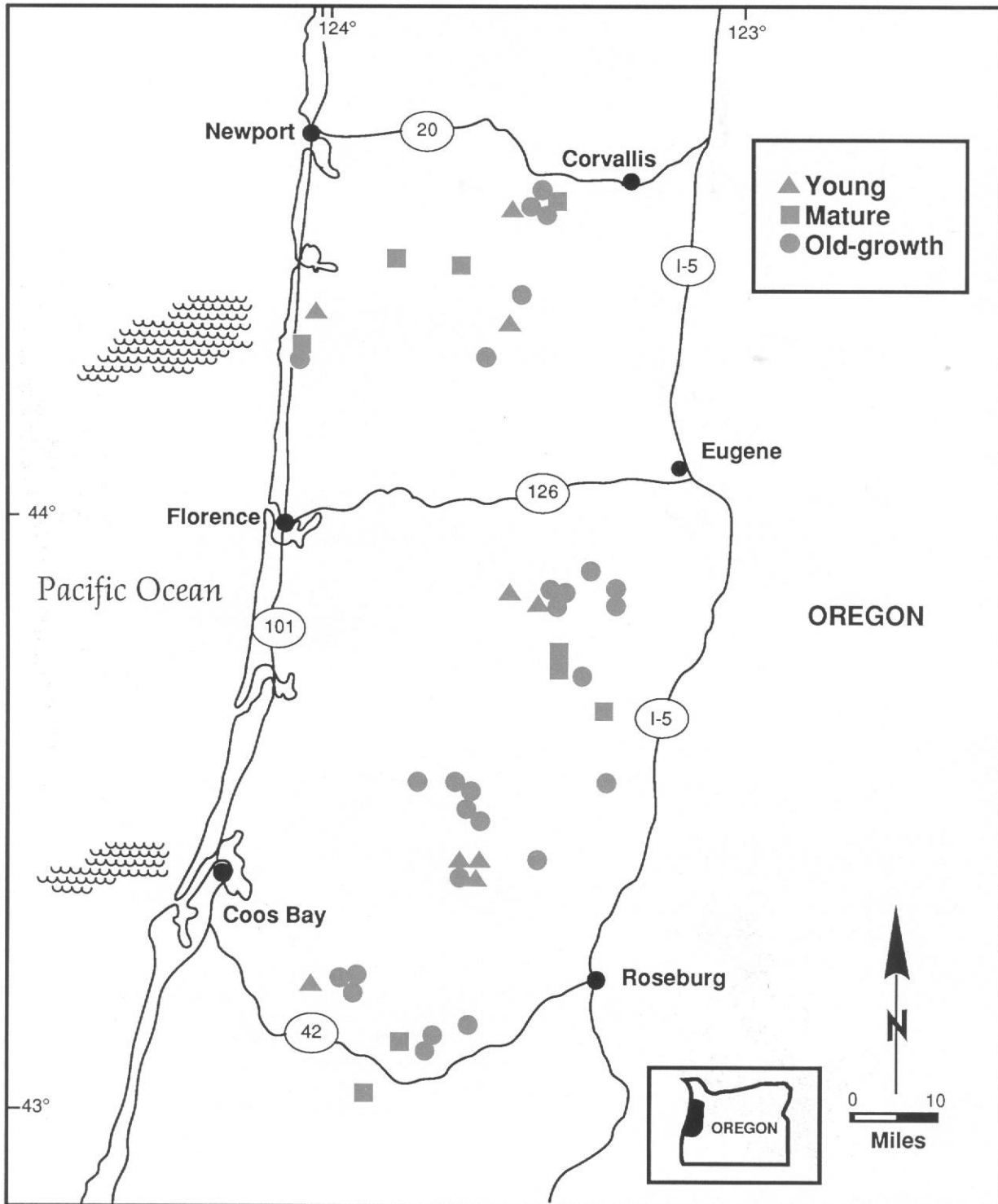


**Part 4**  
**Diurnal Forest Birds of**  
**Oregon and Washington**



Location of study sites.

# Spring Bird Communities in the Oregon Coast Range

Andrew B. Carey, Mary Mae Hardt, Scott P. Horton, and Brian L. Biswell

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## Authors

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## Abstract

Our objectives were to determine the value to birds of old-growth forests relative to mature and young forests in the southern Oregon Coast Range. Special emphasis was placed on cavity-using birds. We studied birds in 45 stands in 1985 and 33 stands in 1986. Over 60,000 individuals of 91 species were counted; 989 observations on the foraging activities of cavity-using birds were recorded; 277 nests of cavity users were found and described; snag densities were estimated by four size-classes and three decay-classes. We calculated a birds-per-area index (BAI) from the counts and diversity indices from the BAI. Bird species diversity and total bird abundance did not differ significantly among the young, mature, and old-growth stands. Fourteen species were most abundant in old growth; 10 were cavity users (including the crevice-nesting brown creeper and the spotted owl). Two species that do not nest in cavities, the western flycatcher and the varied thrush were also abundant in young and mature stands. Two, the marbled murrelet and the olive-sided flycatcher, were rare in young and mature stands. All the cavity users (including the brown creeper) selected very large snags

for nesting; snags of the average sizes used by these birds were larger than those normally produced in young stands. Under current conditions, the cavity-using birds depend on old growth.

## Introduction

“Are there unique features, species, or important values associated with old-growth forests?” ask Franklin and others (1981). They review the literature and ongoing research and conclude that old-growth forests provide specialized habitats and differ from both natural and managed younger forests. Research shows some differences between managed forests and old-growth forests in avian community composition (Hagar 1960) and total bird abundance and constancy of abundance (Bowles 1963). And although 18 or more species of vertebrates appear to find optimal conditions in old growth, quantitative avifaunal studies across stages of forest development are lacking in the Douglas-fir forests of western Oregon and Washington (Meslow and Wight 1975, Meslow and others 1981). The Old-Growth Forest Wildlife Habitat Program was chartered to quantify the value of old growth to wildlife (Carey and Spies, this volume; Ruggiero and Carey 1984). We began our research in the Oregon Coast Range in 1985 under the aegis of the Old-Growth Program.

Our objectives were to determine the value to birds of old growth relative to young and mature Douglas-fir forests in the Oregon Coast Range. In particular, we wanted to

determine if the bird communities in old growth differed from the bird communities in mature and young forest in total abundance, diversity (numbers of species and the degree to which the communities were dominated by a few species), composition of species, and structure (ranked abundance of the species) because these are all components of biodiversity; simple presence or absence of species does not reflect all the important aspects of biodiversity, and few species in the Pacific Northwest are so specialized that they would be expected to be confined to old growth (Meslow and others 1981). We also wanted to determine which species reached maximum abundance in old growth and which, if any, were found exclusively in old growth. We placed special emphasis on cavity-using birds because Mannan and others (1980), in an unreplicated study, report cavity-using birds to be strikingly more abundant in old growth than in younger stands. And Cline and others (1980), Mannan and others (1980), and Meslow and others (1981) express concern over the loss to timber management of large, Douglas-fir snags that are important to cavity-using birds.

Franklin and others (1981) list some structural features unique to old-growth (as compared to young and mature) forests that could be important to birds; we wished to determine whether these features were important. These features and their putative value to birds (and the tests we made) include:

- Large, old Douglas-fir trees have deeply furrowed bark that provides a unique environment for bark arthropods and may be important foraging substrates for bark-foraging birds, especially the brown creeper. We test the hypotheses: (a) young, mature, and old-growth stands do not differ in the density of large (>100 cm in diameter-at-breast height, d.b.h.) Douglas-fir; (b) abundance of bark-foraging birds is not positively correlated with the densities of large Douglas-fir trees; (c) bark-foraging birds do not differ in abundance among young, mature, and old-growth stands; (d) brown creeper abundance is not correlated with the density of large Douglas-fir trees; (e) brown creeper abundance does not differ among young, mature, and old-growth stands. Rejection of the last two hypotheses would imply that brown creepers forage in large trees out of proportion to their availability relative to small trees. We examined the foraging behavior of brown creepers to test this implicit hypothesis.
- Two or more age-classes of conifers that form an overstory, midstory, and sometimes an understory result in a vertical diversity of coniferous foliage that may support a diversity and abundance of birds that forage among the foliage of trees (foliage foragers) that exceeds that in young or mature forests. We test the hypotheses: (a) foliage-height diversity does not differ among young, mature, and old-growth stands; (b) the abundance of foliage foragers

does not differ among young, mature, and old-growth stands; (c) the diversity of foliage foragers does not differ among young, mature, and old-growth stands; (d) the diversity of foliage foragers is not correlated with foliage-height diversity; (e) the abundance of foliage foragers is not correlated with foliage-height diversity.

- Large, standing, dead trees may provide important nesting substrate for cavity-using birds. We test the hypotheses: (a) the density of large snags does not differ among young, mature, and old-growth stands; (b) the abundance of cavity-using birds does not differ among young, mature, and old-growth stands; (c) cavity-using birds do not use large snags for nesting out of proportion to their availability relative to small snags.
- Spatial diversity of vegetation brought about by gaps in the canopy caused by the death of large trees may provide for a greater diversity and abundance of birds in the understory and on the ground. We test the hypotheses: (a) spatial diversity of vegetation does not differ among young, mature, and old-growth stands; (b) the diversity and abundance of birds associated with the forest floor do not differ among young, mature, and old-growth stands.

Our final objective was to determine if the complex moisture-temperature gradient governing plant community composition in the Pacific Northwest (Franklin and Dymess 1973) resulted in differences in bird species diversity or species abundances among old-growth stands on different parts of the gradient (wet, mesic, and dry sites). Franklin and others (1981) discuss the value of streams in old growth. We do not address streams here because the influence of small streams and seeps on upland, spring bird communities in the Oregon Coast Range was reported by Carey (1988).

## Methods

### Experimental Design

Study stands were selected under the vegetation community ecology portion of the Old-Growth Program (Carey and Spies, this volume), but we were unable to find enough stands for three complete replicates of the Program's design: three young, three mature, three wet old-growth, three dry old-growth, and three mesic old-growth stands. Forty-five stands were studied in 1985: 8 young, 10 mature, 14 mesic old-growth, 8 dry old-growth, and 5 wet old-growth stands (see frontispiece). In 1986, because of cuts in funding, only 33 stands were studied: 6 young, 8 mature, and 10 mesic old-growth, 5 dry old-growth, and 4 wet old-growth stands. Young and mature stands were not classified into moisture-classes, but spanned the same moisture gradient that the old-growth stands spanned. We could not find stands of 100 ha or more as called for in the research plan. Stand size

averaged 29 ha, ranging from 14 to 62 ha. Two small old-growth stands studied in 1985 were replaced with larger stands in 1986. Study stands were in four large clusters: between Corvallis and Yachats, west of Drain, northwest of Roseburg, and between Roseburg and Coos Bay, Oregon. The clusters covered the southern Coast Range western hemlock forest type but also included the coastal Sitka spruce forest type near Yachats, the Umpqua Valley margin mixed-conifer forest type northwest of Roseburg, and the southwest Oregon mixed-evergreen forest type near Remote. Each cluster contained young, mature, and old-growth stands, but not enough stands of each type to be treated separately.

