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Final
8/29/02

RELATIONSHIPS BETWEEN FOREST STRUCTURE AND BREEDING BIRD ABUNDANCE IN THE SOUTHWEST CASCADE MOUNTAINS OF WASHINGTON

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Abstract. Understanding the influence of stand structure on the distribution and abundance of breeding avifauna is critical if forests are to be managed with the needs of birds in mind. To this end, we conducted a two-year study (1998–1999) of breeding bird communities in Douglas-fir (*Pseudostuga menziesii*) - Western Hemlock (*Tsuga heterophylla*) forests in the southwest Cascade Mountains of Washington to assess relationships between relative avian abundance and the structural attributes of forest stands. Our specific study objectives were to: (1) describe bird use of three forest treatments that reflected distinct management histories; (2) identify species assemblages with similar distributions among forest stands; and (3) model species-specific bird-habitat relationships. To achieve these objectives, we sampled 12 forest stands that were classified into one of three common forest treatments on the southwest Cascade Mountains landscape: (1) 8- to 12-year-old regenerating clearcuts ($n = 4$ stands); (2) 40- to 60-year-old managed forest that had been commercially thinned, but not yet clear-cut harvested ($n = 4$ stands); and (3) 150- to 270-year-old mature, naturally regenerated old growth forest ($n = 4$ stands). In each stand, breeding birds were surveyed using fixed-radius point counts in each year of study, and forest structure was measured using an intensive sampling protocol at each point-count location.

Of 81 species recorded, 28 were detected >10 times in each year and therefore retained for further analyses. Seventeen species (61%) differed significantly ($P < 0.05$) in their relative abundance among forest treatments. We used cluster analysis (Ward's minimum-variance linkage method) to further describe breeding bird assemblages and identified three distinct groups of species with similar distributions among forest stands: "clearcut associates", such as the Song Sparrow (*Melospiza melodia*), Orange-crowned Warbler (*Vermivora celata*), and Willow Flycatcher (*Empidonax trailii*); "commercial thin associates", such as

Hermit/Townsend's Warbler (*Dendroica occidentalis/townsendi*) and Gray Jay (*Nucifraga columbiana*); and "old growth associates", such as the Brown Creeper (*Certhia americana*), Varied Thrush (*Ixoreus naevius*), and Golden-crowned Kinglet (*Regulus satrapa*). Community indices (avian abundance and species richness) tended to be highest in clearcuts, moderate in commercial thins, and lowest in old growth, but the differences were not statistically significant ($P = 0.05$ and 0.07, respectively).

Differences in stand structure were reflected by several strong habitat gradients (e.g., canopy cover, density of large-diameter trees, density of shrubs, and amount of coarse woody debris) across forest treatments. We used the information-theoretic approach and Akaike's information criterion to build species-specific habitat models for 19 bird species and explained an average of 67% of the variation in relative avian abundance using a reduced set of habitat variables. In particular, robust models were derived for the American Robin (*Turdus migratorius*; $R^2 = 0.96$), Willow Flycatcher ($R^2 = 0.94$), Song Sparrow ($R^2 = 0.87$), Orange-crowned Warbler ($R^2 = 0.87$), and Winter Wren (*Troglodytes troglodytes*; $R^2 = 0.87$). Overstory canopy cover was an especially important habitat variable, appearing in the models of 11 (39%) species. Other significant variables included density of shrubs (especially for ground-nesting birds), percent cover of berry-producing shrubs (especially for fruit-eating birds), and density of large-diameter coniferous trees (for mature forest associates). Our results suggest that numerous bird species in Douglas-fir - Western Hemlock forests of the southwest Cascade Mountains are strongly associated with specific habitat attributes, many of which we have identified in this paper. Implications of our results for forest management include that changes in the amount of overstory cover will have the greatest influence on birds. Where canopy cover is reduced below, or increased above, a threshold level of approximately 25–50% cover, we offer insights into which species of breeding birds will change in occurrence or density.

Key words: avian abundance, bird-habitat relationships, canopy cover, forest avifauna, songbirds, forestry, habitat, old growth forest, silviculture.

INTRODUCTION

It is well known that North American forests provide important breeding and wintering habitat for many bird species (DeGraaf et al. 1991, Rappole 1996). Such forests are not only important to birds, but also for meeting the increasing demands for wood products, recreation, and aesthetic values of an ever-expanding human population. Given these demands, management of forests is inevitable, widespread, and generally increasing in intensity (Sallabanks et al. 2001). While there have been numerous studies on the effects of timber harvest on bird populations, relatively few studies have identified specific relationships between structural attributes within forest stands and the distribution and abundance of bird species or species' groups (Sallabanks et al. 2000). Without knowledge of which stand structures potentially operate as proximate mechanisms driving the abundance of bird species, effective management recommendations lack an empirical basis for implementation (Marzluff et al. 2000, Sallabanks et al. 2000).

In the Pacific Northwest, several studies have described general associations between birds and forest conditions that vary with respect to age class or management history (Ruggiero et al. 1991 and references therein, Hagar et al. 1996, Aubry et al. 1997, Hallett and O'Connell 1997, O'Connell et al. 2000, Pearson and Manuwal 2001). In the southwest Cascade Mountains of Washington, however, quantitative relationships between the abundance of breeding birds and specific habitat attributes have not been thoroughly described. In the Oregon Coast Range, Carey et al. (1991) described the relationship between breeding birds and forest stages (young forests 40–72 years, mature 80–120 years, and old growth 200–525 years old) rather than specific habitat attributes. Gilbert and Allwine (1991) related bird abundance in the western Oregon Cascade range to specific habitat attributes across a chronosequence of forest ages ranging from 30 to 500 years, but only had one stand less than 60 years old. Manuwal's (1991) and Huff and Raley's (1991) studies of habitat characteristics and songbirds also focused on older forests (>55 years old) in the Southern Cascade Range. A more recent study in managed forest of western Washington (Aubry et al. 1997), examined the effects of fragmentation on relative bird abundance in western Washington, using simple correlation to examine relationships between each species' abundance and habitat characteristics. Finally, O'Connell et al. (2000) looked at bird communities in mature (40–60 year-old second growth) riparian forests, mature and recently clear-cut harvested upland forests, and mature riparian forests of different buffer widths surrounded by clear-cuts forests.

Knowing which structural habitat features are of greatest importance to birds is one of the highest ranked information needs of forest managers in the Pacific Northwest (Arnett and Sallabanks 1998). To begin to meet this information need for the region, we studied breeding bird communities during 1998 and 1999 in the Douglas-fir (*Pseudostuga menziesii*) - Western Hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1988) of the southwest Cascade Mountains of Washington. We counted birds and extensively sampled a wide array of habitat features in clearcut, commercially-thinned, and old growth forest treatments. Our specific study objectives were to: (1) describe bird use of three distinct forest treatments; (2) identify species assemblages with similar distributions among forest stands; and (3) model species-specific bird-habitat relationships. To enhance our study's applicability to current management, we end our paper with a discussion, based upon our results, of how forestry practices that modify forest structure might influence the distribution and abundance of breeding avifauna.

METHODS

Study area

Our study was conducted in the Douglas-fir - Western Hemlock zone of the southwest Cascade Mountains of Washington. Data were collected in three principal forest types (treatments): (1) 8- to 12-year-old managed forest (regenerating clearcuts); (2) 40- to 60-year-old managed forest that had been commercially thinned, but not yet clear-cut harvested; and (3) 150- to 270-year-old mature, naturally regenerated old growth forest. Four replicates of each forest type were selected for study, spanning a variety of state, federal, and private ownerships (Sallabanks and Quinn 2000). Actual study plots were forest stands approximately 32 ha in size that matched these structural stage descriptions. We chose 32 ha because this was approximately equivalent to the maximum stand size available in our study area. While we would have preferred to work with larger plots (to increase sample points within stands), we could only work with what was available on the southwestern Washington Cascade Mountains landscape.

Criteria for selecting study plots

One goal of our study was to make inferences for as much of the forest (in structural stages described above) within the southwestern Cascades region of the Washington State Douglas-fir - Western Hemlock zone (e.g., the population) as possible. This would require that study plots be randomly selected from all potential plots that constituted that population. To achieve this, we identified a population of suitable study plots and randomly selected from among that population, as long as our sample did not create logistical bottlenecks for field staff that had to conduct surveys at all plots. We controlled for major factors that could influence within-stand bird population dynamics, such as the amount and type of disturbance in the immediate vicinity of the study plot (stand), size of study plot, and disturbance history of the study plot. We recognized that there also were potentially important influences of longitude, latitude, and elevation on the composition of bird communities in forests of the western Cascades (e.g., Huff and Raley 1991) and controlled for such factors during plot selection where possible. In January of 1998, we began identifying potential study plots by working with state resource agencies and private timber companies. All study plots were as homogeneous as possible with respect to forest structural stage. Where necessary, we obtained permission from landowners to use privately owned land and were assured that the study plots would not be disturbed by forest management activities for at least two years.

