natural forests. Canopy tree retention harvest systems have been widespread in the PNW for the last 5–7 yr. Thus, we could examine only relatively young retention units. The habitat value of these stands after they achieve canopy closure is still unknown.

The habitat variables we selected for developing the bird habitat functions were based on tree density by diameter class. This was done for several reasons. These data were available for each of the five studies. Moreover, these variables are likely to be available for other stands, allowing the habitat functions to be used to predict bird abundance in other landscapes. Thirdly, previous studies have found that these variables explain relatively large amounts of variation in bird abundance and are correlated with other important habitat attributes, e.g., canopy cover, understory cover, and foliage height diversity (Marcot 1984, Hansen and Hounihan 1995).
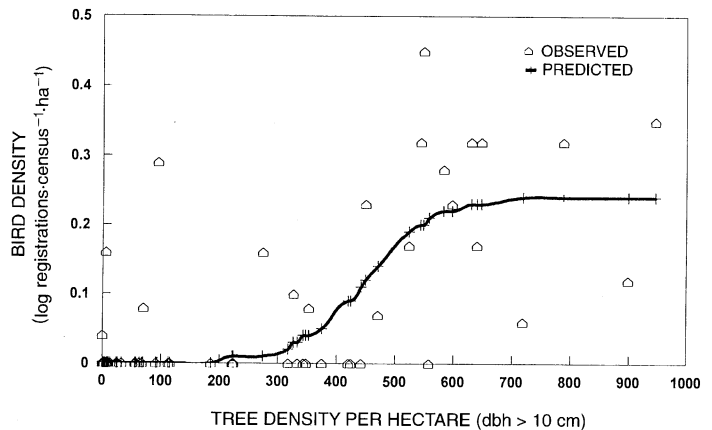
SWAINSON'S THRUSH

FIG. 9. Observed and predicted relationships between Swainson's Thrush density and tree density (TOT2_5) across 67 stands in the central Oregon Cascades. The predicted relationship is based on the function listed for this species in Table 5.

When possible, it is clearly desirable to consider a wide range of habitat variables in assessing animal habitat relationships (e.g., stand and landscape scale geomorphic, climate, and vegetation variables). Doing so in this study might have improved our analysis of some of the habitat relationships. However, our results indicate that tree density by size class was strongly associated with the abundance of several bird species. The fact that land managers can easily manipulate tree size class distribution makes these habitat measures additionally useful for conservation and management.

Two groups of tree density variables were analyzed in this study: tree density in each of the four size classes (TOT2, TOT3, TOT4, TOT5); and total tree density (TOT2_5), mean dbh (DBHMEAN), and variation in dbh (DBHSD). Neither DBHMEAN nor DBHSD was selected in the stepwise regressions for any of the bird species. These variables were related to the abundance of some bird species, but typically in a nonlinear fashion. In these cases, the first variable set was associated with more of the variation than the second. The fact that DBHMEAN and DBHSD were calculated using modal values of each diameter class probably reduced their utility in this study.

Habitat use and natural history of bird species

The bird habitat relationships found here are generally consistent with those in previous studies and are interpretable based on the natural history of many of the species. The open-canopy species, Dark-eyed Junco and White-crowned Sparrow, feed and nest on or near the ground of open, shrubby habitats (Morrison and Meslow 1983). The American Robin often feeds on the ground where there is little understory biomass. All three species were found to be negatively associated with tree density by Marcot (1984) and Hansen and Hounihan (1995). Vega (1993) found that the Lazuli Bunting showed a similar pattern, although the sample size was too small to allow inclusion of this species in our analysis. These species may avoid open stands with canopy trees either because nest predation rates are elevated in such stands, or because overstory cover may reduce primary productivity and food availability for these species (Vega 1993, Hansen et al. 1994). These findings are important in suggesting that not all open-canopy bird species benefit from canopy tree retention.