Douglas-fir was a dominant species in each stand. Young stands were 40 to 72 years old; mature stands were 80 to 120 years old, old-growth stands were 200 to 525 years old. One old-growth stand had a mixed-aged canopy of trees 130 years old and old-growth trees of unknown age, d.b.h. of 100 cm or more, and density of 17.4 per hectare. The old-growth and mature stands and three of the young stands originated after catastrophic wildfire. Five of the eight young stands originated after human disturbance (logging or clearing) as evidenced by stumps, old roads, or railroad grades.

### Sampling Plan

We located 12 points 100 m apart along a transect through each stand; our stands were not large enough to use the Program's recommended 150 m between points. Because stands were small and we maintained a 75-m buffer along stand edges, the points systematically covered the interior of each stand. The smallest stands were too small for 12 points. One stand had only 7 points (dropped in 1986), one had 10 points (dropped in 1986), and three had 11 points (two dropped in 1986). These points served as centers for nested circular plots for describing vegetation and for bird counts; they also delineated segments of 30-m-wide strip transects used to sample snags.

### Sampling Techniques

Birds-Pilot studies (Manuwal and Carey, in press) compared line transects, variable-circular plots, and territory mapping as methods for estimating bird abundance and describing bird communities for contrasting young, mature, and old-growth forests. Variable-radius circular plots (Reynolds and others 1980) with 12 sampling points and six visits gave the best return per unit effort in determining species presence and abundance, but densities differed from territory mapping by 13 to 41 percent. Major differences were overestimates from counting birds more than once, particularly birds of species whose home ranges were large relative to spacing between the plots or that could be detected at long distances (for example, more than 75 m).

With the pilot study as the basis for our sampling, we recorded all birds seen or heard during 6 to 11, early morning, 8-minute visits during late April, May, and June at each of the sampling points in the stands. Species not commonly recorded at sampling points were recorded if seen while the observer walked between points and during searches for nests and observations of foraging behavior that immediately followed the count surveys; 4 to 5 hours were spent in each stand on a sampling day. Sampling was not done on windy or rainy days. The minimum number of visits to a stand was six in a year. We tried to visit stands with less than 12 points more often than the stands with 12 points (appendix tables 14, 15). For example, the maximum was 11 visits to the stand with 7 points. In 1985, all but three stands had six to eight visits, with the range caused by rainy days, observer illness, and other random events. In 1986, all but two stands were visited seven times (the two had six visits). As predicted by the pilot study, species richness reached an asymptote before 72 8-minute counts (six visits to a stand with 12 points) had been done.

We estimated the distance to each bird detected that was not flying through or over the stand during the 8-minute counts. Distance estimation was aided by two flags 25 m from each point, flags midway between points, and by rangefinders. Distances more than 100 m were not recorded because we and our field biologists concluded that estimating distances beyond 100 m with a 20-percent precision was impossible.

We made a strong effort to avoid counting the same bird more than once from the same point. We and our field biologists believe that we were successful in minimizing double counting. If a bird could be heard from more than one point, it was recorded only at the point closest to it. The average (among species) third quartile of detection distances was  $51 \pm 0.4$  (SE) m and did not differ among young, mature, and old-growth stands. Because we used only detections within the third quartile for calculating abundance indices (see section on data analysis), any bias (dependence) from assigning a bird to only one point should have been minimized.

**Controlling for differences among observers**-Eleven biologists counted birds in 1985 and eight counted in 1986. Five counted birds in both years. All had experience in bird identification before employment, and all were trained for 2 to 3 weeks before sampling each year they participated in sampling.

Training consisted of instruction and practice in the field and written protocols that documented objectives, methods, assumptions of techniques, and consequences of violating assumptions. Protocols were reviewed in group discussions and implemented in the field both by groups and by pairs of biologists. All were provided with binoculars, field guides to

bird identification, recordings of bird calls and songs in northern California and southern Oregon, as well as opportunities to review recordings based on national and regional bird calls and songs. A written, phonetic guide to bird calls and songs (Carey and others 1990) was developed by the group, based on their experiences in the southern Coast Range, and all observers were provided with a copy. Training in bird identification, identification of calls and songs, and aural distance estimation in the field was provided to the group before sampling began; individuals had opportunities to practice alone. The biologists were trained in the use of rangefinders and ocular estimation of distance on courses with targets at various, measured distances. Targets were placed at measured distances near offices so rangefinders could be calibrated daily (flags 25 m from each station allowed checking of rangefinders during actual surveys).

During surveys, rangefinders were used to check ocular and aural estimates of distances to birds. Flags at 25-m intervals along the transect allowed observers to continually check their distance estimates for birds that were too far away to be visually or aurally located in a specific tree. We and our field biologists believed that we maintained a high degree of accuracy in bird identification and distance estimation throughout the sampling.

Observers were in three Oregon locations in 1985, with four in Corvallis, two in Lorane, and five in Winchester: In 1986, three biologists were in Corvallis and five were in Sutherlin. Within each geographic area, observers were systematically rotated among the stands being sampled; young, mature, and old-growth stands were sampled in each area. Biologists in each geographic area (three areas in 1985, two areas in 1986) regularly met to discuss the birds seen and heard and to review one another's data sheets. Regular telephone contact was maintained between the geographically separated groups during the sampling season to discuss methodology and the birds being seen and heard.

**Nests and foraging behavior-**After each morning's bird counts, we searched the stands for nests and recorded foraging behaviors of cavity-using birds. Nests, nest trees, and nest environments were described (Nelson 1989). For foraging behaviors, we recorded the vertical location by foliage strata (upper, middle, or lower canopy; understory; shrub layer; ground), the horizontal location (mainstem; inner, center, or outer branch; log), the species of tree, the substrate (bole; large, medium, or small branch; twig; shrub), the condition of the tree (live good, live poor, snag decay-class), the d.b.h. of the tree (0-9, 10-19, 20-49, 50-99, and  $\geq 100$  cm), the dominance status of the tree (suppressed, subordinate, dominant/codominant), and the object (foliage, bark, live wood, dead wood, flower, bud, insect, and other) for the first foraging activity observed for each bird seen.

**Vegetation-Vegetation** was characterized on two scales: 13-m-radius plots for ground cover, shrub, and midstory variables; and 25-m-radius plots for site and overstory variables. Cover variables included fallen trees by three decay-classes (combined from Franklin and others 1981): 1, intact; 2, bark sloughing to absent, sapwood well-decayed; 3, tree completely in contact with the ground, bark absent, and all wood well-decayed). Other cover variables were herbs, ferns (mostly sword fern), berry-producing deciduous shrubs (mostly blueberry and blackberry), other deciduous shrubs (mostly oceanspray, filbert, and maple), evergreen shrubs (mostly salal, Oregongrape, Pacific rhododendron), broad-leaved evergreen midstory trees, deciduous midstory trees, and needle-leaved midstory trees. Overstory variables included canopy cover of three classes of trees (deciduous, broad-leaved evergreen, and needle-leaved evergreen), counts of snags by three decay-classes (combined from Cline and others 1980): 1, bark and branches mostly intact, sapwood firm; 2, limbs stubs to limbs absent, sapwood soft; 3, well-decayed, bark and sapwood sloughed). We also counted trees by diameter-classes (10-49 cm, 50-99 cm, and 1100 cm) for Douglas-fir, western hemlock, cedars-Port-Orford-cedar, incense-cedar, and western redcedar, Pacific madrone, giant chinkapin, bigleaf maple, other conifers (mostly grand fir), and other deciduous trees. Snags sampled along the transects were measured and described in more detail than those in the circular plots, and their use for nesting and roosting by cavity-using birds was compared to that of snags generally available (Nelson 1989).

### Data Analysis

Observations of moving birds, birds more than 75 m from a sampling point, or birds recorded only once in a stand were discarded before calculating indices of birds per effort (BEI) and birds per area (BAI). We did this to avoid counting individual birds more than once, eliminate the observations with the most error (the most distant observations), reduce among-observer differences in effective detection distances, eliminate transient species from the counts, and maintain comparability with the results of the bird community studies in the Oregon Cascade Range, the southern Washington Cascade Range, and the regional analysis of the Old-Growth Program data.

The recorded observations for each species were examined to determine if the rate of cue (call, song) emission varied with time. The black-headed grosbeak, Swainson's thrush, and western tanager were not detected during the early counts. We subtracted the sampling done in the first 5 to 18 days (depending on species) from the effort to adjust for the periods when each species was not present (or not singing). From these reduced data, we calculated bird species richness (number of species by stand) and an index to abundance based on effort-mean number per count per species per stand (BEI).

For analyses related to community structure and bird species diversity, we calculated an index to abundance based on area sampled per species (BAI). Placing the birds on an area-sampled scale allowed calculation of diversity indices and examination of community structure (ranked abundance) (Hutto and others 1986). Such analyses cannot be done reliably with simple count data.

First, we eliminated effort and observations of observers who seemed to have especially poor sensitivity to the calls or songs of particular species (these are known as "window species" for that observer, Kepler and Scott 1981). Poor sensitivity was defined as having a mean number per count less than 50 percent of the median (among observers) mean number per count. For the 2 years, 15 of 929 observer-bird species combinations were dropped. Window species did not appear to reflect differences in the hearing, experience, or awareness of the observers. They seemed to be unique interactions between particular species and individual observers.

We then examined the detections-versus-distance curves by stand type to determine if differences existed among young, mature, and old-growth stands (we found none). From the distributions of birds detected over distance, we calculated the third quartile detection distance for each species. We used this distance as an effective radius of detection for that species and calculated the area sampled around each point. The third quartile proved to be a good approximation of the shoulder in the detection curve—the distance at which a marked decline in numbers of birds was detected. The abundance index was calculated as the numbers of cues of individual birds detected within the third quartile divided by the area sampled (number of points times area sampled per point times the number of visits per point). Abundances are reported on a birds-per-40-ha scale. We calculated coefficients of variation for the density indices for each stand and stand-class.

For species that were detected mostly ( $\geq 270$  percent) by their songs, we deleted observations of nonsinging birds; later we doubled the BAI of the songs-only species, on the assumptions we were recording only males and that all males were mated (Emlen 1977, Reynolds and others 1980).