Breeding bird abundance

We estimated relative abundance of breeding birds using the fixed-radius point-count censusing technique (Hutto et al. 1986) during the songbird breeding seasons of 1998 and 1999. Each 32 ha study plot contained eight 50 m count stations. All stations were at least 200 m apart, at least 100 m from stand boundaries, and centered within stand interiors to the extent possible. We visited each station five times between late-April and mid-July in each year of study. Consecutive samples of the individual stands were made at different times of the day (e.g., 0600–0730 hr, 0730–0900 hr, and 0900–1030 hr). Observers rotated through stands on consecutive visits so that no stand was censused by any individual observer more than once in a given year to minimize observer bias in detecting and identifying birds (e.g., Cyr 1981, Bart and Schoultz 1984). Furthermore, intensive training in sampling protocols (e.g., estimating 50 m from count stations) and familiarization with all bird species likely to be encountered occurred for several weeks each year prior to data collection (see Kepler and Scott 1981). We conducted counts only on days that were free from inclement weather, such as rain or strong wind. All detections (vocal or visual) of individual birds were tallied by species, and recorded as either being inside or outside the 50 m radius circle centered on the point-count station. Counting lasted 10 min at each station, with detections separated between the first 5- and the second 5-min intervals to maintain data compatibility with other monitoring programs (e.g., USFS; Huff et al. 2000). Birds flying above the forest canopy were recorded as such. Any individual birds known to have been recorded at a previous station within a stand were not recorded a second time.

Habitat characteristics

Intensive sampling of forest structural attributes and vegetation composition occurred systematically throughout all 12 study plots (six in 1998 and six in 1999). Protocols followed those of Aubry et al. (1997) and Hallett and O'Connell (1997), with a few modifications from Sallabanks (1994, 1995). We established two 11.3 m radius subplots at each 50 m count station for a total of 16 vegetation subplots per forest stand. The first subplot was centered over the count station center point, and the second was located 30 m from the station's center point in a random direction. At the center of each subplot, we measured slope with a clinometer, aspect with a compass, percent canopy cover using a moosehorn (Robinson 1947), and height to both the top and bottom of the canopy also using a clinometer.

Within each 11.3 m radius subplot, we sampled different components of the vegetation at three spatial scales: (1) a 0–2 m radius circle; (2) a 0–5 m radius circle; and (3) a 0–11.3 m radius circle. At the smallest spatial scale (0–2 m), we identified all forbs to species, estimated their stem diameter, and tallied individual stems by species. At the intermediate spatial scale (0–5 m), we identified all shrubs to species, estimated their stem diameter, and tallied individual stems by species. Also included at this scale were tree seedlings with diameters too small to measure at breast height (DBH). At the largest spatial scale (0–11.3 m), we did the following: (1) identified all living trees to species and measured individual tree DBH; (2) recorded all snags (standing dead trees) as we did live trees, recording species (whenever possible) and DBH; (3) sampled cut stumps by identifying tree species (again, whenever possible), as well as diameter (at the top of the stump) and height; and (4) recorded numbers of rootballs (fallen trees with exposed root systems), regardless of size and tree species.

We also conducted ocular estimates of cover at the smallest scale (0–2 m) for the following cover types: (1) berry-producing deciduous shrubs <1 m in height; (2) broad-leaved evergreen shrubs <1 m in height; (3) other deciduous shrubs <1 m in height; (4) tree seedlings <1 m in height; (5) ferns; (6) leaf/needle litter; (7) moss; (8); bare soil; (9) rocks; (10) forbs; (11) grasses; (12) *Lobaria* lichen; (13) branches; (14) fine woody debris (e.g., twigs, decayed log fragments); (15) coarse woody debris (e.g., intact down logs); (16) cut stumps; and (17) other (e.g., saprophytes, above-ground roots, tree and snag boles). Ocular estimates were made to the nearest 5% independent of all other cover types. To increase accuracy, the 0–2 radius circle was divided into four quadrants and ocular estimates were conducted separately for each quadrant. To reduce observer bias, two observers performed the ocular estimates simultaneously and their data were averaged.

Data analysis

For this analysis, we included only those birds detected within 50 m radii of observers (limited distance counts) to avoid including birds that may have been outside the sample stand. All detections, regardless of distance from observers, are reported in Appendix 1. Within each year, bird detections were first averaged among point counts within each visit to a sample stand on a species-by-species basis. For each bird species, visits within each year were then averaged to yield a mean number of detections per point count per visit per year. Finally, to avoid generating spurious results for species detected too infrequently, the bird data set was further reduced by limiting subsequent analyses to those species detected >10 total times in year. For all analyses, we used Statistica (version 5.5 for Windows, StatSoft, Inc. 2000).

Before analysis, we tested avian count data for deviations from normality using Shapiro-Wilks' *W* test and for homogeneity of variance using Levene's test (StatSoft, Inc. 2000). Generally, the error distributions of common species (>100 detections) were normal and their variances were homoscedastic. For the less common species included in our analysis, standard transformations (e.g., logarithmic, square root) did not significantly improve normality or homoscedasticity in the majority of cases and so were not used. Fortunately, the analysis of variance is robust, operating well even with considerable heterogeneity of variances, as long as sample sizes are approximately equal (Glass et al. 1972). The analysis of variance is also robust with respect to the assumption of the underlying population's normality, the validity of the analysis being affected only slightly by even considerable deviations from normality, especially as sample sizes increase (Zar 1996).

Habitat data were first summarized into 150 variables that represented the diverse array of plant species, size classes, and structural attributes of our study sites. These variables were comprised of two physical features (slope and aspect), three measures of overstory (canopy cover, tree height, and height to the bottom of the canopy), percent cover (17 cover types; see Methods: Habitat characteristics, above), shrub density (25 species), forb density (20 species), tree density (4 size classes x 18 species), stump density (4 size classes), snag density (3 size classes), and density of rootballs (4 size classes). For each variable, we then averaged data among the two vegetation subplots at each avian count station to yield mean values per point count per forest stand. To reduce the size of the data set for subsequent analyses, we screened all variables for multicollinearity (correlations among independent variables; Legendre and Legendre 1983, Morrison et al. 1987, 1992). Where a pair of habitat variables was highly intercorrelated ($r > 0.75$), the variable with the least biological meaning and/or greatest difficulty to measure was removed from consideration for inclusion in further analyses. To further reduce the number of variables, we finally pooled some variables together. For example, small- (0–10 cm DBH) and medium- (11–25 cm DBH) sized trees were lumped together to form a single variable, as were large- (26–60 cm DBH) and giant- (>60 cm DBH) sized trees. In this way, our original list of 150 variables was reduced to 22 variables with low intercorrelations (Appendix 2).

To correct deviations from normality, the arcsine transformation was applied to percent cover of overstory canopy (CCOV; see Appendix 2 for definitions of variable codes), berry-producing deciduous shrub (BPSB), broad-leaved evergreen shrub (BLSB), other deciduous shrub (ORSB), tree seedling (TRSD), fern (FERN), herb (HERB), fine woody debris (FNWD), coarse woody debris (CSWD), and other (OTHR). Natural log transformations (log [variable + 1]) were applied to density of small/medium deciduous trees (SMDEC), shrub stems (SHRB), forb stems (FORB), and large/giant snags (LGSNG). All other habitat variables were normally distributed (nonsignificant Shapiro-Wilks' *W* tests) and homoscedastic (nonsignificant Levene's tests) and were therefore left untransformed. Transformed variables are denoted by a "T" at the end of mnemonic codes (e.g., BLSBT).

We first compared relative abundance of each bird species, as well as abundance of all species combined and species richness, among forest treatments (clearcuts, commercial thins, and old growth) using repeated measures ANOVA (with year as the repeated measure). We used multiple univariate *F*-tests to examine variation in abundance of each species among treatments, testing for effects of treatment, year, and treatment x year interaction. To identify groups of species with similar distributions, we used cluster analysis to combine species into a smaller number of groups based on their relative abundance. Before cluster analysis, we standardized all variables as (raw score – [mean / standard deviation]). We then clustered these standardized species data on City-block (Manhattan) distance using Ward's minimum-variance linkage method (McGarigal et al. 2000).

We also compared habitat characteristics among forest treatments using a similar approach as we did for birds. We used repeated measures ANOVA (with count station [two vegetation subplots] within a forest stand as the repeated measure) and performed multiple univariate *F*-tests to examine variation in habitat characteristics among treatments.

To examine bird-habitat relationships, we used generalized linear model multiple regression analysis (GLZMOD; McCullagh and Nelder 1989). One advantage of the generalized linear model over the general linear model (of which, for example, multiple regression is a special case) is that it can be used to describe relationships for dependent variables that are nonlinearly related to the independent (predictor) variables. To develop species-level habitat models using GLZMOD, we used the information-theoretic approach (Burnham and Anderson 1998), first building a set of *a priori* "candidate models" based upon existing biological knowledge of each bird species. To do this we gleaned information from the scientific literature, our own unpublished data, and personal observations. This approach avoided "data dredging," development of over-fitted models, and discovery of spurious effects that are typical of more traditional multiple regression techniques, especially stepwise procedures (James and McCulloch 1990, Burnham and Anderson 1998).

Models were built using a log link function (McCullagh and Nelder 1989), assuming that dependent variables were normally distributed. From the *a priori* set of candidate models we then selected an estimated "best" approximating model using Akaike's information criterion corrected for small-sample bias (AIC_c; Hurvich and Tsai 1995). After selecting the "best" model, we assessed its overall performance (i.e., how well did the model "fit" the data) using the Likelihood-ratio Chi-square goodness-of-fit statistic. For each independent (predictor) variable included in the "best" model, we then tested the significance of its regression coefficient using the Wald statistic (W; Dobson 1990). Considering all habitat variables (Appendix 2), we performed this modeling procedure for all bird species with >10 total detections in each year of study.

