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Populations of breeding birds, and structure and composition of
vegetation were examined in managed and old-growth mixed-coniferous
forests in northeastern Oregon. Forest stands examined were
approximately 85 and over 200 years of age, and were dominated by
Douglas-fir (Pseudotsuga menziesii) and ponderosa pine (Pinus
ponderosa) trees. Components of vegetation that distinguished old-
growth forests from managed forests included large trees (51+ cm dbh)
and snags (31+ cm dbh), small understory grand fir (Abies grandis)
trees (2.5-10 cm dbh), and tree height diversity. Each of these com-
ponents could be associated either directly or indirectly with dif-
ferences in bird populations between managed and old-growth forests.
Bird species diversity and vertical and horizontal structural diver-
sity of vegetation were greater in old-growth forests than in managed
forests; thus, our results supported the contention that bird species
diversity is correlated with vegetation 'patchiness'. However, the
usefulness of correlations between avian diversity and vegetation
structure for management purposes is questioned. Managed forests sup-
ported a higher total density of breeding birds than old-growth
forests due to the abundance of several species that appeared to

prefer structurally open habitats. Total density and species richness of birds in guilds (based on general location of foraging and nesting) differed between managed and old-growth forests. However, consistent responses (in terms of density) among bird species within guilds did not exist. If remaining old-growth forests are eliminated from areas under intensive management for timber in northeastern Oregon, some species of birds will increase in density, some will decrease, and a few may be extirpated on a region-wide basis. Methods of maintaining habitat for those species that will decline in density following removal of old-growth forests are suggested.

Bird Populations and Vegetation Characteristics in Managed

and Old-Growth Forests, Northeastern Oregon

by

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PREFACE

The following dissertation was prepared in manuscript form. The anticipated outlet for publication is the Journal of Wildlife Management.

BIRD POPULATIONS AND VEGETATION CHARACTERISTICS IN MANAGED AND OLD-GROWTH FORESTS, NORTHEASTERN OREGON

INTRODUCTION

The structure and composition of vegetation in coniferous forests of western North America are being altered by logging and silvicultural practices (e.g. Beuter et al. 1976). These alterations influence the distribution and abundance of birds by changing the basic configuration of vegetation, described as the niche-gestalt by James (1971), and the availability of nest-sites, shelter, and sources of food -- proximate and ultimate factors, respectively, in habitat selection (see Hilden 1965 for review). One change that is occurring in forest vegetation in the Pacific Northwest is a reduction of 'old-growth' forests. Franklin et al. (1981) defined old-growth forests as those "that have developed over a long period essentially free of catastrophic (including human) disturbance". Old-growth forests are being eliminated because they are valuable sources of timber, and because silvicultural perscriptions dictate that they be replaced with younger, faster-growing forests. At current rates of harvest, all old-growth forests not associated with some form of reserve system (< 5% of the original landscape) will be liquidated within 4 decades (Franklin et al. 1981). Furthermore, on lands managed intensively for timber, predicted schedules of harvest (i.e. every 40-135 yrs) will not allow anything approaching old-growth forest conditions to redevelop.

Concern over the reduction of old-growth forests focuses on the putative idea that these stands have distinctive structural

characteristics (e.g. Franklin et al. 1981), and thus potentially provide habitats for birds (and other animals) that are not available in younger stands. Several species of birds are thought to be closely associated with, and in some cases dependent upon old-growth forests for food or nest-sites (Meslow and Wight 1975, Franklin et al. 1981). But with the exception of information on 2 of these species -- the northern spotted owl (Strix occidentalis caurina) (Forsman 1976, 1980, Forsman et al. 1977), and the pileated woodpecker (Dryocopus pileatus) (Bull and Meslow 1977, McClelland and Frissell 1979) -- few quantitative data exist.

Our study was designed to investigate avian populations in undisturbed, old-growth forests and in managed forests near or at rotation age (i.e. age at final harvest). We believe that a comparison of avian populations between these 2 habitats will illuminate some of the potential consequences of liquidating older forests. The general hypothesis tested in this study was that differences in the structure and composition of vegetation between managed and old-growth forests influence densities of some avian populations by altering the quantity of habitat suitable for foraging and nesting. There were 3 objectives. First, compare bird populations between managed and old-growth forests to determine those species whose densities differ markedly between the 2 habitats. Second, quantitatively describe the structure and composition, or specific components of vegetation used by selected species of birds when foraging and nesting. And 3rd, examine how differences in

densities of selected species influence the structure of guilds, and

avian community parameters (i.e. total density and species diversity).