Many sources of bias and error are possible in count indices and cue-density indices (Dawson 1981, Emlen 1977, Hutto and others 1986, Verner 1985; see Ralph and Scott 1981 for an extensive treatment). But our BAI require fewer assumptions and incorporation of less error and bias than the abundance index, BEI (Carey 1983, Ramsey and others 1987, Raphael 1987a). Our BAI is a measure of bird density only to the extent that bird call-and-song counts per unit area are a measure of density. Some birds may not be counted, and

some may be counted twice. If such a sampling error differs among bird species, among groups of observers, or among stand types, then the BAI (and the BEI) would be biased.

Placing the birds on an area-sampled scale helped to account for differences in detectability among species. Elimination of long-distance detections and window species was designed to reduce among-observer variability. The remaining among-observer variability was evenly apportioned among the stands through our systematic rotation of observers. Calculating species-by-species third quartiles of detection distances was an effort to reduce the errors in identification of species and estimation of distances in the area of marked decline in detectability. We could not use mathematical models of the decline in detectability because the 27 species for which we had numbers of detections sufficient to model detectability differed markedly in the shape of the detectability curves. And we could not relate the shape of the detectability curve to either the cue quality (strength and pitch of calls and songs) or to the vertical position of the species in the canopy. Therefore, we could not choose a model to fit all species, or several models that could be applied to species of like songs and calls or like positions in the canopy.

In both years, five species exhibited "spikes" (high counts in the first few meters followed by a sharp reduction in counts and eventual additional decline in detectability), six species had "donuts" (low counts in the first few meters, followed by higher counts, then by declining counts), four species had spikes and donuts, and eight species differed in pattern between years. We could not relate patterns to cue quality or usual location of the species in the canopy. Deletion of nonsong cues from songs-only species did reduce the spikes. Using the third quartile distances typically encompassed the bulk of the donut. Thus, we effectively reduced some of the error from differences among species. Error in the BAI was likely to be greater in the less abundant and less detectable species, simply because of sample sizes. We chose diversity indices (Magurran 1988) and made comparisons of community structure with these errors in mind.

Margalef's index (MI) accounts for variability in species richness by weighting the number of species by the total number of birds present; thus, MI based on BAI should be a better measure of richness than number of species based on simple counts. The Berger-Parker index (BPI) expresses the degree to which the most abundant species dominates the community and is thus robust to errors in the estimates of species of low abundance. We used Kendall's coefficient of concordance (Zar 1984) to test differences among age-classes and moisture-classes in the ranked abundance of species, and we used Kendall's coefficient of rank correlation and its graphical representation (Sokal and Rohlf 1981) to display the results of the analyses of ranked abundance. We applied this analysis only to species that occurred in at least 90 per-

cent of the stands in any one stand type (young, mature, dry old-growth, mesic old-growth, wet old-growth) to eliminate rare species from the data set. In 1985, these tests were based on the 16 most abundant species, and, in 1986, on the 14 most abundant species. All these species were detected 100 times or more during the counts. Error in the estimates of species of low abundance was not important to the analyses of community structure.

We used direct gradient analyses (box-and-whisker plots and scatter plots) to explore our data. We were particularly interested in how much variability was in each variable-where that variability lay in relation to stand-age and environmental gradients, how observations on each variable were distributed in a statistical sense, and how variability changed along the distributions. Correlation coefficients (linear correlations, correlations with log-transformed variables, and rank correlations) were used to identify redundancies among the variables and to quantify bird species' responses to gradients and relations between gradients.

Parametric and nonparametric (Kruskal-Wallis tests) analyses of variance, Mann-Whitney U-tests, and median tests were used to examine the statistical significance of comparisons among categories. Bartholomew's test for gradients in proportions was used to examine patterns of abundance (proportions of stands in which the species was present) of birds of low abundance across age-classes (Fleiss 1973); all recorded observations were used to determine presence and absence. Because our study sites and sampling points were not Selected randomly, levels of significance are biased. But because we intentionally sampled a wide range of variation in stands in the southern Coast Range, we maximized variability and the significance levels should be conservative (Gauch 1982)-our P-values are probably larger than those a random sample would have produced. The generalizability of statistical or mathematical models and predictions derived from the data is unknown, however. As with any study, extrapolation beyond the bounds of the conditions examined would be risky; the degree of risk is unknown. We recognize that the power of statistical tests is low when variability is high and sample sizes are small. We caution the reader that failure to detect differences under these conditions does not necessarily indicate that differences do not exist, only that the data did not support rejection of the null hypothesis.

We examined bird community attributes and species' abundances on two levels of gradients. The first level included stand age (in years, sometimes log-transformed), stage of forest development (young, mature, old-growth), and moisture categories (dry, mesic, wet). These first-level gradients reflect complex interactions of site and the process of forest development.

The second level included gradients based on cover-classes and counts made at the sampling points or along transects. These values were averaged for each stand, classes were combined, and the BPI was calculated. The second-level gradients we developed were density of trees 100 cm or more in d.b.h.; diversity of canopy conifer sizes (BPI based on density of trees in the three size-classes); density of broad-leaved evergreens (Pacific madrone and giant chinkapin) in the canopy; density of slightly to moderately decayed snags 50 cm or more in d.b.h.; density of slightly to moderately decayed snags 100 cm or more in d.b.h.; cover of deciduous trees in the midstory and understory; cover of ferns, herbs, and berry-producing shrubs less than 2 m tall; cover of evergreen shrubs less than 2 m tall; and the proportion of cover less than 2 m tall that was ferns, herbs, and berry-producing shrubs.

## Results

### Characteristics of Old-Growth Stands

Old-growth stands were easily distinguishable from young and mature stands on the basis of density of Douglas-fir trees by diameter-class (table 1). Discriminant analysis using the three density variables correctly classified 93.6 percent of the stands ( $P < 0.01$ ); one mature stand was classified as old growth, one as young; one young stand was classified as mature. The density of coniferous trees 100 cm or more in d.b.h. was positively correlated with stand age (fig. 1,  $r = 0.78$ ,  $P < 0.01$ ).

The vertical diversity of conifers (as measured by the BPI) in the canopy was positively correlated with stand age (fig. 2,  $r = 0.51$ ,  $P < 0.01$ ) and varied almost three-fold among stands. The BPI was significantly different among the young, mature, and old-growth stand types (Kruskal-Wallis test,

**Table 1-Density of Douglas-fir by diameter-class and age-class of stands in the southern Oregon Coast Range, 1985-86; 8 young, 10 mature, and 29 old-growth stands were sampled**

Diameter-class	Age-class	Density (stems per hectare)		
		Mean	Standard error	Mode
10-49 cm	Young	269.7	29.0	213.4
	Mature	118.8	19.2	74.8
	Old	<b>27.4</b>	<b>6.2</b>	<b>.0</b>
50-99 cm	Young	<b>29.3</b>	<b>6.9</b>	<b>20.4</b>
	Mature	<b>64.4</b>	<b>8.1</b>	<b>54.0</b>
	Old	<b>24.8</b>	<b>2.6</b>	<b>33.6</b>
≥ 100 cm	Young	1.5	.6	.0
	<b>Mature</b>	<b>6.6</b>	<b>2.6</b>	<b>.0</b>
	Old	<b>22.3</b>	<b>1.8</b>	<b>16.6</b>



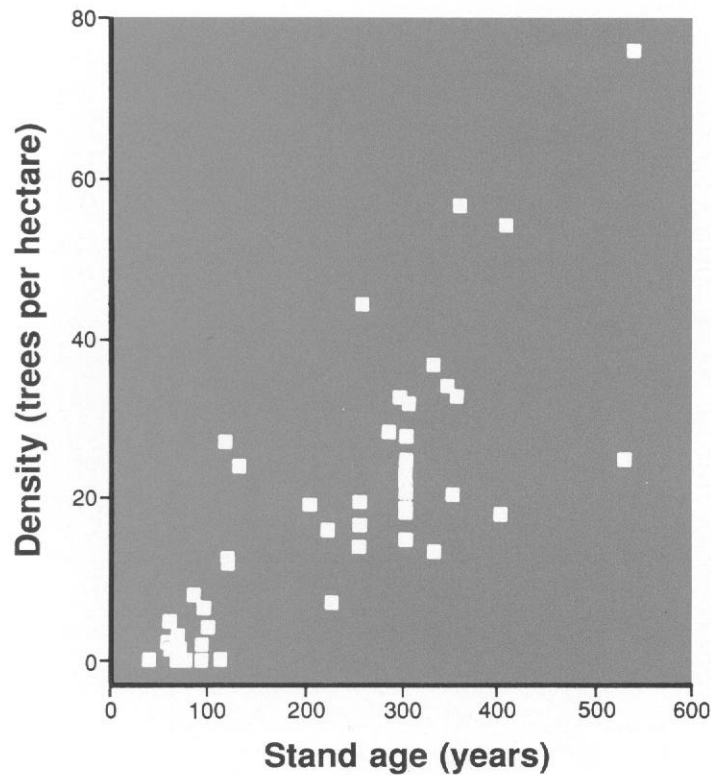


Figure 1—The density of trees 100 cm or larger in d.b.h. versus stand age in the southern Oregon Coast Range, 1985-86.

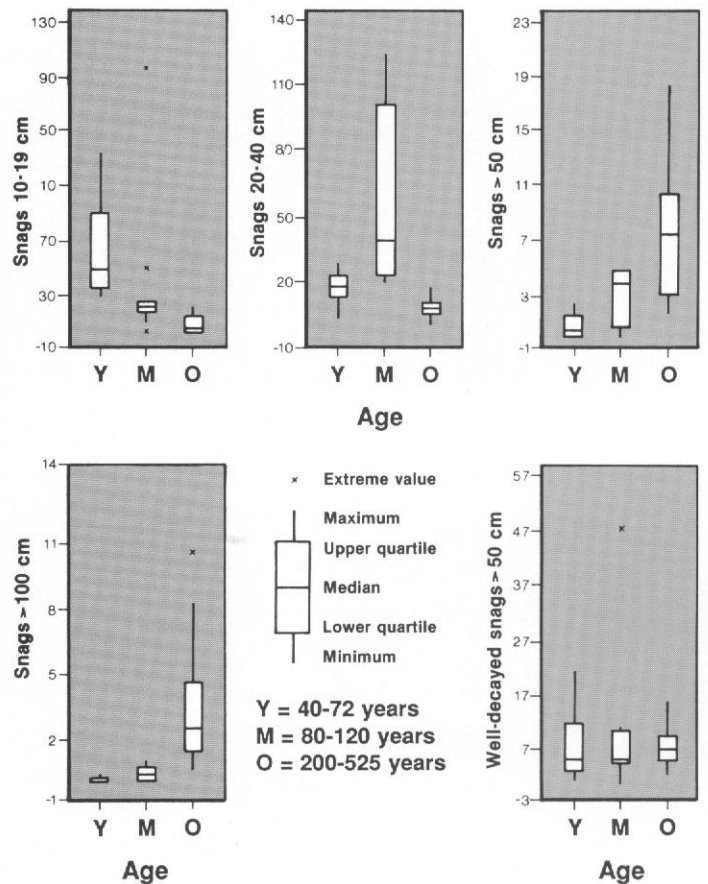


Figure 3—Snag densities by size-class and stand age-class in the southern Oregon Coast Range, 1985-86.