RESULTS

Distribution of birds among forest treatments

During our two-year study, we detected 9,938 individuals representing 81 bird species; most detections occurred in clearcuts, fewer in commercial thins, and fewer still in old growth forest (Appendix 1). Considering only limited distance counts (those birds detected within 50 m of observers), overall avian abundance ($F_{2,9} = 4.15$, $P = 0.05$) and species richness ($F_{2,9} = 3.73$, $P = 0.07$) tended to vary among forest treatments, with both numbers of birds and numbers of species being highest in clearcuts and lowest in old growth (Fig. 1). Avian abundance did not vary between years ($F_{1,9} = 0.29$, $P = 0.60$), nor was there an interaction between treatment and year ($F_{2,9} = 0.33$, $P = 0.72$). In contrast, more bird species were detected on point counts in 1999 compared with 1998 ($F_{1,9} = 7.03$, $P = 0.03$; Fig. 1b), although there was no interaction between treatment and year for this index of the avian community ($F_{1,9} = 1.40$, $P = 0.30$).

Twenty-eight species were detected frequently enough (>10 times in each year) to be included in species-specific analyses. Of these 28 species, 17 (61%) differed significantly ($P < 0.05$) in their abundance among forest treatments (Table 1). Note that the *P*-values reported in Table 2 and elsewhere are those derived directly from independent *F*-tests and do not reflect correction for performing multiple tests. We chose not to correct for experiment-wise error (e.g., with Bonferroni correction) because such techniques tend to be overly conservative (Rice 1989) and may therefore mask biologically interesting results. Consequently, we urge readers to interpret our results cautiously and examine empirical data (reported in tables) rather than *P*-values *per se*. Several species exhibited a strong association with clearcuts, being almost exclusively found in this forest treatment (e.g., Common Yellowthroat [scientific names in Appendix 1], Orange-crowned Warbler, Song Sparrow, Spotted Towhee, White-crowned Sparrow, and Willow Flycatcher; Table 1). Other species tended to avoid clearcuts (e.g., Brown Creeper, Chestnut-backed Chickadee, Pacific-slope Flycatcher, Varied Thrush, and Winter Wren). Differences in species' abundance between commercial thins and old growth were less apparent, although there were some exceptions (e.g., Hermit/Townsend's Warbler in commercial thins and Varied Thrush in old growth; Table 1).

Seven species exhibited differences between years. The Orange-crowned Warbler ($F_{1,9} = 11.37$, $P = 0.01$), Swainson's Thrush ($F_{1,9} = 10.58$, $P = 0.01$), Brown Creeper ($F_{1,9} = 10.24$, $P = 0.01$), Evening Grosbeak ($F_{1,9} = 7.48$, $P = 0.02$), and Varied Thrush ($F_{1,9} = 5.71$, $P = 0.04$) were more abundant in 1999 relative to 1998. In contrast, the Chestnut-backed Chickadee ($F_{1,9} =$

7.65, $P = 0.02$) and Pacific-slope Flycatcher ($F_{1,9} = 7.05$, $P = 0.03$) were more abundant in our first year of study. Only two species exhibited treatment x year interactions (Orange-crowned Warbler, $F_{2,9} = 9.66$, $P = 0.01$; Swainson's Thrush, $F_{2,9} = 5.17$, $P = 0.03$).

Cluster analysis revealed three distinct groups of birds (Fig. 2). The robustness of general-purpose classifications is maximized by cutting hierarchical trees within the maximum range of resemblance coefficients (linkage distance, d_{xy}) for which the number of clusters remains constant (Romesburg 1984). In our hierarchical tree, this range was $502.64 > d_{xy} > 208.35$, and within this range, bird species clustered into one of two groups: (1) Song Sparrow–Dark-eyed Junco ($n = 12$ species); and (2) Steller's Jay–Pacific-slope Flycatcher ($n = 16$; Fig. 2). This initial cut essentially separated those species associated with clearcut forest (cluster 1) with those associated with more mature forest treatments (cluster 2). The next most robust place to cut the hierarchical tree was at $208.35 > d_{xy} > 127.96$. This cut divided cluster 2 above (Steller's Jay–Pacific-slope Flycatcher) into two new groups to yield a three-cluster solution: (1) Song Sparrow–Dark-eyed Junco ($n = 12$ species); (2) Steller's Jay–Hermit/Townsend's Warbler ($n = 9$); and (3) Varied Thrush–Pacific-slope Flycatcher ($n = 7$; Fig. 2). For the most part, the second cut separated species with greater abundance in commercial thins from those with greater abundance in old growth.

Variation in habitat characteristics among forest treatments

Of the 22 habitat variables included in analyses, 10 (45%) differed among forest treatments (Table 2). Among the types of ground cover assessed using ocular estimates, we found more berry-producing deciduous shrubs in clearcuts and more coarse woody debris in old growth; herbaceous plants were equally common in clearcuts and commercial thins, but relatively lacking in old growth (Table 2). Stem counts conducted at small spatial scales revealed greater densities of forbs and shrubs in clearcuts relative to old growth forest. Among the standing tree categories, only the large tree component differed among forest treatments, with large/giant conifers and large/giant snags occurring in greater densities in old growth stands. Finally, all three measures of overstory structure (canopy cover, tree height, and height to the bottom of the overstory canopy) differed among forest treatments (Table 2). Of all habitat variables measured, canopy cover showed the most marked differences among forest treatments ($F_{2,9} = 105.21$, $P = 0.0000$) being an order of magnitude greater in old growth relative to clearcut forests. Tree height also increased from young to more mature forest types. Height to the bottom of the overstory canopy was the same in both commercial thins and old growth forest, but nonexistent in clearcuts because of the lack of a canopy in that forest treatment (Table 2).

Bird-habitat relationships

Best approximating models were developed for the relative abundance of 19 (68%) of the 28 bird species included in analyses (Table 3). For eight species (Black-headed Grosbeak, Black-throated Gray Warbler, Common Yellowthroat, Evening Grosbeak, Hutton's Vireo, Red-breasted Nuthatch, Steller's Jay, and Western Tanager), none of the habitat variables that we examined were found to be significantly correlated with abundance. For the MacGillivray's Warbler, abundance was negatively correlated with CCOVT and SMDECT, but the overall performance of the best approximating model was not significant (Likelihood-ratio $\chi^2 = 1.06$, $P = 0.59$). Models of abundance for all other species provided a statistically significant "fit" to the data, especially for Song Sparrow (Likelihood-ratio $\chi^2 = 115.66$), Spotted Towhee ($\chi^2 = 51.73$), and White-crowned Sparrow ($\chi^2 = 51.09$).

Overall, the amount of variance explained by the habitat variables considered in our analyses was relatively high. Models of abundance for American Robin ($R^2 = 0.96$), Willow Flycatcher ($R^2 = 0.94$), Orange-crowned Warbler ($R^2 = 0.87$), Song Sparrow ($R^2 = 0.87$), and Winter Wren ($R^2 = 0.87$) exhibited the highest values of R^2. Excluding the Gray Jay, for which our best approximating model explained little variation ($R^2 = 0.03$), values of R^2 for the remaining 18 species exhibited a mean ± SE of 0.67 ± 0.05 (Table 3).

Of the 22 habitat variables considered in analyses, three were never selected for inclusion in bird-habitat models: LGSNGT (density of large/giant snags), STMP (density of stumps), and OTHRT (percent ground cover of bare soil, rock, and other miscellaneous cover types; Table 3). Percent overstory canopy cover (CCOVT) was the variable selected most often and which appeared in 11 (39%) of the 28 species' models (positively correlated with abundance of six species; negatively correlated with abundance of five species). Also important were SMCON (density of small/medium conifers; eight models [positive in five; negative in three]), LGCON (density of large/giant conifers; seven models [positive in four; negative in three]), and SHRBT (stem density of shrubs; seven models [positive in five; negative in two]). For some species, best approximating models contained only two variables (suggesting simple bird-habitat relationships; e.g., Brown Creeper, Spotted Towhee, and Willow Flycatcher) and for others they contained as many as 6 variables (suggesting more complex relationships; e.g., Hairy Woodpecker).

DISCUSSION

Variation among forest treatments

The three forest treatments that we sampled in this study represented a gradient in forest structure from management-induced early-seral stands with little overstory cover and few large trees and snags (i.e., clearcuts) to late-seral stands with high canopy cover and a significant component of large trees and snags (i.e., old growth). Specifically, canopy cover increased more than eleven-fold from 8% in clearcuts to 91% in old growth (Table 2). The density of large/giant trees increased from 2 trees/ha in clearcuts to 240 trees/ha in old growth. Similarly, the density of large/giant snags increased from 25 snags/ha in clearcuts to 230 snags/ha in old growth. Coarse woody debris increased from clearcuts, through commercial thins, to old growth. The densities of forbs and shrubs were highest in clearcuts, moderate in commercial thins, and lowest in old growth. These gradients in habitat characteristics clearly define the three forest treatments that we sampled and are typical of management-induced successional stages in Douglas-fir - Western Hemlock forests of the western Cascade Mountains of Washington (e.g., Aubry et al. 1997).

Habitat gradients, such as those we have described here, are well known to influence the structure and dynamics of avian communities (e.g., James and Wamer 1982, Cody 1985, Adams and Morrison 1993, Hansen et al. 1995, Rodewald and Yahner 2000). Consistent with this thesis, we found >60% of the bird species that we examined to differ in their abundance among the forest treatments that we studied. Several species exhibited particularly strong associations with clearcut forests, including Orange-crowned Warbler, Rufous Hummingbird, Song Sparrow, Spotted Towhee, Swainson's Thrush, White-crowned Sparrow, and Willow Flycatcher (Table 1).

Previous studies in western Washington have described similar relationships with early-seral forests for several of these species (e.g., O'Connell et al. 2000).