Open-canopy habitats with large trees have not been well studied in the region, and these results are the first to associate MacGillivray's Warbler, Western Bluebird, and Western Tanager with this habitat type. MacGillivray's Warbler is a foliage gleaner often associated with shrubs (Morrison and Meslow 1983, Marcot 1984). We also observed it foraging in the canopies of dispersed conifers, and this may explain its greatest abundance in the retention stands. The Western Tanager is an aerial-sallying insectivore that is often seen high in the canopies of edge habitats. It is also known to be associated with deciduous tree volume in conifer-dominated stands (Marcot 1984). The Western Bluebird forages from low perches and on the ground where understory is sparse (Marcot 1984). It may have been more abundant in retention than in clear-cut stands because of the greater abundance of low perches. Another possibility is that coarse woody debris, which this bird uses for nesting, was more prevalent in retention stands. The existence of this guild is evidence in support of the practice of retaining canopy trees in harvest units.

The guild found in structurally complex closed-canopy habitats is well-studied and has been the focus of conservation interests. The abundances of Brown Creeper, Chestnut-backed Chickadee, Hammond's Flycatcher, Pacific-slope Flycatcher, and Winter Wren have been correlated with attributes of older natural forests, such as large trees, large snags, and/or western hemlock trees (Carey et al. 1991, Gilbert and Allwine 1991, Manuwal 1991). The Hermit/Townsend's Warbler is somewhat intermediate in association between this guild and the structurally simple closed-canopy guild. It has been found to reach peak abundances in young and mature natural forests in Oregon and Washington (Carey et al. 1991, Gilbert and Allwine 1991), especially in stands with canopy gaps (A. J. Hansen et al., *unpublished data*). However, it is also extremely abundant in older managed plantations. Our results suggest that the Pacific-slope Flycatcher and Winter Wren are not uniquely associated with late-seral natural forest, and are also abundant in closed-canopy plantations.

Included in the structurally simple closed-canopy guild are three canopy gleaners (Black-headed Grosbeak, Black-throated Gray Warbler, and Golden-crowned Kinglet) and two ground-foraging insectivores (Hermit Thrush and Swainson's Thrush). The Black-headed Grosbeak has been associated with canopy volume of deciduous and coniferous trees (Marcot 1984), and Golden-crowned Kinglet with conifer density (Marcot 1984, Hansen and Hounihan 1995). Hermit and Swainson's Thrushes are strongly associated with this habitat type, probably because the dense overstory inhibits understory development, allowing these birds access to litter and soil invertebrates.

Effect of canopy tree retention on avian habitats

The results suggest that several species of birds benefit from the retention of canopy trees in harvest units. MacGillivray's Warbler, Western Tanager, and Western Bluebird were primarily associated with retention stands. Also, the four species associated with late-seral stands were not found in clearcuts, but occurred at low densities in the retention stands. Although data are not available for retention stands that have achieved canopy closure, results from a simulation study indicated that the abundance of these late-seral birds will increase

in retention stands following canopy closure and exceed that in clear-cut stands for the first 100 yr following harvest (Hansen et al. 1995).

This combination of late-seral species and retention specialists explains the higher bird species richness and diversity in retention stands than in clearcuts found by Hansen and Hounihan (1995). The simulation study predicted that bird richness would remain significantly higher in retention stands than in clearcuts for 140 yr following harvest (Hansen et al. 1995). Vega (1993) also found bird richness to be higher in retention stands than in clearcuts, but the difference was not statistically significant.

Some of the ecological mechanisms that may underlie these patterns of bird diversity were examined by Hansen et al. (1994). They found that vertical habitat complexity increased with canopy tree density, possibly explaining the positive relationship between overstory bird diversity and canopy tree density. The abundance of relatively palatable plants, however, may be inversely related to canopy tree density. These plants may fuel a food web that enhances the diversity of understory birds in open-canopy stands. Patterns of bird diversity in PNW forests are likely to reflect complex interactions among energy availability, complexity of habitats for nesting, refuging, and feeding, and the life history strategies of the bird species in the community.