$P < 0.01$ ), reflecting that the values of BPI were very small in young stands (median = 1.1) and large in mature (median = 1.5) and old-growth (median = 1.7) stands. The variability of the BPI increased with stand age. Canopy height was correlated positively with stand age ( $r = 0.59$ ,  $P < 0.01$ ). Total canopy cover and cover of coniferous trees in the canopy decreased with stand age (Kruskal-Wallis,  $P < 0.01$ ;  $r = 0.50$  and  $0.49$  respectively,  $P < 0.01$ ).

Total midstory cover increased with stand age ( $r = 0.436$ ,  $P < 0.01$ ) and was much greater in old growth than in mature or young stands (Kruskal-Wallis,  $P < 0.01$ ). The number of coniferous trees in the midstory increased with stand age ( $r = 0.52$ ,  $P < 0.01$ ; Kruskal-Wallis  $P = 0.01$ ).

Small-diameter (10-19 cm) snags decreased rapidly with stand age-class (fig. 3; table 8;  $r = -0.62$ ,  $P < 0.01$ ); 20- to 49-cm-d.b.h. snags were most abundant in mature stands; large (>50-cm d.b.h.), moderately decayed (classes 1 and 2) snags increased with stand age ( $r = 0.60$ ,  $P < 0.01$ ). Very large (>100-cm d.b.h.), moderately decayed snags showed marked association with old growth, being 10 times more

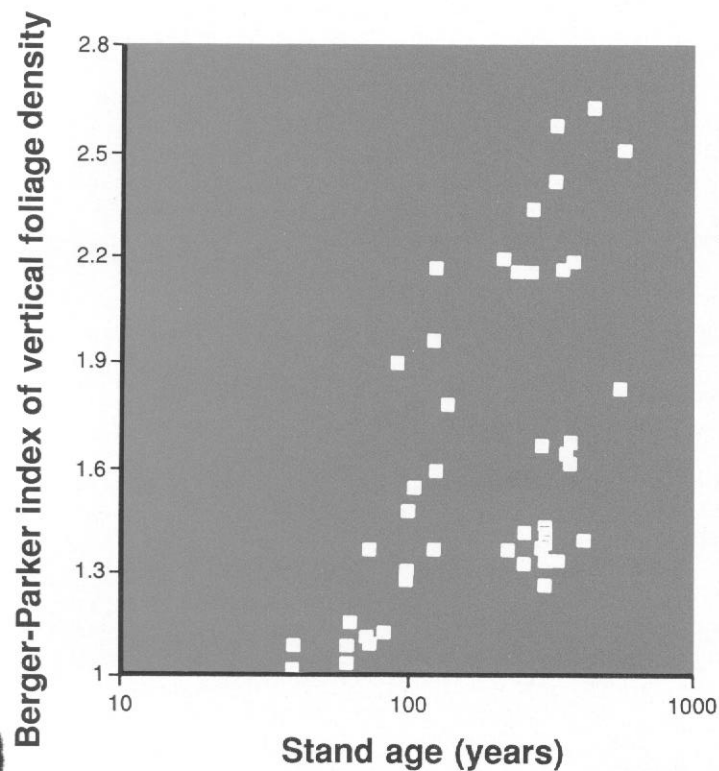


Figure 2—The vertical diversity of conifer foliage in the canopy versus stand age in the southern Oregon Coast Range, 1985-86.

**Table 2—Density of snags by diameter-class and age-class in 8 young, 10 mature, and 29 old-growth stands in the Oregon Coast Range, 1985-86**

Diameter-class	Age-class	Density (stems per hectare)		
		Mean	Standard error	Mode
>100 cm	Young	0.08	0.05	0.0
	Mature	.33	.12	.3
	Old	3.27	.47	1.8
>50 cm	Young	.79	.34	.0
	Mature	4.33	1.52	4.8
	Old	7.32	.84	6.7
20-49 cm	Young	17.63	2.60	13.6
	Mature	55.61	12.62	32.1
	Old	8.35	.84	9.1
10-19 cm	Young	64.90	56.87	36.1
	Mature	39.09	23.17	18.2
	Old	6.95	4.65	6.4

abundant there, on average, than in mature forests (fig. 3, table 2;  $r = 0.73$ ,  $P < 0.01$ ). Very large, moderately decayed snags were not commonly found in young forests (mode = 0.0). Very large, well-decayed (class 3) snags were equally abundant among the age-classes.

No variables measured in the understory were significantly correlated with stand age. The proportion of total vegetative cover that was canopy cover decreased with stand age ( $r = -0.50$ ,  $P < 0.01$ ; Kruskal-Wallis,  $P < 0.01$ ). Significant relations among understory variables and moisture-class were found in old growth. Herbs, ferns, berry-producing shrubs, and total vegetative ground cover increased with moisture (Kruskal-Wallis,  $P < 0.10$ ). Evergreen shrubs, deciduous shrubs, and total shrub cover decreased with moisture (Kruskal-Wallis,  $P < 0.10$ ). The proportion of understory cover that was herbs, ferns, and berry-producing shrubs was highly correlated with moisture (fig. 4;  $r = 0.76$ ,  $P < 0.01$ ; Kruskal-Wallis ranks: 7.5, 15.2, 26.2,  $P < 0.01$ ). The combined cover of evergreen and other deciduous shrubs was negatively correlated with moisture-class (Kruskal-Wallis ranks: 22.2, 13.9, 6.8,  $P < 0.01$ ). The proportion of understory cover that was herbs, ferns, and berry-producing shrubs was negatively correlated with the cover of evergreen and other deciduous shrubs when applied to the old-growth data set ( $r = -0.64$ ,  $P < 0.01$ ) and the total data ( $r = -0.66$ ,  $P < 0.01$ ). Discriminant analysis of preassigned moisture-classes using the understory proportion was significant ( $P = 0.0000$ ) and correctly classified 62 percent of the 29 old-growth stands; 100 percent of the wet stands and 88 percent of the dry stands were correctly classified. Twelve percent of the dry stands were classified as mesic, 38 percent of the mesic stands were classified as dry, and 25 percent of the

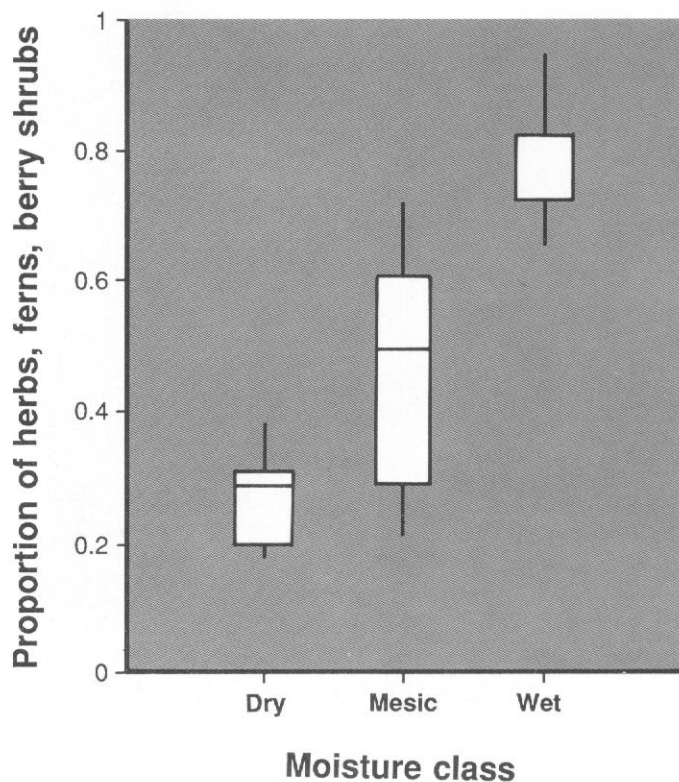


Figure 4—The proportion of cover less than 2 m tall that was composed of herbs, ferns, and berry-producing shrubs by moisture-class of old-growth stands in the southern Oregon Coast Range, 1985-86.

mesic stands were classified as wet. The proportion of understory cover that was herbs, ferns, and berry-producing shrubs proved to be a good indicator of site moisture and of the gradient in understory cover that ranges from forbs and ferns to heavy cover of salal.

#### Birds

We recorded 37,402 birds of 84 species in 1985 and 23,089 of 79 species in 1986. A complete list of the 91 species and their numbers was reported by Carey (1988). When we counted only stationary birds within 75 m of the sampling points and deleted observations of birds that occurred less than twice in each of the stands, we obtained 26,811 observations of 51 species in 45 stands in 1985 and 16,741 observations of 46 species in 33 stands in 1986 (appendix tables 10, 11). Eliminating observations of birds more than 75 m from the observer resulted in a 28-percent reduction in number of observations; combined with BAI calculations, almost 40 percent of observations were discarded. The precision of the estimates, however, was not affected. Coefficients of variation averaged  $43.6 \pm 3.4$  percent for BAI,  $44.1 \pm 6.7$  percent for BEI, and  $38.6 \pm 6.7$  percent for total counts for the 15 most abundant species. Total counts were highly correlated with the BEI ( $r = 0.99$ ,  $P < 0.01$ ) and BAI ( $r = 0.97$ ,  $P < 0.01$ ), indicating that no information was lost within species. The

**Table 3—Species comprising 75 percent of all observations in 45 stands in 1985 and 33 stands in 1986 in the southern Oregon Coast Range**

Species	1985		1986	
	Rank	Number	Rank	Number
Winter wren	1	4589	2	2347
Western flycatcher	2	3725	1	2448
Chestnut-backed chickadee	3	3382	4	1639
Hermit warbler	4	2748	3	1802
Golden-crowned kinglet	5	2225	5	1422
Wilson's warbler	6	1774	6	1075
Brown creeper	7	1365	7	1051
Varied thrush	8	1087	8	875

**Table 4—Mean number of species per stand by age-class and moisture-class, based on counts of stationary birds within 75 m of sampling points in the southern Oregon Coast Range, 1985-86 (species must have occurred at least twice in a stand to be counted)**

Year	Age-class				Moisture-class			
	Young	Mature	Old	$P^a$	Dry	Wet	Mesic	$P$
1985	20.6	20.6	20.8	0.98	21.8	20.2	21.0	0.51
Samples <sup>b</sup>	8	10	27		8	14	5	
1986	20.7	16.4	19.4	0.01	21.2	19.5	17.0	0.24
Samples <sup>b</sup>	6	8	19		5	10	4	

<sup>a</sup> Kruskal-Wallis test.