Just as numerous species were associated with clearcuts, we also documented numerous species associated with more mature forest conditions. Indeed, several species (e.g., Brown Creeper, Chestnut-backed Chickadee, Golden-crowned Kinglet, and Varied Thrush) tended to avoid clearcuts altogether. Previous studies conducted in western forests have reported similar habitat relationships for these mature forest associates (Mannan and Meslow 1984, Mariani and Manuwal 1990, Carey et al. 1991, Tobalske et al. 1991, Adams and Morrison 1993, Hejl et al. 1995, Sallabanks et al. 2002). Unlike for clearcuts, however, few bird species could be clearly distinguished as strong associates with commercial thins or as strong associates with old growth *per se*. Species tended to either be more common in clearcuts, or more common in more mature forest treatments (commercial thins and old growth combined). These patterns likely reflect the fact that clearcuts were the most distinct of the three forest treatments we studied. Commercial thins and old growth, on the other hand, despite some clear differences, also had several structural similarities (e.g., density of large/giant conifers and tree height). Certainly relative to the dense understories and open canopies of clearcuts, commercial thins and old growth were structurally quite similar. Along these lines, it is important to recognize that commercial thinning helps accelerate succession by promoting understory development. Harvest-aged stands that are not commercially thinned may be similar to the closed-canopy forests studied by Aubry et al. (1997), who showed that these forests typically have lower avian species richness and lower overall abundance of birds than clearcut, pre-canopy, and commercially-thinned harvest-aged forests. The fact that the stands we studied had been commercially thinned may therefore be one reason why they contained somewhat similar breeding bird assemblages to old growth forests.

Abundance of several species differed between years. Such annual variation is typical (Franzreb and Ohmart 1978, Szaro and Balda 1979, Hejl et al. 1988), with numbers often responding to weather-related migration patterns, annual differences in immigration rates from, or emigration rates to, surrounding landscapes, and reproductive success in previous years. Despite significant differences in relative abundance between years for seven species, we observed interaction effects between forest treatment and year for only two species (Orange-crowned Warbler and Swainson's Thrush). The paucity of such interaction effects, even in the face of annual variation in abundance, suggests that the association of most species with different forest treatments remained relatively consistent. Indeed, for both the Orange-crowned Warbler and Swainson's Thrush, the reason for the interaction effect was simply due to an increased abundance in clearcuts in 1999 relative to 1998.

Forest bird assemblages with similar distributions

Associations between bird species and forest treatments were more clearly defined using cluster analysis. Our analyses identified three distinct groups of species (Fig. 2), where each member of a group had similar variation in relative abundance among forest stands as other members of the same group. Presumably, similar variation in relative abundance among forest stands reflects similar relationships with habitat gradients present within those stands. Grouping bird species into well-defined assemblages is one of the main goals of analyzing bird habitats (Wiens 1989) and provides forest managers with a useful way to consider "species sets" that respond collectively to changes in habitat structure. Managing forest birds on a species-by-species basis is not often a viable option (unless a species is listed as threatened or endangered) and so knowing which species in a community have similar habitat relationships is important information.

Cluster 1 consisted of 12 species (Fig. 2), 10 of which (83%) were significantly more abundant in clearcuts relative to commercial thins and old growth (Table 1). We therefore considered this group of birds to be "clearcut associates". Cluster 2 was comprised of nine species (Fig. 2). Although only two species in this cluster differed significantly in their abundance among forest treatments (Hermit/Townsend's Warbler and Gray Jay), seven of the nine species (78%) tended to be more common in commercial thins (Table 1). For this reason, we considered species in cluster 2 to be comprised mostly of "commercial thin associates". Finally, cluster 3 was comprised of seven species (Fig. 2), five of which (71%) were significantly more abundant in old growth forest (Table 1). We therefore considered most species in cluster 3 to be "old growth associates".

Bird-habitat models and predictors of avian abundance

Significant relationships between relative abundance and habitat variables were derived for many bird species included in our analyses. Many such relationships provided some insight into why forest birds were distributed among forest treatments in the patterns we observed. For example, negative correlations between abundance and overstory canopy cover were found for several species classified as clearcut associates (Table 3), and as we also have shown, clearcuts had significantly lower canopy cover than other forest treatments included in our study (Table 2). In terms of understory structure, clearcuts also had dense shrub layers (Table 2). Shrub density was an important variable in the habitat models for Orange-crowned Warbler and Wilson's

Warbler (Table 3), both of which were significantly more abundant in clearcuts (Table 1), and both of which were considered clearcut associates (Fig. 2). Both the Orange-crowned Warbler and Wilson's Warbler nest on or near the ground, where nest predators presumably have more difficulty locating nests in densely-vegetated understories. Similarly, the Dark-eyed Junco also nests on the ground, often building its nest among grasses and/or beneath coarse woody debris. Both HERBT and CSWDT were included in the habitat model for the junco, being positively correlated with relative abundance. Our classification of Swainson's Thrush as a clearcut associate also is consistent with Evans Mack and Yong (2000), who describe this migratory thrush as preferring to nest in the understory, particularly in thickets of deciduous shrubs or conifer saplings within moist coniferous forests.

Habitat models for species more abundant in commercial thins and old growth forest typically contained variables such as tree height (e.g., Varied Thrush and Hermit/Townsend's Warbler), large-diameter trees (e.g., Gray Jay, Golden-crowned Kinglet, and Brown Creeper), and of course, overstory canopy cover (e.g., Winter Wren and Chestnut-backed Chickadee). Our results for the Brown Creeper reiterate those reported by Mariani and Manuwal (1990), who also found positive correlations between creeper abundance, closed overstory canopies, and large-diameter trees in forests of the southern Washington Cascade range. Elsewhere in western forests, Adams and Morrison (1993) report similar findings. The importance of a large tree component for the Golden-crowned Kinglet also has been documented for forests in Washington state by O'Connell et al. (2000), as well as elsewhere in the Pacific northwest (Mannan and Meslow 1984, Sallabanks et al. 2002).

Berry-producing shrub species (e.g., *Rubus* spp. and *Vaccinium* spp.) entered habitat models as significant variables for two frugivorous thrushes, the American Robin and

Swainson's Thrush. Berry-producing shrubs also were found to be positively correlated with relative abundance of the American Robin by O'Connell et al. 2000. Flowering shrubs in general (berry-producing and other deciduous shrubs) also were important predictor variables for abundance of Rufous Hummingbird (Table 3), perhaps because they provide an important food resource (sugar) for this migratory nectarivore. The abundance of berry- and nectar-producing shrubs in clearcuts likely contributed to the increased abundance of these bird species in this forest treatment.

Although the variance in relative abundance explained by the habitat variables we considered was high for several species (e.g., American Robin and Willow Flycatcher), some species' models still had values of R^2 in the 0.40–0.60 range. Such values of R^2 suggest that other factors not measured influenced avian abundance, or that there is substantial random variability in the distribution of these species across forest treatments. Birds may respond to a wide range of habitat features at various spatial and temporal scales (Verner et al. 1986, Saab 1999). Birds also may exhibit significant annual variation in their relationship with habitat features, including landscape-level factors such as patch size and percent cover (Gutzwiller and Barrow 2001). We therefore conclude that a significant proportion of the unexplained variation in some models may simply reflect random variation in species' associations with habitat characteristics over a range of spatial and temporal scales.

Throughout this discussion, we have assumed that relative bird abundance provides a meaningful estimate of habitat quality. Nonetheless, studies of species-habitat associations are known to be limited (Wolff 1995), and relationships between abundance and habitat quality (as indicated by reproductive success, for example) have rarely been examined. Numerous studies, mostly on birds, have noted that abundance or density is not necessarily an accurate indicator of habitat quality (Van Horne 1983, Vickery et al. 1992, Hagan et al. 1996). Although not the focus of this paper, we did monitor nests (*n* = 681 nests of 40 bird species) in the stands in our sample and have correlated estimates of nesting success with avian abundance (Sallabanks and Quinn 2000). For six of 11 species analyzed (Brown Creeper, Chestnut-backed Chickadee, Dark-eyed Junco, Song Sparrow, Willow Flycatcher, and Winter Wren), "area-level productivity" (number of young fledged per unit area) and relative abundance were positively correlated; in fact, only for the Pacific-slope Flycatcher and Varied Thrush did we question the reliability of point-count surveys for habitat quality assessments. Unfortunately, even with data on birth and death rates, or the source of recruits, identifying whether or not a population or a habitat is functioning as a source, sink, or "pseudo-sink" is difficult (Watkinson and Sutherland 1995). Although we cannot therefore rule out the possibility that forest stands with relatively high avian abundance were operating as sink habitats, we consider it unlikely based on our analyses of nesting success (Sallabanks and Quinn 2000). With this in mind, readers should temper our conclusions accordingly.

Management implications

Combining results from our analyses provides numerous consistent relationships between bird species (and species' assemblages), forest treatments, and habitat characteristics of forest stands that should be of benefit to forest managers in western Washington. The amount of overstory canopy cover, for example, appears to be an important proximate mechanism that drives the distribution and abundance of numerous bird species. In our study, many of the strongest relationships between avian abundance and canopy cover were positive, and numerous species differed significantly in their distributions among forest treatments, being more abundant in commercial thins and old growth. For such species (e.g., Brown Creeper, Chestnut-backed Chickadee, Golden-crowned Kinglet, Varied Thrush, and Winter Wren; see Table 3), intensive timber harvest, such as a clearcut, would render forest habitat unsuitable and cause the loss of these species from mature forest stands.