STUDY AREA

The study was conducted on the Wallowa-Whitman National Forest in northeastern Oregon. Forest stands examined were centered approximately 8 km east of Medical Springs, Union County, Oregon. Franklin and Dyrness (1973) classified the area as part of the Abies grandis vegetation zone. This zone is the most extensive midslope forest zone in eastern Oregon and Washington, and although grand fir is the climax tree species, fire has maintained pure and mixed seral stands of ponderosa pine, Douglas-fir, western larch (Larix occidentalis), and lodgepole pine (Pinus contorta). Most of this forest zone has been subjected to varying degrees of selective logging.

METHODS

Selection of Stands

Bird populations and the structure and composition of vegetation were compared between stands of mixed conifers approximately 85 and over 200 years of age. We examined 4 stands in each age class; stands within an age class were selected to be as similar as possible.

The 85-year-old managed stands had been thinned in 1971 from approximately 10,000 to 330 stems per ha (5.5 m spacing). These stands were near rotation age (projected to be 70-100 yrs), and generally represented the structure of an 'older managed forest'.

All of the 200+-year-old (old-growth) stands were free from human disturbance with 1 exception -- a few ponderosa pine trees (< 5) had been removed from 1 stand in the early 1900's. These areas represented some of the oldest remaining stands of mixed conifers on the Wallowa-Whitman National Forest.

Old-growth stands were approximately 50 ha in size; managed stands varied from 65-75 ha. Elevations of all stands ranged from 1,350-1,550 m. All stands were on west- or southwest-facing slopes, and Douglas-fir and ponderosa pine trees were dominant.

Measurement and Analysis of Vegetation

Fifteen sampling points were established in each stand. The 1st point was randomly selected from a 1 ha square near the edge of the stand; remaining points were located every 100 m along a predetermined compass line.

All trees over 2.5 cm in diameter at breast height (dbh) were sampled using 0.05 ha circular plots centered on the established points (Mueller-Dombois and Ellenberg 1974). Trees were placed in size classes based on diameter and height. Diameter (dbh) classes were: 1 = 2.5-10 cm, 2 = 11-30 cm, 3 = 31-50 cm, and 4 = 51+ cm. Heights of trees were measured with an Abney level; height classes were at 5 m intervals between 0-50 m. Canopy volume of all trees was estimated using the method described by Sturnam (1968).

Standing dead trees (snags) over 10 cm dbh and over 3 m tall were sampled at each point using 0.5 ha circular plots. Size classes of snags were based on dbh and were equivalent to tree dbh classes 2, 3, and 4. Presence or absence of cavities and evidence of woodpecker foraging were noted for each snag (Mannan et al. 1980).

A randomly oriented '+' was centered on each point; the 4 segments of the '+' were each 15 m in length. Arboreal cover was measured using the method described by Emlen (1967). Briefly, 60 vertical sightings -- 1 per m along the 15 m line in each quadrant -- were taken to determine the percentage of 'hits' on the canopy. Percent cover of shrubs was measured using the line-intercept method (Canfield 1941). Percent cover of herbs and grasses was visually estimated in 12 rectangular plots (20 x 40 cm) (Mueller-Dombois and Ellenberg 1974). The plots were located 3 to a line, 1 every 5 m. Sixteen parameters describing the structure and composition of vegetation were generated at each point from the above measures (Table 1).

Discriminant function analysis with stepwise inclusion of variables (Klecka 1975) was used to determine the vegetation parameters that separated old-growth stands from managed stands. All points from all

stands were included in the analysis. The computer program in the Statistical Package for the Social Sciences (SPSS) was employed (Nie et al. 1975). The method of entry of variables into the analysis was the maximum F ratio (minimum Wilk's lambda) for the test of difference between group centroids.