<sup>b</sup> Number of stands sampled with around 84 8-minute counts each.

correlation between total counts and BAI was much lower across species ( $r = 0.74$ ,  $P < 0.01$ ), reflecting the information gained by accounting for differences in detectability.

The same eight species accounted for 75 percent of all observations in both years (table 3). Seven species were recorded in 1985 that were not recorded in 1986: black-capped chickadee (39 observations, primary habitat: deciduous and deciduous/conifer forests), mountain quail (three observations, early stages of forest development), ruby-crowned kinglet (two observations, late stages of coniferous forest development), ruffed grouse (two observations, deciduous forests), Townsend's solitaire (seven observations, early and late stages of forest development), white-breasted nuthatch (two observations, late stages of forest development), and western woodpecker (two observations, late stages of forest development) (habitat associations from Brown 1985). Species recorded only in 1986 were chipping sparrow (four observations, early stages of forest development) and house wren (seven observations, shrub stages of forest development). Lists of species' BAI by age-class are in appendix tables 12, 13. Sampling efforts are in appendix tables 14, 15.

**Table 5—Mean values of Margalef's index (MI) of richness and the Berger-Parker index of dominance (BPI) applied to avian species birds-per-area index by age- and moisture-class in the southern Oregon Coast Range, 1985-86**

Index year	Age-class				Moisture-class			
	Young	Mature	Old	$P^b$	Dry	Mesic	Wet	$P$
MI, 1985	3.2	3.2	3.1	0.99	3.3	3.0	3.2	0.34
BPI, 1985	4.6	4.0	4.1	.39	3.9	4.2	4.0	.47
Samples <sup>a</sup>	8	10	27		8	14	15	
MI, 1986	3.3	2.6	3.0	0.01	3.3	3.0	2.6	0.14
BPI, 1986	4.5	4.6	4.8	.89	5.6	4.5	4.4	.15
Samples <sup>a</sup>	6	8	19		5	10	4	

<sup>a</sup> Number of stands sampled per class.

<sup>b</sup> Kruskal-Wallis test.

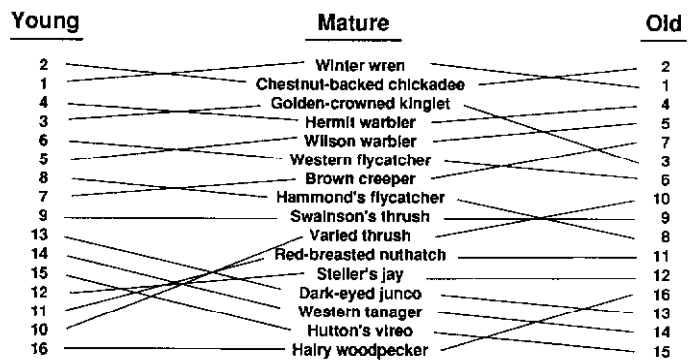


Figure 5—The ranked abundance of bird species in young, mature, and old-growth stands in the southern Oregon Coast Range, 1985.

### Species Diversity

The mean number of species per stand (based on counts) did not vary with age-class (Kruskal-Wallis,  $P = 0.98$ ) or moisture-class ( $P = 0.51$ ) in 1985. In 1986, mature stands had fewer species than young or old-growth stands (table 4; Kruskal-Wallis,  $P < 0.01$ ), but no significant difference was found among moisture-classes (Kruskal-Wallis,  $P = 0.24$ ). The difference in richness was due to the absence of some uncommon species in the mature stands. Margalef's index to richness displayed the same pattern as the counts—mature stands had fewer species than young and old-growth stands in 1986 but not in 1985 (table 5). Margalef's index did not differ significantly among moisture-classes. The Berger-Parker index of dominance (and evenness) showed no differences among stand types (table 5).

### Patterns of Abundance

The mean number of birds counted per stand in 1985 (570) did not differ significantly ( $P = 0.85$ ) among age-classes; in 1986, fewer birds were counted in mature stands (mean = 471) than in young (mean = 489) and old-growth (mean = 528) stands (analysis of variance,  $P < 0.05$ ). Ranked

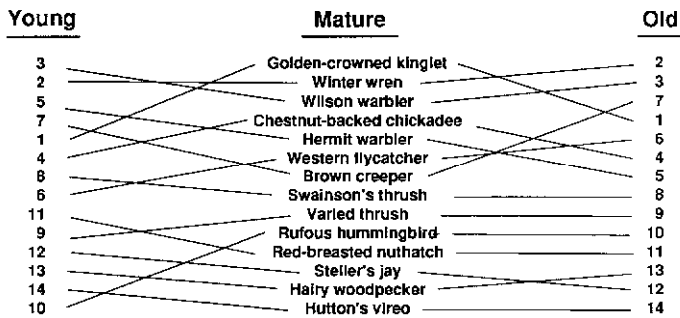


Figure 6—The ranked abundance of bird species in young, mature, and old-growth stands in the southern Oregon Coast Range, 1986.

Table 6—Mean birds-per-area indices (numbers per 40 ha) of birds associated with old-growth forests in the southern Oregon Coast Range, 1985-86

Species	Age-class			$P^a$
	Young	Mature	Old-growth	
Brown creeper	16.66	28.66	34.24	**
Chestnut-backed chickadee	52.06	61.88	101.62	**
Hairy woodpecker	.74	1.10	1.79	*
Olive-sided flycatcher	.06	.03	.47	*
Pileated woodpecker	.02	.25	.41	**
Red-breasted nuthatch	3.14	6.48	9.30	**
Red-breasted sapsucker	.12	.90	1.02	**
Varied thrush	4.82	15.12	14.75	**
Western flycatcher	49.28	34.57	60.84	**
Woodpeckers <sup>b</sup>	.88	2.25	3.22	**
Other cavity users <sup>c</sup>	71.88	97.08	145.27	**
Bark foragers <sup>d</sup>	20.68	37.39	46.35	**

<sup>a</sup> \*  $P < 0.10$  in 1 year; \*\*  $P < 0.10$  in 2 years; Kruskal-Wallis test.

<sup>b</sup> Hairy woodpeckers, pileated woodpeckers, and red-breasted sapsuckers.

<sup>c</sup> Red-breasted nuthatch, chestnut-backed chickadee, brown creeper, and northern pygmy-owl.

<sup>d</sup> Hairy woodpecker, pileated woodpecker, red-breasted sapsucker, brown creeper, and red-breasted nuthatch.

abundance did not differ among age-classes in 1985 (for 16 species, fig. 5) or in 1986 (for 14 species, fig. 6) (Kendall's coefficient of concordance,  $P < 0.01$ , Kendall's coefficient of rank correlation,  $P < 0.01$  for all pairwise comparisons). Nine species reached maximum abundance in old growth (table 6), including all the common cavity-using birds. The varied thrush was more abundant in mature and old-growth stands than in young stands. The varied thrush was the only species associated with old forests that also showed a preference for a moisture-class (wet stands in both years, Kruskal-Wallis test,  $P < 0.05$ ). Moisture preferences of other species will be discussed below in relation to the gradient in proportion of understory cover that was herbs, ferns, and berry-producing shrubs. Woodpeckers as a group, other cavity users as a group, and bark gleaners reached maximum abundance in old growth (table 6). Foliage foragers (black-throated gray

Table 7—Mean bird-per-area indices of species associated with young forests in the southern Oregon Coast Range, 1985-86

Species	Age-class			$P^a$
	Young	Mature	Old-growth	
Black-headed grosbeak	3.90	0.79	0.37	*
Dark-eyed junco	7.76	4.39	2.06	*
Evening grosbeak	2.96	5.66	1.63	**
Hammond's flycatcher	27.97	20.26	6.94	**
Hermit warbler	69.59	41.18	48.34	*
Hutton's vireo	6.66	.78	1.62	**
Nashville warbler	1.84	.69	.71	*
Purple finch	4.12	.74	1.70	**
Orange-crowned warbler	3.20	1.18	1.41	*
Warbling vireo	2.41	.12	.26	*
Western tanager	5.12	1.34	1.46	*

<sup>a</sup> \*  $P < 0.10$  in 1 year; \*\*  $P < 0.10$  in 2 years; Kruskal-Wallis test.

Table 8—Mean proportion of young, mature, and old-growth stands in which selected species of low abundance occurred in the southern Oregon Coast Range, 1985-86; all observations recorded were used

Species	Age-class			$P^a$
	Young	Mature	Old-growth	
Hairy woodpecker	0.88	1.00	1.00	*
Northern flicker	.56	.88	.93	**
Northern pygmy-owl	.38	.75	.59	*
Olive-sided flycatcher	.31	.38	.78	**
Pileated woodpecker	.69	.94	1.00	**
Red-breasted sapsucker	.31	.44	.87	**
Spotted owl	.00	.00	.24	**
Marbled murrelet <sup>b</sup>	.00	.50	.83	*
Vaux's swift <sup>b</sup>	.00	.29	.39	**

<sup>a</sup> Test of the hypothesis that the species increased in abundance with age-class, using Bartholomew's test for a gradient in proportions; \*  $P < 0.05$ , \*\*  $P < 0.01$ .

<sup>b</sup> Data from 1986 only.

warbler, chestnut-backed chickadee, golden-crowned kinglet, Hammond's flycatcher, hermit warbler, Hutton's vireo, purple finch, western flycatcher, western tanager, black-headed grosbeak, and yellow-rumped warbler) and forest-floor birds (American robin, blue grouse, dark-eyed junco, hermit thrush, song sparrow, Swainson's thrush, varied thrush, Wilson's warbler, winter wren, and wren) as groups did not differ significantly in abundance among age-classes ( $P > 0.10$ , 1985 and 1986). Eleven species were most abundant in young stands (table 7). One, the purple finch, was listed by Brown (1985) as preferring old growth; our data suggest that it does not.

Proportional occurrences of species of low abundance reinforced many of the associations with old growth shown by densities in table 6 (table 8). All of these species showed a

significant increase in abundance across the three age-classes (Bartholomew's test,  $P < 0.05$ ). In addition, the northern flicker and northern pygmy-owl increased in abundance with stand age. All patterns displayed in tables 4 to 6 were consistent between years, except that evening grosbeaks were less than one-tenth as abundant in old-growth and mature stands and twice as abundant in young stands in 1986 as in 1985. All abundances were of the same magnitude between years except that chestnut-backed chickadees were one-third, orange-crowned warblers one-fourth, and western tanager one-half as abundant in 1986 as in 1985.