The importance of overstory canopy cover to forest birds has other important implications for management, however. For example, if forest managers could harvest trees and still leave a relatively closed overstory canopy, many bird species would likely remain unaffected. Several species, such as Varied Thrush, Winter Wren, and Hairy Woodpecker, had positive relationships with canopy cover, but not necessarily with large-diameter trees and snags (i.e., old growth characteristics *per se*). Neither did the abundance of other species that were classified as old growth associates, such as Pacific-slope Flycatcher and Chestnut-backed Chickadee, appear to be positively correlated with the density of large-diameter trees. Therefore, there is some evidence from our study that selective tree removal, or thinning from below, may be one option available to forest managers that would still leave suitable forest habitat for the majority of bird species. Our results also suggest, however, that some bird species are closely tied to both overstory canopy cover and large-diameter trees characteristic of old growth forest *per se*. Such species include Brown Creeper and Golden-crowned Kinglet, two forest birds that would likely be negatively affected by almost any type of timber harvest in old growth forest.

Not all bird species are likely to respond negatively to intensive timber harvest, however. We found the abundance of several species to be positively correlated with habitat features characteristic of young forests, such as an open canopy, shrubby understories, and a lack of a large tree component. Such species included Orange-crowned Warbler, Willow Flycatcher, Song Sparrow, and White-crowned Sparrow (Table 3), and these species would benefit from intensive overstory tree removal. Indeed, numerous species were identified as clearcut associates in our study, many of them responding to different habitat attributes, but all of which were characteristic of early-seral forests. Although the trends were not statistically significant, we also recorded more birds, and more species, in clearcuts relative to more mature forest treatments (Fig. 1).

The critical factor defining the threshold at which harvest operations begin to influence birds in Douglas-fir - Western Hemlock forests of the southwest Cascades Mountains of Washington consistently appears to be the amount of canopy cover retained in a stand. O'Connell et al. (2000) reported similar findings from their study of forested riparian management zones in Washington. Following clearcutting of mature upland forest, O'Connell et al. (2000) found seven species to change in abundance pre- versus post-treatment. Three of these species (Dark-eyed Junco, Spotted Towhee, and White-crowned Sparrow) were negatively associated with canopy closure and three (Chestnut-backed Chickadee, Pacific-slope Flycatcher, and Winter Wren) were positively associated with canopy closure. Based upon our data, a reduction in the amount of canopy cover below approximately 25–50% is the range within which the majority of bird species appear to begin to respond to changes in stand structure, both positively and negatively. If foresters can work with wildlife biologists to develop logging prescriptions that allow for the removal of commercially-valuable timber yet retain moderate canopy cover, we believe the impacts of forest management on breeding birds can be minimized. Where an intensive thin is necessary, either for economical or ecological reasons (e.g., salvage operations in response to insect outbreaks), we have offered empirical evidence of how avian community composition is likely to change, both in terms of species' gains and species' losses, in response to such management. By identifying a number of habitat attributes that influence avian abundance, perhaps we also have provided managers with some options to help mitigate the impacts of timber harvest on forest birds.

ACKNOWLEDGMENTS

This study was funded by Washington State Department of Natural Resources (DNR) as Personal Services Contract No. 98-037 between DNR and the Sustainable Ecosystems Institute, and Champion Pacific Timberlands, Inc. In particular we thank Cheryl Quade, Tami Grant, and Nikki Housh of DNR for administering this contract and providing project support from its inception. For logistical support in the field we thank Dr. Douglas Runde of Weyerhaeuser Company and Jessica Eskow of Champion Pacific Timberlands. Weyerhaeuser also provided two field vehicles. For providing access to study plots we are grateful to the following: Weyerhaeuser Company, Champion Pacific Timberlands, DNR, U.S. Forest Service, and the University of Washington Pack Experimental Forest. We also thank members of the Landscape and Wildlife Advisory Group (LWAG) for their support and advice throughout this project, especially Cheryl Quade and Dr. Daniel Varland for serving as the primary LWAG contacts. Finally, the following assisted with data collection: Nathan Blackburn, Jeanne Hammond, Robert Kaler, Greg Levandoski, Doug Milek, Anna Noson, Heidi Packard, Tom Parker, Peter Sanzenbacher, Jennifer Soules, Heather Wilson, and Julian Wood. We owe much of the success of this study to Tom Parker and Jennifer Soules, field team leaders in 1998 and 1999, respectively.

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Appendix 1. Bird species detected in forests of the southwest Cascade Mountains, Washington, 1998–1999. Numbers are summarized by forest treatment and year, and represent all detections, regardless of distance from observers (umlimited distance counts). Species are listed alphabetically.

			Total number of detections per forest treatment					
			Clearcut ($n = 4$)		Commercial Thin ($n = 4$)		Old Growth ($n = 4$)	
No.	Common name	Scientific name	1998	1999	1998	1999	1998	1999
1	American Crow	*Corvus brachyrhynchos*	2	9	4	18	1	4
2	American Goldfinch	*Carduelis tristis*	55	52	1	3	0	0
3	American Robin	*Turdus migratorius*	68	104	98	126	68	38
4	Band-tailed Pigeon	*Columba fasciata*	8	5	9	2	14	18
5	Barred Owl	*Strix varia*	0	0	1	0	2	1
6	Belted Kingfisher	*Ceryle alcyon*	0	1	0	4	0	0
7	Bewick's Wren	*Thryomanes bewickii*	8	15	3	1	0	0
8	Black-capped Chickadee	*Parus atricapillus*	5	1	0	0	1	0
9	Black-headed Grosbeak	*Pheucticus melanocephalus*	45	25	6	1	2	2
10	Black-throated Gray Warbler	*Dendroica nigrescens*	0	2	33	33	4	0
11	Blue Grouse	*Dendragapus obscurus*	10	22	0	1	5	10

12	Blue-winged Teal	*Anas discors*	1	0	0	0	0	0
13	Brown Creeper	*Certhia americana*	3	1	32	63	68	92
14	Brown-headed Cowbird	*Molothrus ater*	0	2	2	0	0	0
15	California Quail	*Callipepla californica*	0	1	0	0	0	0
16	Canada Goose	*Branta canadensis*	3	10	0	10	0	12
17	Cassin's Vireo	*Vireo cassinii*	1	0	2	0	0	0
18	Cedar Waxwing	*Bombycilla cedrorum*	14	9	2	1	1	0
19	Chestnut-backed Chickadee	*Parus rufescens*	33	16	106	79	145	119
20	Chipping Sparrow	*Spizella passerina*	0	1	0	1	0	0
21	Common Merganser	*Mergus merganser*	1	0	0	0	0	0
22	Common Nighthawk	*Chordeiles minor*	0	1	0	0	0	0
23	Common Raven	*Corvus corax*	6	11	13	18	10	7
24	Common Snipe	*Gallinago gallinago*	0	1	0	0	0	0
25	Common Yellowthroat	*Geothlypis trichas*	107	87	0	0	0	0
26	Cooper's Hawk	*Accipiter cooperi*	0	0	0	1	0	0
27	Dark-eyed Junco	*Junco oreganus hyemalis*	128	94	123	75	18	19
28	Downy Woodpecker	*Picoides pubescens*	0	1	0	0	0	1
29	Evening Grosbeak	*Coccothraustes vespertina*	24	26	53	67	12	25

30	Golden-crowned Kinglet	*Regulus satrapa*	5	9	66	42	117	87
31	Golden-crowned Sparrow	*Zonotrichia atricapilla*	3	0	0	0	0	0
32	Gray Jay	*Nucifraga columbiana*	5	6	43	39	23	26
33	Great Blue Heron	*Ardea herodias*	1	0	0	0	0	0
34	Great Horned Owl	*Bubo virginianus*	0	0	1	0	0	0
35	Hairy Woodpecker	*Picoides villosus*	18	14	30	32	24	23
36	Hammond's Flycatcher	*Empidonax hammondii*	0	0	0	8	2	1
37	Hermit Thrush	*Catharus guttatus*	0	7	1	0	12	1
38	Hermit/Townsend's Warbler	*D. occidentalis/townsendi*	0	6	141	95	66	61
39	Hutton's Vireo	*Vireo huttoni*	5	15	35	22	2	6
40	Killdeer	*Charadrius vociferus*	3	1	0	0	0	0
41	MacGillivray's Warbler	*Oporornis tolmiei*	167	88	12	5	0	1
42	Mallard	*Anas platyrhynchos*	0	0	9	0	0	0
43	Mourning Dove	*Zenaida macroura*	0	0	0	0	0	1
44	Northern Flicker	*Colaptes auratus*	33	40	14	11	11	10
45	Northern Goshawk	*Accipiter gentilis*	0	0	0	0	0	1
46	Northern Harrier	*Circus cyaneus*	3	3	0	0	0	0
47	Northern Pygmy-owl	*Glaucidium gnoma*	0	0	2	1	3	11