Prior to entry into the discriminant function analysis, variables that departed significantly from a normal distribution (Sokal and Rohlf 1969) were transformed. Proportions were transformed using the arcsin transformation (arcsin $\sqrt{proportion}$), and densities were transformed using the square root transformation ($\sqrt{density} + 0.5$) (Sokal and Rohlf 1969). In addition, highly correlated variables were eliminated from the analysis by including only 1 of every pair of variables with correlation coefficients over 0.7 (Noon 1981). Variables were chosen for inclusion based on their potential ease of ecological interpretation.

Johnson (1981) recommended caution when using discriminant function analysis in studies of wildlife habitat because assumptions of the technique -- multivariate normal distribution of variables and equal variance-covariance matrices among groups -- are frequently violated. Others (Klecka 1975, Lachenbruch 1975, Pimentel and Frey 1978) have argued that discriminant function analysis is robust and remains useful even when the above assumptions are not met. Because we were more interested in the use of discriminant function analysis as a descriptive technique than as a technique for testing the differences among group means, we chose to use the method even though our data failed to meet the required assumptions in several analyses (see Table 2).

Measurement and Analysis of Bird Populations

We used the variable circular plot method (Reynolds et al. 1981) to census birds. The 15 points established in each stand served as census stations. Starting at sunrise, distances to all birds detected were recorded for 8 minutes at each station in 1 stand. Censusing birds at 15 stations required approximately 2.5 hours. The order in which the 8 stands were visited, and the initial census stations were selected randomly. Each stand was visited 5 times between 15 May and 15 July in 1978, 1979, and 1980. Data from all years were combined and inflection points for each species (with > 20 observations) were determined using the method developed by Ramsey and Scott (1978). For those species with fewer than 20 observations, inflection points were arbitrarily set at 100 m. Because of the comparatively low number of females detected, only territorial males were used in the analyses. Estimates of densities of territorial males were doubled to obtain estimates of total densities (Emlen 1971, Franzreb 1976). Scientific names of all species that occurred on our study areas are given in Table 5.

Selected species of birds were observed to determine vegetation used when foraging and nesting. Species selected were those whose densities differed markedly between managed and old-growth forests (i.e. over 2 times greater in 1 habitat than the other). Structure and composition of vegetation around nests were measured as described previously; centers of plots were located directly below the nests. Discriminant function analysis was used to determine the variables

that separated vegetation around nest-sites from vegetation around random-sites in either managed or old-growth forests (Titus and Mosher 1981).

Foraging behavior of selected species was quantified by following an individual (identified to species and sex) and recording information about its activities every 15 seconds for a period of 5 minutes, or until the bird could not be relocated (Landres and MacMahon 1980). Information recorded at every interval included activity (e.g. type of foraging behavior, territorial behavior, resting, preening, etc.), stratum (e.g. air, ground, part of tree, etc.), species of stratum (if appropriate), and an estimate of the height at which the activity occurred. Observations of behavior were recorded at various times of the day from sunrise to late afternoon. An effort was made to avoid obtaining more than 1 set of observations per individual per day. Only observations of males are reported in this paper because the number of observations of females generally was small.

Consecutive observations of foraging behavior are time-dependent, and thus violate the assumption of independence when testing for significance (Balda 1969). However, Landres and MacMahon (1980) argued that for birds that actively pursue prey in trees, the 15-second time interval was adequate to insure independence of consecutively recorded behavior. To examine the amount of bias in our data, we randomly selected 1 observation from each set of observations for each species. Results obtained from the random subset were nearly

identical to the results from the entire data set, so we treated the observations as if they were independent (see results).

Two species of flycatchers of the genus Empidonax were present on our study areas -- the dusky flycatcher (E. oberholseri) and Hammond's flycatcher (E. hammondii). Because we could not separate these species in the field, they were lumped under Empidonax during the censuses. To approximate the proportions of each species in managed and old-growth forests, we collected 20 flycatchers (9 from old-growth forests and 11 from managed forests) in early June 1981. Individuals taken were those 1st detected at randomly selected stations. Specimens were identified to species and sex using the ratio of the 9th and 5th primaries, length of the tarsus and rectrices, and width and length of the bill (Johnson 1963). Proportions of each species in the samples were multiplied by the total density of Empidonax in both habitats to obtain the densities reported in this paper. Another sample of 19 flycatchers collected at nests in mid-July 1980, generally supported the results of this collection.