Three species that were not commonly found within 75 m of the sampling points were the marbled murrelet, the spotted owl, and Vaux's swift. They showed a pattern of increasing abundance with age-class (table 8; Bartholomew's test,  $P < 0.05$ ). The marbled murrelet was recorded only in mature and old-growth stands near Corvallis (Carey 1989; Nelson and others, in press).

### Responses to Gradients

Bark foragers (hairy woodpeckers, pileated woodpeckers, red-breasted sapsuckers, brown creepers, and red-breasted nuthatches) were not significantly correlated (using Pearson product-moment correlation) with the density of large trees in 1985 and showed only a weak positive Pearson correlation in 1986 ( $r = 0.45$ ,  $P < 0.01$ ) because of a positive response by the red-breasted nuthatch. A simple linear regression of bark-forager abundance on large-tree density had a positive slope significantly different from zero ( $P < 0.05$ ) in both years. When we truncated the gradient at 20 large trees per hectare (about the mean value for trees  $\geq 100$ -cm in d.b.h. in old growth) the increase in the slope was marked. When we examined the correlations between large trees and bark-forager abundances for young and mature stands separately from old growth, significant positive Pearson correlations were found in both years (1985,  $r = 0.71$ ; 1986,  $r = 0.75$ ;  $P < 0.01$ ). Brown creeper abundances were positively correlated with the density of large trees in both years ( $r = 0.75$  in 1985,  $P < 0.01$ ;  $r = 0.62$  in 1986,  $P < 0.05$ ). Positive Pearson correlations were found for pileated woodpeckers in 1985 and red-breasted sapsuckers in 1986. Spearman rank correlations were positive and significant in both years for brown creepers and bark foragers, as a group, across the entire large-tree gradient ( $P < 0.10$ ).

Few positive Pearson correlations were found between cavity-using birds and densities of small, medium, large, and very large snags. When we examined young and mature stands alone, the red-breasted nuthatch, chestnut-backed chickadee, brown creeper, and northern pygmy-owl, as a group, were positively correlated with the density of very large ( $\geq 100$ -cm d.b.h.) snags ( $r = 0.71$  in 1985,  $P < 0.01$ ;  $r = 0.73$  in 1986,  $P < 0.05$ ). Chestnut-backed chickadees accounted for most of

this positive response ( $r = 0.62$  in 1985,  $P < 0.05$ ;  $r = 0.67$  in 1986,  $P < 0.05$ ). Positive rank correlations ( $P < 0.10$ ) were found between very large snags and all cavity-nesting species, brown creepers, woodpeckers as a group, and other cavity nesters as a group in both years (except hairy woodpeckers in 1985 and northern flickers in 1985 and 1986). Rank correlations with very large snags (0.28-0.55) were higher than rank correlations with large snags (0.17-0.45), indicating that very large snags accounted for a substantial portion of the correlations with large snags.

Only one consistent pattern of positive response was obtained when we examined forest-floor-associated birds relative to the proportion of vegetative cover less than 2 m tall that was herbs, ferns, or berry-producing shrubs, which is also a site-moisture indicator, and the cover of evergreen shrubs. The varied thrush was positively correlated with the proportion of herbs, ferns, and berry-producing shrubs in both years ( $P < 0.05$ , Pearson's  $r = 0.44$ -0.54) and negatively correlated with evergreen shrubs in both years ( $P < 0.05$ , Pearson's  $r = -0.43$  in both years), reflecting its preference for wet sites. Rank correlations between ground-associated birds as a group and the proportion of herbs, ferns, and berry-producing shrubs were positive in both years ( $r = 0.35$ , 0.37,  $P < 0.05$ ).

We found no consistent pattern of positive responses between the abundance and diversity (MI, BPI) of foliage foragers and coniferous foliage-height diversity (BPI). Similarly, we found no consistent pattern of positive responses when we examined the diversity of hardwood-associated species (black-throated gray warbler, black-headed grosbeak, Hutton's vireo, purple finch, Swainson's thrush, warbling vireo, black-capped chickadee, ruffed grouse, and downy woodpecker) in relation to total deciduous hardwood cover (shrub, understory, and midstory). Rank correlations between the abundance of hardwood-associated birds as a group and hardwood cover were significant in both years ( $r = 0.33$ , 0.44,  $P < 0.05$ ).

### Nests

We located 277 active nests of nine species of cavity-using birds. All species preferred Douglas-fir snags more than 50 cm in d.b.h. Mean nest-tree d.b.h. ranged from 54 cm for the northern pygmy-owl to 113 cm for the red-breasted sapsucker; the mean was 94 cm (Nelson 1989).

### Foraging Behavior

We recorded 989 foraging bouts by six species of cavity-using birds (table 9). Pileated woodpeckers concentrated their activities in the upper and mid-canopy in Douglas-fir, as did red-breasted nuthatches. Pileated woodpeckers concentrated on tree boles, whereas the nuthatches used small, medium, and large branches in addition to the tree bole. Pileated

**Table 9-Percentage of common ( $\geq 14$  percent) foraging activities by bird species, location in the forest, tree characteristics, and object for cavity-using birds in the Oregon Coast Range, 1985-86**

	Red-breasted sapsucker	Hairy woodpecker	Pileated woodpecker	Chestnut-backed chickadee	Red-breasted nuthatch	Brown creeper
Sample size	99	156	33	323	65	313
Vertical location:						
Upper canopy	19		<b>54</b>	17	38	
Midcanopy	47	35	22	36	49	30
Lower canopy	23	14		22		30
Understory		26		20		32
Horizontal location:						
Mainstem	86	72	83		37	87
Inner branch				16		
Center branch				35	40	
Outer branch				52	16	
Tree species:						
Douglas-fir	44	71	82	43	71	65
Western hemlock	15			21		17
Bigleaf maple	35					
Substrate:						
Tree bole	84	72	75	12	31	89
Large branch				20	22	
Medium branch				48	19	
Small branch					29	
Tree condition:						
Live	85	64	35	92	76	84
Decay-class 1			34			
Decay-class 2		23	24			
Diameter-class:						
0-9 cm				22		
10-19 cm						
20-49 cm	59	38		34	26	41
40-100 cm	28	45	48	43	65	41
>100cm			40			
Tree status:						
Suppressed	18	19		27		
Subordinate	44	22		20		24
Dominant	34	52	80	44	80	62
Object:						
Foliage				54		
Bark	24	48	34		14	79
Dead wood		30	51		31	
Live wood (sap)	60				32	

**woodpeckers** preferred large trees ranging from live trees in good condition to snags that were slightly to moderately decayed. Nuthatches concentrated on live trees.

Red-breasted sapsuckers and chestnut-backed chickadees also used the upper canopy, but made greatest use of the middle to lower canopy, as did hairy woodpeckers and brown creepers. Sapsuckers, woodpeckers, and creepers concentrated

on the boles of trees, whereas chickadees foraged among branches, especially the outer branches. Chickadees foraged mostly on small branches. Douglas-fir was the primary species used, but sapsuckers also used bigleaf maple and western hemlock. All concentrated on live trees in good condition, with hairy woodpeckers making significant use of moderately decayed snags. Chestnut-backed chickadees foraged across diameter-classes, whereas woodpeckers and creepers tended

to prefer dominant trees with diameter-classes reflecting stand age; sapsuckers used subordinate trees the most, followed by dominant trees, and thus foraged on smaller trees, on average, than did woodpeckers and creepers. Chickadees concentrated on foliage, sapsuckers on live wood (sap), hairy woodpeckers on dead wood and bark, and creepers on bark.

Foraging behavior mostly was consistent across the stand age-classes. Pileated woodpeckers were seen rarely in young and mature stands (4 of 42 observations). Pileated woodpeckers were observed foraging on fallen trees more (15 percent), a greater variety of trees, more on snags, and more on trees more than 100 cm in d.b.h. in old growth than in young or mature stands. Hairy woodpeckers used branches on trees more in old growth than in younger stands (42 percent bole use in old growth versus 84 percent and 73 percent in mature and young stands, respectively). Hairy woodpeckers used more live trees in poor condition and slightly decayed trees in mature and old-growth stands than they did in young stands. They also foraged more on large trees in old-growth than in young and mature stands; trees 20 to 49 cm in d.b.h. were used the most in young and mature stands. Only three red-breasted sapsuckers were observed foraging in young stands. Red-breasted nuthatches tended to use the lower canopy more as stand age increased (percentage of use = 0, 8, and 12 in young, mature, and old-growth stands) and increased their use of very large trees. In young stands, nuthatches selected trees greater than 50 cm in d.b.h. over trees 20 to 49 cm in d.b.h. But in mature stands, they selected for the 20- to 49-cm diameter-class. Use of diameter-classes by chickadees reflected availability. Nuthatches foraged more on dead wood in young stands (27 percent) than in mature (0 percent) or old-growth stands (6 percent).

## Discussion

### Forest Development

The Douglas-fir-dominated forests of the southern Oregon Coast Range displayed a clear pattern of development over the range of ages we studied: 40 to 525 years. Both the distribution of diameter at breast height in live trees (table 1) and the patterns of abundance of snags (fig. 3) provide good models of forest development: attainment of dominance by some trees, suppression of subordinate trees, and the opening of the canopy through death of dominant trees. Young stands were characterized by high densities of 10- to 49-cm d.b.h. Douglas-firs (table 1); high stocking rates had resulted in mortality from suppression that produced high densities of small- and medium-diameter snags (table 2, fig. 3). Relatively large numbers of well-decayed large snags from the previous stand were carried over into the young and mature stands. Young stands were even-aged, had low values for coniferous foliage-height diversity (fig. 2), and high values of canopy cover, Midstory and understory layers were undeveloped.

Mortality from competition (suppression) continued into the mature age-class, which also tended to be even-aged and to have a low foliage-height diversity. Canopy cover decreased with age, but mortality in the mature stands began to produce snags of the size and condition favored by cavity-nesting birds (moderately decayed snags >50-cm d.b.h.; Cline and others 1980, Nelson 1989). Mature stands were approaching a phase of rapid development, including increases in tree size, abundance of large snags, and vertical stratification of the canopy.

Tree size (fig. 1) and foliage-height diversity (fig. 2) continued to increase with age through the oldest stands studied. Mortality rates of dominant trees slowed; however, the slightly to moderately decayed snags most used by cavity-using birds (mean diameter of snags used for nesting was 94 cm, Nelson 1989) occurred in much lower densities in old growth than the smaller snags did in the younger stands (fig. 3). Tree death in young and mature stands is usually due to suppression, but tree death in old growth is usually due to butt rot, windthrow, or fire (Franklin and others 1987). Canopy cover was at a minimum, and midstory and understory development at a maximum, in old-growth stands. Because of the wildfire history of the Coast Range, 500 years is about the maximum age of old-growth stands there (Juday 1976); 500 years is also the time of peak accumulation of coarse woody debris, including snags (Spies and others 1988). The structure of the old-growth (200-525 years old) forests differs significantly from young and mature forests. Attendant to these structural differences are compositional differences in the makeup of the overstory, the development of a shade-tolerant midstory and understory, and, depending on moisture conditions, a greater development of shrub and forest-floor vegetation.