48	Olive-sided Flycatcher	*Contopus borealis*	15	16	0	0	0	2
49	Orange-crowned Warbler	*Vermivora celata*	110	164	2	6	1	1
50	Osprey	*Pandion haliaetus*	0	0	0	0	1	0
51	Pacific-slope Flycatcher	*Empidonax difficilis*	23	17	209	88	149	116
52	Pileated Woodpecker	*Dryocopus pileatus*	0	1	6	7	7	7
53	Pine Siskin	*Carduelis pinus*	4	4	2	4	0	2
54	Purple Finch	*Carpodacus purpureus*	4	1	16	29	0	2
55	Red Crossbill	*Loxia curvirostra*	0	34	0	0	0	3
56	Red-breasted Nuthatch	*Sitta canadensis*	9	6	41	19	44	63
57	Red-breasted Sapsucker	*Sphyrapicus nuchalis*	0	0	3	1	5	3
58	Red-tailed Hawk	*Buteo jamaicensis*	1	0	0	1	1	0
59	Ruby-crowned Kinglet	*Regulus calendula*	1	8	0	0	0	0
60	Ruffed Grouse	*Bonasa umbellus*	1	5	1	1	0	0
61	Rufous Hummingbird	*Selasphorus rufus*	49	79	5	8	4	8
62	Sharp-shinned Hawk	*Accipiter striatus*	0	1	0	0	0	0
63	Song Sparrow	*Melospiza melodia*	235	201	6	6	1	1
64	Spotted Owl	*Strix occidentalis*	0	0	0	0	1	0
65	Spotted Towhee	*Pipilo maculatus*	147	114	6	14	5	3

66	Steller's Jay	*Cyanocitta stelleri*	53	55	25	33	48	40
67	Swainson's Thrush	*Catharus ustulatus*	70	113	53	35	10	26
68	Townsend's Solitaire	*Myadestes townsendi*	2	0	0	1	0	0
69	Tree Swallow	*Tachycineta bicolor*	1	0	0	0	0	0
70	Varied Thrush	*Ixoreus naevius*	43	42	50	60	133	130
71	Vaux's Swift	*Chaetura vauxi*	0	0	0	0	2	0
72	Violet-green Swallow	*Tachycineta thalassina*	0	0	0	0	1	0
73	Warbling Vireo	*Vireo gilvus*	24	21	9	5	0	0
74	Western Tanager	*Piranga ludoviciana*	11	8	60	34	8	6
75	Western Wood-pewee	*Contopus sordidulus*	0	0	0	0	0	1
76	White-crowned Sparrow	*Zonotrichia leucophrys*	47	38	1	7	0	2
77	Willow Flycatcher	*Empidonax trailii*	210	186	1	1	1	0
78	Wilson's Warbler	*Wilsonia pusilla*	89	44	38	29	21	18
79	Winter Wren	*Troglodytes troglodytes*	71	64	379	408	373	280
80	Yellow Warbler	*Dendroica petechia*	0	1	0	0	0	0
81	Yellow-rumped Warbler	*Dendroica coronata*	8	3	1	1	2	0
	Total No. Detections		1,993	1,912	1,756	1,557	1,429	1,291

Appendix 2. Habitat variables used in analyses of bird-habitat relationships in forests of the southwest Cascade Mountains, Washington, 1998–1999. A "T" at the end of a variable name indicates that data for that variable were transformed for analysis.

Variable	Units	Description
BLSBT	%	Percent ground cover by broad-leaved evergreen shrubs <1 m in height
BPSBT	%	Percent ground cover by berry-producing deciduous shrubs <1 m in height
ORSBT	%	Percent ground cover by other deciduous shrubs <1 m in height
TRSDT	%	Percent ground cover by tree seedlings <1 m in height
FERNT	%	Percent ground cover by ferns
HERBT	%	Percent ground cover by herbaceous vegetation (includes forbs, grasses, *Lobaria* lichen, and moss)
FNWDT	%	Percent ground cover by fine woody debris (includes leaf/needle litter and small branches)
CSWDT	%	Percent ground cover by coarse woody debris (includes down logs and stumps)
OTHRT	%	Percent ground cover by bare soil, rock, and other cover types (includes saprophytes, above-ground roots, tree and snag boles)
FORBT	no./ha	Density of forb stems (all species combined)
SHRBT	no./ha	Density of shrub stems (all species combined)

SMCON	no./ha	Density of small- (0–10 cm DBH) and medium- (11–25 cm DBH) sized coniferous trees
LGCONT	no./ha	Density of large- (26–60 cm DBH) and giant- (>60 cm DBH) sized coniferous trees
SMDECT	no./ha	Density of small- (0–10 cm DBH) and medium- (11–25 cm DBH) sized deciduous trees
LGDEC	no./ha	Density of large- (26–60 cm DBH) and giant- (>60 cm DBH) sized deciduous trees
SMSNG	no./ha	Density of small- (0–10 cm DBH) and medium- (11–25 cm DBH) sized snags (both coniferous and deciduous)
LGSNGT	no./ha	Density of large- (26–60 cm DBH) and giant- (>60 cm DBH) sized snags (both coniferous and deciduous)
STMP	no./ha	Density of cut stumps (all size classes combined)
RTBL	no./ha	Density of rootballs
CCOVT	%	Percent overstory canopy cover
TRHT	m	Height of a "representative" tree within the vegetation subplot (essentially the same as measuring the height to the top of the overstory tree canopy)
CBOT	m	Height to the bottom of the overstory tree canopy (measures the amount of "space" between the forest floor and the overstory tree canopy)

Table 1. Results of repeated measures ANOVA for differences in relative abundance of breeding birds among three forest treatments in the southwest Cascade Mountains, Washington, 1998–1999. Species with >10 total detections within 50 m of point-count stations in each year were included in analyses and are listed alphabetically. *P*-values are not corrected for experiment-wise error rates.

	Mean ± SE no. birds (x10) / forest treatment			ANOVA	
Bird Species	Clearcut ($n = 4$)	Comm. Thin ($n = 4$)	Old Growth ($n = 4$)	$F_{(2,9)}$	P
American Robin	2.55 ± 0.46	3.10 ± 0.48	1.11 ± 0.30	3.22	0.0884
Black-headed Grosbeak	1.25 ± 0.30	0.09 ± 0.07	0.06 ± 0.04	5.52	0.0273
Black-throated Gray Warbler	0.03 ± 0.03	1.38 ± 0.51	0.11 ± 0.11	2.11	0.1770
Brown Creeper	0.00 ± 0.00	2.48 ± 0.49	3.87 ± 0.40	12.25	0.0027
Chestnut-backed Chickadee	1.52 ± 0.31	5.29 ± 0.59	7.83 ± 0.65	15.25	0.0013
Common Yellowthroat	5.31 ± 1.13	0.00 ± 0.00	0.00 ± 0.00	2.30	0.1559
Dark-eyed Junco	5.73 ± 0.79	4.42 ± 0.68	0.81 ± 0.17	2.87	0.1088
Evening Grosbeak	0.03 ± 0.03	0.81 ± 0.24	0.23 ± 0.13	2.55	0.1329
Golden-crowned Kinglet	0.38 ± 0.18	3.10 ± 0.49	5.74 ± 0.68	8.82	0.0076
Gray Jay	0.16 ± 0.08	1.54 ± 0.32	0.54 ± 0.13	4.61	0.0418
Hairy Woodpecker	0.51 ± 0.11	1.23 ± 0.26	0.88 ± 0.24	1.89	0.2057
Hermit/Townsend's Warbler	0.13 ± 0.10	4.08 ± 0.68	1.97 ± 0.45	5.38	0.0291
Hutton's Vireo	0.16 ± 0.13	0.78 ± 0.21	0.06 ± 0.04	1.91	0.2040
MacGillivray's Warbler	6.09 ± 0.77	0.29 ± 0.13	0.00 ± 0.00	15.65	0.0012
Orange-crowned Warbler	6.44 ± 0.72	0.16 ± 0.07	0.00 ± 0.00	55.61	0.0000

Pacific-slope Flycatcher	0.67 ± 0.27	5.61 ± 0.89	6.13 ± 0.84	4.80	0.0382
Red-breasted Nuthatch	0.00 ± 0.00	0.41 ± 0.12	1.20 ± 0.34	2.16	0.1718
Rufous Hummingbird	3.56 ± 0.60	0.38 ± 0.12	0.31 ± 0.12	6.45	0.0183
Song Sparrow	10.56 ± 1.26	0.03 ± 0.03	0.03 ± 0.03	7.71	0.0112
Spotted Towhee	6.09 ± 0.75	0.41 ± 0.18	0.10 ± 0.06	12.40	0.0026
Steller's Jay	0.36 ± 0.12	0.38 ± 0.12	0.89 ± 0.27	0.39	0.6849
Swainson's Thrush	3.11 ± 0.72	0.92 ± 0.26	0.54 ± 0.13	13.54	0.0019
Varied Thrush	0.54 ± 0.18	1.01 ± 0.26	2.28 ± 0.33	8.29	0.0091
Western Tanager	0.33 ± 0.15	1.25 ± 0.38	0.28 ± 0.12	1.32	0.3150
White-crowned Sparrow	0.99 ± 0.21	0.06 ± 0.04	0.00 ± 0.00	10.47	0.0045
Willow Flycatcher	9.84 ± 1.75	0.00 ± 0.00	0.00 ± 0.00	18.97	0.0006
Wilson's Warbler	2.84 ± 0.51	1.48 ± 0.33	0.84 ± 0.22	4.50	0.0442
Winter Wren	2.60 ± 0.74	16.45 ± 1.47	12.44 ± 1.00	8.26	0.0092

Table 2. Results of repeated measures ANOVA for differences in habitat characteristics among three forest treatments in the southwest Cascade Mountains, Washington, 1998–1999. Habitat variable codes are defined in Appendix 2 (note that for those variables that were transformed for analysis, untransformed values are reported in the table). *P*-values are not corrected for experiment-wise error rates.