RESULTS

Vegetation in Managed and Old-Growth Forests

Inherent in the hypothesis being tested in this study was the assumption that the structure and composition of vegetation in managed and old-growth forests were different. A linear function of the density of small trees (DT1), the densities of large trees and snags (DT4, DS34), and tree height diversity (THD) separated the 2 habitats (Fig. 1, Table 2). Values of all discriminating parameters were greater in old-growth forests than in managed forests (Tables 3, 4). One discriminating parameter -- the density of small trees -- was positively correlated (r = 0.80, P < 0.001) with the density of grand fir trees (DGF).

In addition to statistically separating 2 or more groups, discriminant function analysis can be used as a classification technique. Classification is the process of assigning each case (in our study, cases are random-sites or nest-sites) to a group based on its discriminant score. The adequacy of a discriminant function can be checked by classifying the cases used to generate that function and examining the percentage grouped correctly (Klecka 1975). Of the 120 random-sites in managed and old-growth forests, 93% were correctly classified (Table 2). Old-growth forests sometimes included patches that were similar to managed forests (7 misclassifications of 60 sites), but managed forests only rarely included patches that resembled old-growth forests (1 misclassification of 60 sites) (Table 2).

Profiles of canopy volume of managed and old-growth forests clearly depict differences in the number of canopy layers and tree species composition between the 2 habitats (Fig. 2). Total canopy volume in old-growth stands (23,662 m^3/ha) was over twice that in managed stands (11,256 m^3/ha) due primarily to the presence of understory grand fir trees (Fig. 2, Tables 3, 4).

The coefficient of variation of tree density among plots was used to index horizontal diversity of vegetation in each habitat (Wiens 1974, Roth 1976). This index was greater in old-growth stands (93%) than in managed stands (46%), and suggested that when viewed in 0.05 ha plots, old-growth forests were considerably more 'patchy' than managed forests. In both habitats, however, there was a continuum from dense to open patches (Fig. 3). In managed stands, the dense, or 'closed' patches were composed of either ponderosa pine or Douglas-fir, while in old-growth stands these patches generally were composed of grand fir in the understory, and Douglas-fir and grand fir in the overstory. Open patches in both habitats were dominated by ponderosa pine.

Avian Community Parameters

Species Composition. - The assemblage of bird species was similar on managed and old-growth stands; 90% of all species detected (n = 48) occurred in both habitats. Nonparametric rank correlation analyses (Steel and Torrie 1960) were performed each year to generate measures of community similarity (Webb 1977). Correlation coefficients (0.58, 0.58, and 0.53 for 1978, 1979, and 1980, respectively, $P < 0.001$)

suggested that the rank ordering of species by density in the 2 habitats were similar. However, the substantial amount of variation that remained unexplained in the correlations indicated that some differences in the orderings existed (Table 5). Furthermore, location of nest-sites, observations of behavior, and frequency of occurrence all suggested that some species bred in 1 habitat, but not the other. Species that nested in old-growth stands, but not, or at least infrequently in managed stands were the goshawk, pileated woodpecker, Vaux's swift, and Swainson's thrush. Species that nested in managed stands but not in old-growth stands were the dusky flycatcher and mourning dove.

Density and Diversity. - Density of breeding birds was greater (P < 0.05) in managed stands than in old-growth stands; this relationship was consistent in all years (Table 5). In contrast, bird species diversity was greater (P < 0.01) in old-growth stands than in managed stands; this relationship also was consistent throughout the study (Table 5). Both components of the diversity index -- species richness and evenness of distribution of individuals among the species (Tramer 1969) -- were greater in old-growth stands than in managed stands in all 3 years (Table 5).

Variation Among Years. - Total density and diversity of birds fluctuated significantly (P < 0.05) among years in old-growth stands (Table 5). Avian diversity also fluctuated (P < 0.05) among years in managed stands, but variations in total density were not significant (Table 5). Densities of species within each habitat did not necessarily follow the patterns set by total density, but many (both

migrant and resident species) differed markedly among years (e.g.
Cassin's finch and mountain chickadee) (Table 5).