### Bird Communities

Bird communities in the southern Coast Range were dominated by eight common species (table 3); no marked differences were observed in community structure (figs. 5,6) among young, mature, and old-growth forests. Total abundance of birds was about equal among age-classes. Species diversity, as measured by richness, Margalef's index, and the Berger-Parker index, did not differ in a biologically significant way among age-classes, although mature stands seemed to support a slightly less rich and less abundant bird community. All three age-classes were closed-canopied, maturing coniferous forest; all the study stands were in landscapes dominated by forest communities.

Forty percent of the bird species present in spring communities were migrants and, of these, only the Vaux's swift (a cavity nester) and the olive-sided flycatcher showed an association with old growth. About one-fourth of the resident

birds were cavity users; all showed an association with old growth; and, in addition, the marbled murrelet and the winter wren increased in abundance with stand age.

Bird communities in old growth differed from those in young and mature stands, primarily in the abundance and diversity of cavity-using birds (including the crevice-nesting brown creeper and the sometimes cavity-using spotted owl). This compositional change in the bird communities was continuous throughout the age gradient studied, with young forests supporting the fewest cavity users and old-growth forest supporting the most. The cavity users that were abundant in young stands, the brown creeper and the chestnut-backed chickadee, were the only two that made significant use of well-decayed (class 3) snags for nesting (Nelson 1989). As carryovers from the old-growth stands preceding the young and mature stands, these large and very large, well-decayed snags were equally abundant in the three age-classes studied. Our findings suggest that given present conditions, cavity-using birds depend on old growth to support the numbers of birds necessary to ensure viable populations.

#### **Hypotheses Examined**

**Large trees**-Old growth is unique in the number of large, live trees, and bark-foraging birds showed a strong ( $r = 0.73$ ) numerical response to large-tree density in young and mature stands. Brown creepers, especially, showed a consistent, positive association with large trees throughout the age gradient and increased in abundance with age, being twice as abundant in old-growth as in young stands. Creepers selected the dominant trees in each age-class for foraging and concentrated their foraging on the bark on the tree boles. But brown creepers were abundant birds-even more abundant; in young stands than many of the species associated with young stands (tables 6,7). Large, live trees may not be a necessity for creepers, but they certainly contribute to maintaining large populations. We conclude that live, old-growth trees are an important habitat element for bark-foraging birds, particularly brown creepers.

The other bark foragers were cavity-using birds whose association with large, live trees may reflect, in part, their associations with large, dead trees. They did not concentrate their foraging on the bark on the boles of large, live trees to the extent creepers did. Indeed, the hairy woodpecker used large branches on old, live trees as well as the boles. The red-breasted nuthatch used branches more than boles. The pileated woodpecker used snags as well as live trees. And the red-breasted sapsucker foraged on a greater variety of species than the brown creeper did.

**Vertical diversity**-Old growth had a much greater vertical diversity of coniferous foliage than young or mature stands did. But the foliage-foraging species did not respond numerically to the gradients in diversity or stand age. The diversity

of foliage foragers did not increase with increasing foliage-height diversity. Greater foliage-height diversity (and the attendant diversity of species) of old growth apparently did not strongly influence the bird communities.

**Snags**-The abundance and diversity of cavity-using birds was positively correlated with large snags. Snags used by cavity-nesting birds began to increase in availability in mature stands but were abundant only in old-growth stands. Ten of the 14 species associated with old growth (tables 6,8) are cavity users. Two, the spotted owl and Vaux's swift, are dependent on old growth (Carey 1989). The only cavity-nesting species that was abundant in young stands was the chestnut-backed chickadee, which used well-decayed, large snags as well as moderately decayed, large snags for nesting. Large, and especially very large, moderately decayed snags are of major importance to cavity-using birds. These kinds of snags may be difficult to maintain in managed stands.

**Spatial diversity**-We found that canopy cover decreased and midstory development increased with age, but understory vegetation reflected moisture more than canopy cover. Bird species responding to ground cover less than 2 m tall seemed to be responding to the abundance of forbs and berry-producing bushes relative to evergreen shrubs on a wet-to-dry gradient, rather than to stage of forest development, although the varied thrush responded to both. We found no clear pattern of increased ground cover with age. Spatial diversity associated with old growth apparently did not exert a strong influence on bird communities.

#### **The Value of Old Growth to Birds**

Old growth seems especially important to cavity-using birds. These birds select large snags out of proportion to their availability even in the midst of abundant, small snags (<50-cm d.b.h.) (Nelson 1989). Mean diameter at breast height of snags used for nesting was 94 cm-an old-growth diameter. The bulk of the snags used were of diameters that do not occur until after at least 80 years of growth.

The pileated woodpecker, hairy woodpecker, and red-breasted sapsucker were rare in young stands and most abundant in old growth, though not as abundant as the secondary cavity users. The home-range size of woodpeckers exceeds our average stand size, however; the average home-range size of the pileated woodpecker in the Oregon Coast Range is 480 ha (Mellen 1987). Thus, the presence of old-growth stands may provide nesting habitat for woodpeckers and allow them to forage in nearby younger forests to a greater degree than would be possible without old growth.

The chestnut-backed chickadee was most abundant in old growth but also abundant in younger stands. The red-breasted nuthatch was three times as abundant in old growth as in young stands but still relatively abundant in young stands.



These small species prefer large, tall snags (Nelson 1989). But unlike most other cavity-using birds (Nelson 1989) chickadees nested in large, well-decayed snags. Young stands developing after harvest of second-growth stands would be devoid of these large, well-decayed snags. Loss of these carryovers from old growth would reduce the quality of young stands as chickadee habitat.

The Vaux's swift uses large, hollow snags for nesting (Gabrielson and Jewett 1940). These swifts will forage over clearcuts, but 56 of the 61 swifts we recorded in the Coast Range were in old growth. The large, hollow trees used for roosting and nesting are not commonly found in young or mature stands (Carey 1989).

The brown creeper, strictly speaking, is not a cavity nester; rather it builds a nest under loose bark (Ehrlich and others 1988). The heavily furrowed bark of old-growth Douglas-firs has been postulated as harboring an abundant arthropod fauna that serves as food for brown creepers (Mariani 1987). Our data show that brown creepers prefer to forage on the largest trees available and that creeper abundance increases with the abundance of large trees. Creepers were abundant in all age-classes. They preferred large snags for nesting (mean d.b.h. was 83 cm) and selected the largest snags available; nest-snag diameter increased with age. Creepers used both moderately and well-decayed snags more frequently than the cavity-using birds did (with the exception of the chestnut-backed chickadee).

The only noncavity nester closely tied to old growth was the olive-sided flycatcher, an aerial insectivore that nests high on the branches of coniferous trees (Ehrlich and others 1988, Gabrielson and Jewett 1940). The tall trees and broken canopy of old growth provides a much better foraging environment than the dense, closed-canopy young and mature forests in the Coast Range.

Western flycatchers, although most abundant in old growth, were abundant in the other age-classes as well. The varied thrush was most abundant in mature and old-growth stands,

but relatively abundant in young stands as well. The association with older stands might reflect a subtle influence of canopy openings on ground cover or an influence of tall canopies on ground moisture.

Little information exists on the inland ecology of marbled murrelets; Nelson and others (in press) reviewed what is known about the marbled murrelet in Oregon. Additional information on the ecology of murrelets is needed before the importance of old growth to them can be determined.

We found no evidence that other bird species we studied found old growth to be a more favorable environment than young or mature stands. Many species, however, were not sampled adequately. And we studied the bird communities only during the spring. We believe our data were sufficient to conclude that loss of old growth would negatively affect cavity-using bird populations. We predict that effects would be severe for woodpeckers, the Vaux's swift, and the spotted owl.

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## Appendix

**Table 10—Mean standardized counts (number per stand visit) of birds within 75 m of sampling points in young, mature, and old-growth forests in the southern Oregon Coast Range, 1985**

Species	Stand age-class		
	Young (n = 8)	Mature (n = 10)	Old (n = 27)
American robin	1.00	1.53	0.81
Band-tailed pigeon	.09	.14	.12
Black-capped chickadee	.00	.05	.16
Black-headed grosbeak	.83	.21	.08
Black-throated gray warbler	1.31	.34	.39
Blue grouse	.00	.13	.09
Brown creeper	2.05	4.30	4.86
Chestnut-backed chickadee	7.11	8.76	12.34
Common raven	.00	.00	.05
Dark-eyed junco	2.14	1.06	.68
Downy woodpecker	.00	.04	.00
Evening grosbeak	.89	2.40	.72
Golden-crowned kinglet	6.71	7.63	6.44
Gray jay	.34	.68	.30
Hairy woodpecker	.45	.37	.61
Hammond's flycatcher	3.59	2.99	1.08
Hermit thrush	1.22	.34	.50
Hermit warbler	11.33	7.59	8.81
Hutton's vireo	1.26	.25	.24
MacGillivray's warbler	.00	.00	0.13
Mountain quail	.00	.00	0.02
Nashville warbler	.21	.16	0.04
Northern flicker	.04	.04	0.10
Northern pygmy-owl	.00	.00	0.03
Olive-sided flycatcher	.00	.00	0.15
Orange-crowned warbler	.75	.26	0.31
Pileated woodpecker	.00	.17	0.14
Pine siskin	.09	1.05	0.71
Purple finch	1.25	.18	0.36
Red-breasted nuthatch	1.12	2.98	3.28
Red-breasted sapsucker	.00	.17	0.28
Red crossbill	.00	.08	0.00
Ruby-crowned kinglet	.00	.03	0.00
Ruffed grouse	.00	.00	0.01
Rufous hummingbird	.24	.11	0.41
Rufous-sided towhee	.00	.00	0.09
Song sparrow	.00	.00	0.08
Spotted owl	.00	.00	0.01
Steller's jay	.68	1.47	1.37
Swainson's thrush	3.83	4.91	3.77
Townsend's solitaire	.00	.03	.03
Varied thrush	1.42	3.93	3.61
Warbling vireo	.17	.00	.00
Western flycatcher	10.46	8.98	2.88
Western tanager	1.78	.60	.71
Western wood-pewee	.00	.00	.01
White-breasted nuthatch	.00	.03	.00
Wilson's warbler	6.49	6.40	4.73
Winter wren	11.58	13.97	15.35
Wrentit	.24	.62	.25
Yellow-rumped warbler	.41	.00	.04