Habitat Variable	Mean ± SE value / forest treatment Clearcut ($n = 4$)	 Comm. Thin ($n = 4$)	 Old Growth ($n = 4$)	ANOVA $F_{(2,9)}$	 P
BLSBT	3.46 ± 1.21	10.00 ± 2.11	8.22 ± 1.72	1.99	0.1926
BPSBT	17.94 ± 2.20	10.63 ± 1.31	2.32 ± 0.45	10.03	0.0051
ORSBT	2.15 ± 0.92	2.07 ± 0.72	0.68 ± 0.28	1.24	0.3349
TRSDT	6.27 ± 1.29	3.46 ± 1.30	5.16 ± 1.84	0.65	0.5466
FERNT	11.14 ± 1.86	19.08 ± 2.66	9.18 ± 1.95	1.70	0.2372
HERBT	24.58 ± 1.85	24.02 ± 2.88	9.71 ± 1.58	6.64	0.0169
CSWDT	13.11 ± 1.58	21.91 ± 1.65	47.60 ± 3.02	23.15	0.0003
FNWDT	11.21 ± 1.97	5.02 ± 0.78	11.89 ± 1.98	0.96	0.4178
OTHRT	6.31 ± 2.35	3.11 ± 0.57	6.00 ± 1.66	0.90	0.4391
FORBT	42,255.77 ± 8,209.80	23,713.82 ± 5,466.14	5,846.91 ± 715.99	11.71	0.0031
SHRBT	8,844.76 ± 1,643.88	2,608.07 ± 449.69	1,177.71 ± 299.29	14.03	0.0017
SMCON	1,479.94 ± 300.91	449.15 ± 256.78	1,137.03 ± 311.12	1.17	0.3521
LGCON	1.95 ± 1.27	205.67 ± 12.06	240.73 ± 17.51	60.01	0.0000
SMDECT	1114.58 ± 271.90	787.97 ± 447.34	39.54 ± 25.43	4.01	0.0570
LGDEC	10.91 ± 3.95	28.83 ± 7.88	8.96 ± 3.13	1.67	0.2413

SMSNG	73.62 ± 10.06	69.34 ± 10.53	16.36 ± 4.05	2.85	0.1097
LGSNGT	24.61 ± 7.87	36.64 ± 8.12	230.34 ± 47.76	16.13	0.0011
STMP	32.40 ± 13.47	34.79 ± 6.39	17.26 ± 6.73	0.75	0.4992
RTBL	0.00 ± 0.00	0.39 ± 0.39	3.12 ± 1.77	1.73	0.2318
CCOVT	8.04 ± 3.62	76.13 ± 4.81	91.02 ± 1.83	105.21	0.0000
TRHT	5.05 ± 0.59	23.59 ± 2.65	35.08 ± 3.64	5.02	0.0344
CBOT	0.00 ± 0.00	15.34 ± 0.94	15.09 ± 1.17	19.03	0.0006

Table 3. Regression models indicating habitat variables correlated with abundance of breeding birds in forests of the southwest Cascade Mountains, Washington, 1998–1999. For each dependent variable (bird species) we report only the model with the minimum AIC$_c$, only models with an acceptable fit to the data (significant Likelihood-ratio χ^2 goodness-of-fit statistic), and only model parameters that had statistically significant regression coefficients. Habitat variable codes are defined in Appendix 2.

Dependent variable (bird species)	Best approximating model (minimum AIC$_c$ value)	Likelihood -ratio χ^2	*P*-value	Adjusted R^2
American Robin	Y = –7.56 + 3.84(HERBT) + 0.003(LGCON) – 0.21(SMDECT) + 0.51(SHRBT) + 2.14(BPSBT)	47.45	0.00000	0.96
Black-headed Grosbeak	No significant parameters found	--	--	--
Black-throated Gray Warbler	No significant parameters found	--	--	--
Brown Creeper	Y = –5.64 + 2.74(CCOVT) + 0.006(LGCON)	24.79	0.00000	0.68
Chestnut-backed Chickadee	Y = –1.97 + 2.12(CCOVT) – 0.004(LGCON)	34.62	0.00000	0.80
Common Yellowthroat	No significant parameters found	--	--	--
Dark-eyed Junco	Y = 1.43 + 9.27(CSWDT) + 4.69(HERBT) – 0.91(SHRBT) – 9.70(FNWDT)	27.72	0.00004	0.42

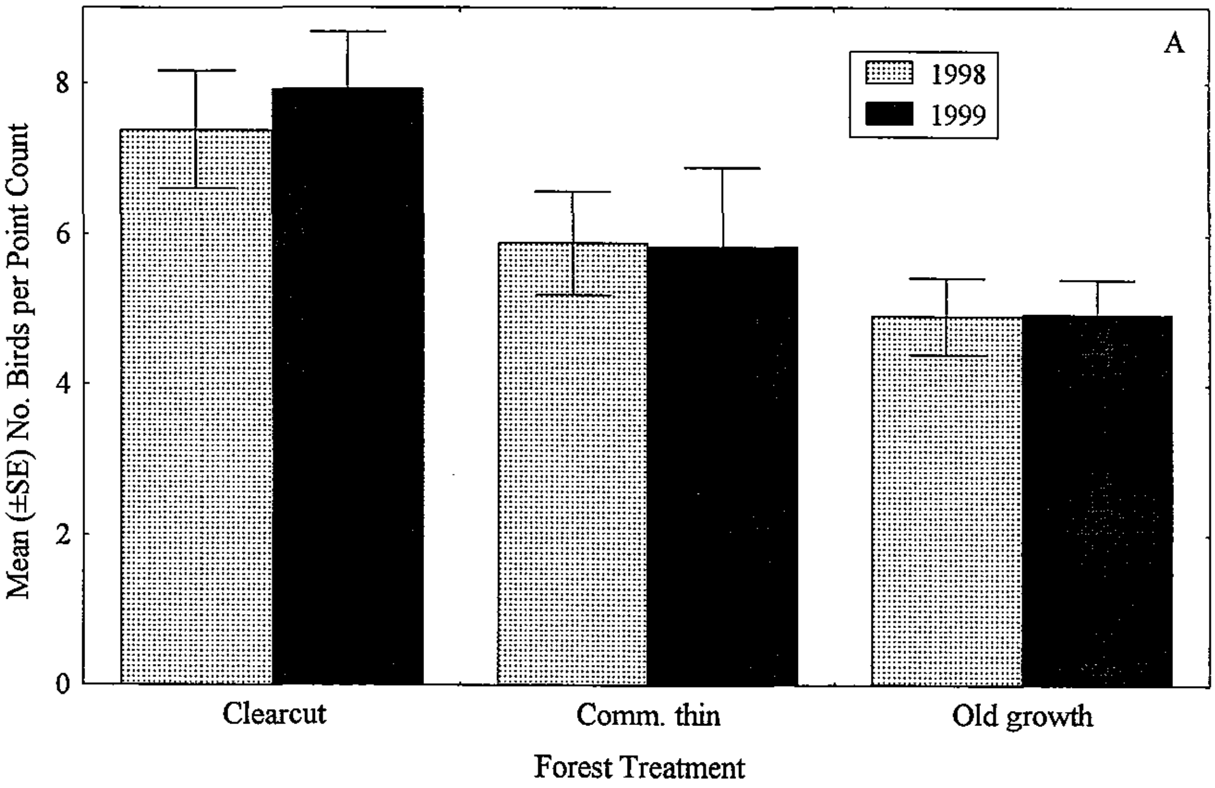
Evening Grosbeak	No significant parameters found	--	--	--
Golden-crowned Kinglet	$Y = -5.64 + 2.74(\mathrm{CCOVT}) + 0.006(\mathrm{LGCON})$	24.79	0.00000	0.62
Gray Jay	$Y = -5.24 + 0.03(\mathrm{LGDEC}) + 0.27(\mathrm{SMDECT}) - 0.0005(\mathrm{SMCON})$	27.76	0.00004	0.03
Hairy Woodpecker	$Y = -3.60 + 0.01(\mathrm{SMSNG}) - 5.20(\mathrm{CSWDT}) + 3.16(\mathrm{CCOVT}) - 0.01(\mathrm{LGCON}) + 0.003(\mathrm{SMCON}) + 0.02(\mathrm{TRHT})$	32.17	0.00000	0.48
Hermit/Townsend's Warbler	$Y = -9.20 - 0.002(\mathrm{SMCON}) + 0.14(\mathrm{TRHT}) + 0.15(\mathrm{LGDEC}) - 0.21(\mathrm{CBOT}) + 0.02(\mathrm{LGCON})$	44.69	0.00000	0.14
Hutton's Vireo	No significant parameters found	--	--	--
MacGillivray's Warbler	Model performance low (did not significantly "fit" the data)	--	--	--
Orange-crowned Warbler	$Y = -7.11 + 1.11(\mathrm{SHRBT}) - 8.22(\mathrm{FERNT}) - 2.14(\mathrm{CCOVT}) - 0.45(\mathrm{TRSDT})$	85.90	0.00000	0.87
Pacific-slope Flycatcher	$Y = -61.38 + 0.002(\mathrm{SMCON}) + 1.28(\mathrm{CBOT}) + 5.93(\mathrm{SHRBT}) - 0.16(\mathrm{LGDEC}) - 0.17(\mathrm{SMDECT})$	38.41	0.00000	0.63
Red-breasted Nuthatch	No significant parameters found	--	--	--
Rufous Hummingbird	$Y = -21.19 + 33.89(\mathrm{ORSBT}) + 0.003(\mathrm{SMCON}) + 17.61(\mathrm{BPSBT})$	46.06	0.00000	0.33