Our data on bird abundance across stand types need to be taken with caution because we do not know if bird abundance is positively correlated with survival and reproduction levels in these stands. Vega (1993) found that artificial bird nests placed at shrub height in retention stands had significantly higher predation rates than those in clearcuts or mature forests. These canopy trees amy serve as perches, allowing nest predators to more easily locate prey nests. This may explain why species that nest on or near the ground, like Lazuli Bunting and White-crowned Sparrow, are much more abundant in clearcuts than in retention stands. More research is needed to determine how the fitness of bird species occurring in retention stands compares with that in other stand types.

Management implications

These results and those of Vega (1993), Hansen and Hounihan (1995), and Hansen et al. (1995) suggest that retaining canopy trees in managed stands enhances structural complexity and provides habitat for many native bird species in the PNW. Some species, however, were negatively associated with canopy tree density, and some other species were primarily associated with closed-canopy plantations. Clearly, no single silvicultural strategy will provide suitable habitat for all species. Moreover, the relationship between bird abundance and canopy density was nonlinear for most species. Thresholds were apparent where small changes

in tree density were associated with large changes in bird abundance.

These individualistic, nonlinear responses of bird species to canopy retention levels emphasize the importance of setting specific management objectives. Managing for "biodiversity" is a hollow goal. Any management action will benefit some species and hinder others. Managers should carefully evaluate which species or community attributes they are most concerned with and design silvicultural strategies accordingly.

Where the goal is to maintain habitats for all native bird species, our results indicate that a range of canopy tree densities and size class distributions should be maintained across the landscape. For example, harvest units retaining <4 trees/ha should provide primary habitats for the open-canopy, structurally simple bird guild. The guild specializing on retention stands will likely achieve peak abundances where ≈4–15 trees/ha are retained. The mature and old-growth bird guild will most benefit from much higher levels of retention. We do not recommend maintaining the even-aged, closed-canopy plantations that are produced by traditional silvicultural practices. The guild of birds reaching peak abundance in this stand type is also numerous in mature and old-growth forest. Moreover, we suspect this guild will be well represented in retention stands after they achieve canopy closure.

Managing for this suite of stand types should accommodate open-canopy specialists as well as species requiring structurally complex stands. Further work is needed, however, to better define the distribution of tree densities and size classes that best promote various biodiversity goals. More study is also needed on the consequences of alternative silvicultural strategies for other taxonomic groups and for socioeconomic considerations.

Application of habitat functions

The habitat functions reported here can be used to predict bird species abundance under alternative land use and climate scenarios (Pulliam et al. 1992, Hansen et al. 1993). The functions could be used with extensive field data such as the USDA Forest Service Continuous Forest Inventory data (Ohmann 1990) to predict bird abundance across current landscapes. Fine-scale vegetation structure can also be quantified from satellite imagery (Cohen and Spies 1992), allowing bird abundance to be extrapolated across subregional landscapes. These habitat functions can also be used in conjunction with computer simulation models to predict forest dynamics and bird diversity under alternative silvicultural strategies (Hansen et al. 1993, 1995).

Caution should be exercised in such applications, however. *The habitat use of some species varies considerably across the region.* For example, the Hermit Warbler was found to be positively correlated with stand age in natural forests in northwestern California

(Ralph et al. 1991), and negatively correlated with stand age in southwestern Washington (Manuwal 1991). Thus, the goegraphic domain of the functions may be limited, and their application to areas other than the west central Oregon Cascades carries an unknown risk of error.

Care is also needed in extrapolating these results to stand types other than those sampled here. Neither closed-canopy plantations with residual large trees nor heavily thinned plantations were considered here. Both stand types are likely to become more common in the PNW in the future.

Another important limitation is that the functions are based only on stand scale measurements of vegetation structure. Other habitat characteristics, such as primary productivity, geomorphology, hydrology, and disturbance history, may also influence habitat quality. Moreover, the main determinants of habitat quality probably vary with spatial and temporal scale, necessitating habitat measurements across a range of scales (Hansen et al. 1993). Unfortunately, such data are not presently available for other than a few well-studied species in the region. Until more such studies are completed, we suggest that it is better to use best current knowledge (e.g., the habitat functions presented here) in management decisions that not to evaluate habitat quality at all. Field studies designed to validate the habitat functions are recommended to ascertain the applicability of the functions to any particular management area.

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