**Table 11—Mean standardized counts (number per stand visit) of birds within 75 m of sampling points in young, mature, and old-growth forests in the southern Oregon Coast Range, 1986**

Species	Stand age-class		
	Young (n = 5)	Mature (n = 8)	Old (n = 19)
American robin	0.76	0.82	0.35
Band-tailed pigeon	.00	.14	.20
Black-headed grosbeak	1.22	.22	.17
Black-throated gray warbler	1.45	.36	.38
Blue grouse	.00	.00	.03
Brown creeper	2.84	4.66	6.08
Chestnut-backed chickadee	3.60	4.89	10.95
Chipping sparrow	.00	.04	.02
Common raven	.00	.00	.10
Dark-eyed junco	2.60	1.48	.65
Downy woodpecker	.00	.00	.02
Evening grosbeak	1.02	.27	.13
Golden-crowned kinglet	4.61	7.50	7.36
Gray jay	.67	.52	.34
Hairy woodpecker	.13	.41	.99
Hammond's flycatcher	6.05	3.32	.96
Hermit thrush	1.63	.25	1.48
Hermit warbler	11.60	6.18	8.79
House wren	.00	.00	.06
Hutton's vireo	1.41	.04	.33
MacGillivray's warbler	.05	.00	.36
Nashville warbler	.07	.00	.00
Northern flicker	.00	.05	.06
Northern pygmy-owl	.00	.04	.02
Olive-sided flycatcher	.00	.00	.07
Orange-crowned warbler	.25	.00	.04
Pileated woodpecker	.00	.00	.23
Pine siskin	.15	.09	.62
Purple finch	.45	.05	.27
Red-breasted nuthatch	1.42	2.91	5.75
Red-breasted sapsucker	.00	.45	.62
Red crossbill	.00	.00	.05
Rufous hummingbird	.33	.13	.46
Rufous-sided towhee	.00	.00	.12
Song sparrow	.20	.00	.08
Spotted owl	.00	.00	.04
Steller's jay	.73	1.04	1.02
Swainson's thrush	5.83	4.83	4.06
Varied thrush	1.27	4.52	5.14
Warbling vireo	.88	.00	.00
Western flycatcher	8.86	7.34	15.17
Western tanager	.98	.15	.48
Wilson's warbler	5.85	5.36	4.85
Winter wren	8.14	11.00	12.69
Wrentit	.17	.16	.24
Yellow-rumped warbler	.07	.00	.07

Table 12—Mean birds-per-area index (numbers per 40 ha) of birds in young, mature, and old-growth forests in the southern Oregon Coast Range, 1985

Species	Stand age-class					
	Young (n = 8) <sup>a</sup>		Mature (n = 10)		Old (n = 27)	
	Mean	N <sup>b</sup>	Mean	N	Mean	N
American robin	2.52	45	4.37	93	2.12	125
Band-tailed pigeon	.13	4	.27	10	.30	28
Black-capped chickadee <sup>c</sup>	.00	0	.00	0	.10	3
Black-headed grosbeak <sup>c</sup>	3.65	29	.75	8	.59	16
Black-throated gray warbler <sup>c</sup>	9.35	54	2.04	15	3.86	69
Blue grouse <sup>c</sup>	.23	2	.41	6	.40	15
Brown creeper	14.22	90	25.85	217	32.74	704
Chestnut-backed chickadee	78.38	325	88.86	492	132.85	1811
Common raven	.84	2	.00	0	.20	16
Dark-eyed junco <sup>c</sup>	5.88	54	3.11	36	1.42	42
Downy woodpecker	.45	1	.11	3	.06	4
Evening grosbeak <sup>d</sup>	2.35	31	9.20	156	2.69	128
Golden-crowned kinglet	54.09	248	73.47	406	62.02	970
Gray jay	1.17	19	1.75	40	1.21	60
Hairy woodpecker	1.05	22	9.92	25	1.42	93
Hammond's flycatcher <sup>c</sup>	23.80	107	20.29	128	8.06	121
Hermit thrush	3.14	37	1.25	20	1.53	58
Hermit warbler <sup>c</sup>	73.62	463	48.23	372	56.58	1170
Hutton's vireo <sup>c</sup>	6.89	41	1.45	12	1.79	37
MacGillivray's warbler <sup>c</sup>	.43	2	.00	0	1.64	22
Mountain quail <sup>c</sup>	.07	1	.18	3	.11	5
Nashville warbler <sup>c</sup>	1.89	11	1.38	11	.86	16
Northern flicker	.23	5	.10	3	.33	25
Northern pygmy-owl	.03	1	.00	0	.12	10
Olive-sided flycatcher	.00	0	.59	1	.65	24
Orange-crowned warbler <sup>c</sup>	5.00	37	2.24	21	1.97	50
Pileated woodpecker	.04	1	.42	14	.38	31
Pine siskin <sup>c</sup>	1.19	15	4.12	70	2.64	122
Purple finch <sup>c</sup>	5.82	49	1.04	12	2.09	57
Red-breasted nuthatch	2.58	52	6.41	169	7.08	465
Red-breasted sapsucker	.62	1	.46	11	.75	48
Red crossbill <sup>d</sup>	.13	3	.19	4	.04	2
Ruby-crowned kinglet	.00	0	.77	1	1.02	3
Ruffed grouse <sup>c</sup>	.00	0	.06	1	.05	2
Rufous hummingbird	6.46	10	5.48	11	13.53	71
Rufous-sided towhee	.19	4	.21	5	.19	12
Song sparrow <sup>c</sup>	.00	0	.15	2	.32	11
Spotted owl	.00	0	.00	0	.07	3
Steller's jay	1.94	36	3.71	82	3.45	212
Swainson's thrush	11.41	103	13.79	148	10.41	286
Townsend's solitaire	.12	2	.09	2	.19	11
Varied thrush <sup>c</sup>	5.59	61	13.59	196	13.85	505
Warbling vireo <sup>c</sup>	1.26	7	.14	1	.06	1
Western flycatcher	48.40	462	36.80	457	62.12	1935
Western tanager <sup>c</sup>	6.50	40	1.92	15	1.89	46
White-breasted nuthatch	.08	1	.07	1	.02	1
Wilson's warbler <sup>c</sup>	42.76	280	39.23	336	30.52	661
Winter wren <sup>c</sup>	76.71	426	89.18	669	107.44	1997
Yellow-rumped warbler <sup>c</sup>	2.96	16	.29	2	1.33	25

<sup>a</sup> Number of stands sampled.

<sup>b</sup> Number of birds counted.

<sup>c</sup> More than 70 percent of the detections of these species were of singing males. Mean densities reported are twice the densities of singing males.

<sup>d</sup> More than 50 percent of all detections of these species were of flying birds not included in the estimates.

Table 13—Mean birds-per-area indexes (numbers per 40 ha) of birds in young, mature, and old-growth stands in the southern Oregon Coast Range, 1986

Stand age-class

Species	Young (n = 6) <sup>a</sup>		Mature (n = 8)		Old (n = 16)	
	Mean	N <sup>b</sup>	Mean	N	Mean	N
American robin	1.84	23	2.10	36	0.91	37
Band-tailed pigeon	.07	1	.53	11	.36	18
Black-headed grosbeak <sup>c</sup>	4.15	26	.83	7	.74	14
Black-throated gray warbler <sup>c</sup>	8.78	48	2.70	20	2.21	39
Blue grouse <sup>c</sup>	.00	0	.00	0	.21	5
Brown creeper	19.09	83	31.47	192	35.75	515
Chestnut-backed chickadee	25.73	105	34.79	200	70.39	957
Chipping sparrow <sup>c</sup>	.10	1	.08	1	.09	3
Common raven	.00	0	.08	1	.37	11
Dark-eyed junco <sup>c</sup>	9.64	52	5.67	42	2.67	47
Downy woodpecker	.00	0	.00	0	.06	3
Evening grosbeak <sup>d</sup>	3.58	40	2.01	31	.57	21
Golden-crowned kinglet	45.75	139	80.95	335	64.12	623
Gray jay	2.28	26	1.50	24	.82	30
Hairy woodpecker	.43	5	1.27	21	2.16	84
Hammond's flycatcher <sup>c</sup>	32.14	130	20.23	113	5.81	77
Hermit thrush <sup>c</sup>	4.60	34	.99	10	3.15	76
Hermit warbler <sup>c</sup>	65.56	369	34.04	262	40.11	733
House wren <sup>c</sup>	.00	0	.00	0	.23	6
Hutton's vireo <sup>c</sup>	6.44	40	.10	1	1.46	28
MacGillivray's warbler <sup>c</sup>	1.06	6	.00	0	1.74	33
Nashville warbler <sup>c</sup>	1.80	5	.00	0	.55	5
Northern flicker	.00	0	.22	5	.15	8
Northern pygmy-owl	.00	0	.12	2	.10	4
Olive-sided flycatcher <sup>c</sup>	.11	1	.00	0	.29	8
Orange-crowned warbler <sup>c</sup>	1.40	9	.11	1	.85	18
Pileated woodpecker	.00	0	.08	2	.43	24
Pine siskin <sup>d</sup>	1.00	11	.13	2	1.56	57
Purple finch <sup>c</sup>	2.41	16	.44	4	1.31	28
Red-breasted nuthatch	3.69	43	6.54	118	11.52	446
Red-breasted sapsucker	.18	2	1.34	23	1.30	53
Red crossbill <sup>c</sup>	.07	1	.30	6	.52	25
Rufous hummingbird	11.08	12	7.42	12	11.76	45
Rufous-sided towhee	.14	1	.21	2	.56	13
Song sparrow <sup>c</sup>	1.13	5	.00	0	.57	8
Spotted owl	.00	0	.00	0	.44	6
Steller's jay	2.08	27	2.65	47	2.14	89
Swainson's thrush	29.96	110	19.22	123	16.35	213
Varied thrush <sup>c</sup>	4.15	31	17.64	179	15.60	371
Warbling vireo <sup>c</sup>	3.55	27	.10	1	.46	11
Western flycatcher	40.15	267	32.33	301	59.55	1305
Western tanager <sup>c</sup>	3.74	22	.76	6	1.02	19
Wilson's warbler <sup>c</sup>	39.12	162	38.25	223	25.88	358
Winter wren <sup>c</sup>	46.59	209	69.91	443	63.51	946
Wrentit	.42	6	.46	9	.45	21
Yellow-rumped warbler <sup>c</sup>	.46	2	.00	0	.51	7

<sup>a</sup> Number of stands sampled.

<sup>b</sup> Number of birds counted.

<sup>c</sup> More than 70 percent of the detections of these species were of singing males. Mean densities reported are twice the densities of singing males.

<sup>d</sup> More than 50 percent of all detections of these species were of flying birds not included in the estimates.