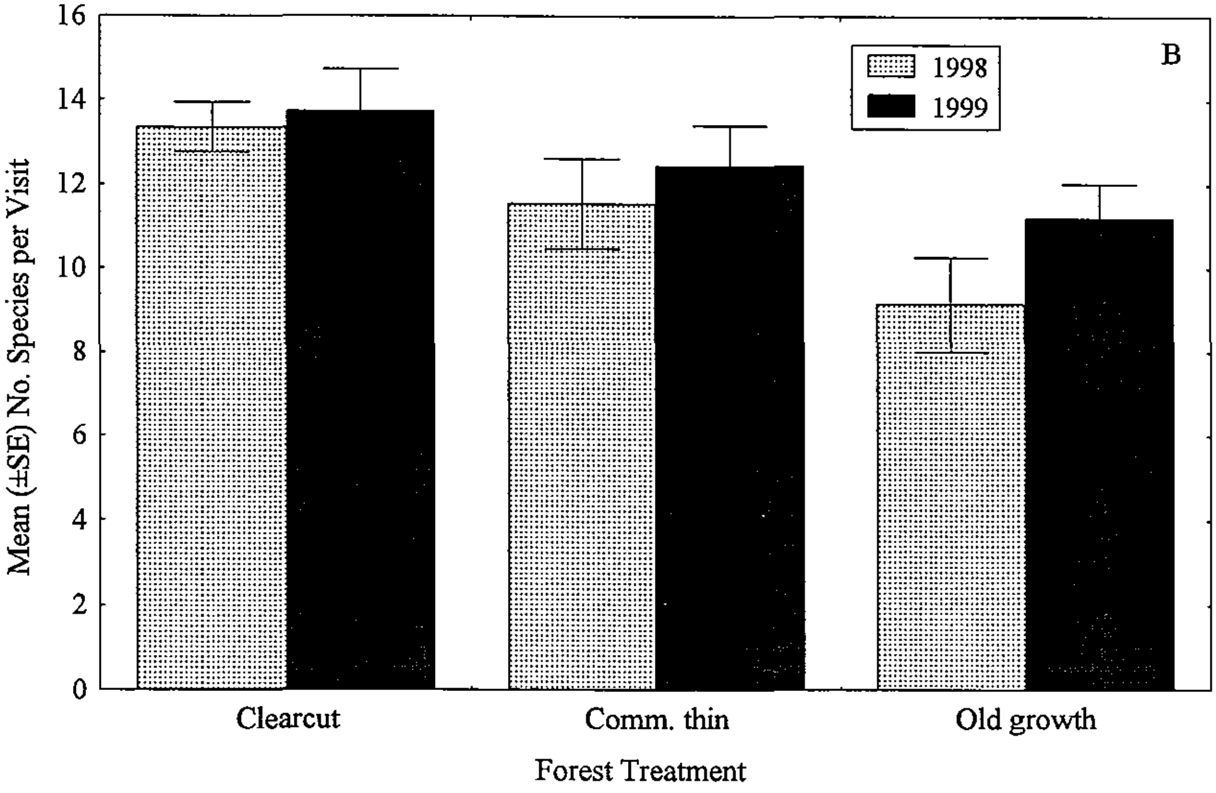
Song Sparrow	Y = 16.26 – 3.57(HERBT) – 9.93(CCOVT) – 1.33(FORBT)	115.66	0.00000	0.87
Spotted Towhee	Y = 1.62 – 3.71(CCOVT) + 4.29(BLSBT)	51.73	0.00000	0.80
Steller's Jay	No significant parameters found	--	--	--
Swainson's Thrush	Y = –5.83 + 0.0009(SMCON) + 8.45(ORSBT) + 3.93(BPSBT) + 3.85(BLSBT)	33.90	0.00000	0.61
Varied Thrush	Y = 0.82 + 8.58(CCOVT) + 0.07(TRHT) – 0.002(SMCON) – 31.44(ORSBT) – 0.05(LGCON)	40.59	0.00000	0.66
Western Tanager	No significant parameters found	--	--	--
White-crowned Sparrow	Y = 2.14 – 5.59(CCOVT) – 0.58(SHRBT) + 8.18(TRSDT)	51.09	0.00000	0.71
Willow Flycatcher	Y = 1.09 – 2.62(CCOVT) – 4.58(ORSBT)	33.58	0.00000	0.94
Wilson's Warbler	Y = –7.13 + 0.0005(SMCON) + 0.51(SHRBT) + 2.65(BLSBT)	21.56	0.00008	0.66
Winter Wren	Y = –5.92 + 2.65(CCOVT) + 0.007(SMSNG) + 0.38(SHRBT)	30.70	0.00000	0.87

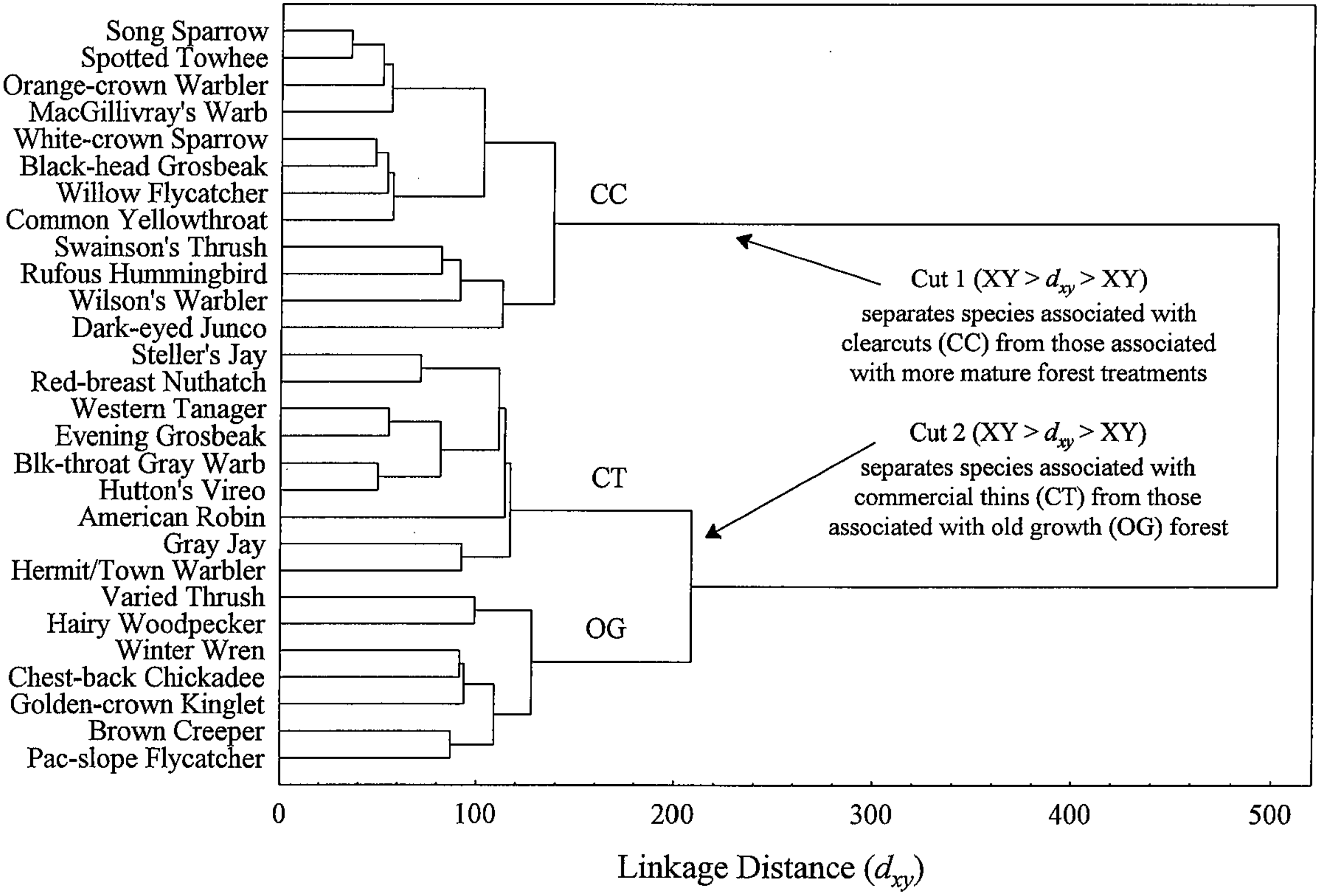
Figure Legends

Figure 1. Differences in the numbers of breeding birds (regardless of species; A) and species richness (numbers of species; B) among three forest treatments studied in the Douglas-fir - Western Hemlock zone of the southwest Cascade Mountains, Washington, 1998–1999.

Figure 2. Cluster analysis hierarchical tree resulting from Ward's minimum-variance linkage fusion (minimization of within-group dispersion) using City-block (Manhattan) distance and standardized data. Bird species with similar distributions among forest stands were clustered together based upon their mean relative abundance estimated during two years of study, 1998–1999, in the southwest Cascade Mountains of Washington.


A
▨ 1998
■ 1999
Mean (±SE) No. Birds per Point Count
0
2
4
6
8
Clearcut
Comm. thin
Old growth
Forest Treatment


B
▨ 1998
■ 1999
Mean (±SE) No. Species per Visit
0
2
4
6
8
10
12
14
16
Clearcut
Comm. thin
Old growth
Forest Treatment



Cut 1 (XY > d_{xy} > XY)
separates species associated with
clearcuts (CC) from those associated
with more mature forest treatments

Cut 2 (XY > d_{xy} > XY)
separates species associated with
commercial thins (CT) from those
associated with old growth (OG) forest