Avian Guilds

Species of birds were placed into guilds (Root 1967) based on
general location of foraging (Holmes et al. 1979) and nesting (Szaro
and Balda 1979) (Table 5). Total densities of birds in most guilds
differed (P < 0.05) between managed and old-growth stands (Table 6).
Species richness in 3 guilds also differd (P < 0.01) between the 2
habitats (Table 6).

Members of the 'hole-nesting' and 'bark-foraging' guilds (the
latter being a subset of the former) generally were more abundant in
old-growth stands than in managed stands (Tables 5, 6). These species
all used snags as nest-sites, and most (especially the woodpeckers)
foraged for insects in the bark and wood of snags. An examination of
snags in both managed and old-growth stands showed that the proportion
used as nest-sites and substrates for foraging generally increased
with the size of the snag (Table 7). Consequently, the density and
proportion of snags used were greater in old-growth stands than in
managed stands (Table 7).

In none of the remaining guilds did all, or even most of the
densities of individual species respond consistently to differences in
the structure and composition of vegetation in managed and old-growth
forests (Table 5). Results were similar when birds were grouped by
'life form' (Thomas et al. 1979).

Habitat Use by Birds Associated with Managed Forests

We did not expect discriminant function analysis to completely separate vegetation around nest-sites of selected species of birds from vegetation around random-sites in either managed or old-growth stands for 2 reasons. First, if adequate samples of plots were taken in managed and old-growth forests, then vegetation around any set of nest-sites within either habitat should resemble closely the vegetation around some subset of random-sites; this subset can be thought of as potential, or in some cases realized nest-sites (Titus and Mohser 1981). Second, all species examined showed some variability in selection of nest-sites. For these reasons, nest-sites and random-sites overlap along the discriminant functions examined below.

Availabilities of tree species and foliage by height class (both based on canopy volume) were generated from information from all stands in either managed or old-growth forests, and not from the territories of the bird species examined. Therefore, non-random selection exhibited by birds, especially with regard to tree species, may be indicative only of selection for a type of within-habitat patch.

Chipping Sparrow. - In comparison to the average site in managed stands, nest-sites of chipping sparrows had greater percent cover of ground vegetation (PRPGRC), greater canopy volume of ponderosa pine trees (CVPP), and lower density of trees in size class 2 (DT2) (Fig. 4, Table 4). These results suggested that chipping sparrows

frequently nested in comparatively large ponderosa pine trees in, or on the edge of openings (Fig. 3h, Table 8). However, the distribution of chipping sparrow nests along the axis of the discriminant function (Fig. 4) indicated that other configurations of vegetation also were used for nesting.

Only 8 nests of chipping sparrows were located in old-growth stands, and no variables met the criterion for entry into the discriminant function analysis of vegetation around these nests and random-sites (α to enter was $P < 0.05$). However, densities of trees in size classes 1, 2, and 3, and the proportion of canopy cover were all lower around nest-sites than around random-sites, while the proportion of ground cover was greater (Table 3). These trends suggested that chipping sparrows were selecting for the more open patches in old-growth forests (Fig. 3d).

In managed stands, chipping sparrows foraged on the ground or in low shrubs 61% of the time. Of the remaining foraging activity, 67% occurred in ponderosa pine trees; this proportion was greater than expected (Fig. 5a, Table 9). Other species of trees were used either less than expected, or in approximately the same proportions in which they occurred (Fig. 5a). When foraging in trees, chipping sparrows generally used the lower portions of the canopy. Foliage in the 0-5 m range was preferred, while foliage above 10 m was avoided (Fig. 6). The sample of observations of chipping sparrows in old-growth stands was small, but patterns observed were similar to those described in managed stands.

Ruby-Crowned Kinglet. - A linear function of the canopy volumes of Douglas-fir, western larch, and grand fir (CVDF, CVWL, CVGF) separated the vegetation around nests of the ruby-crowned kinglet from vegetation around random-sites in managed stands (Fig. 4). Values of all discriminating parameters were greater around the nests (Table 4). Nests most frequently were placed in Douglas-fir or grand fir trees in the middle (14 nests) or lower (6 nests) 1/3 of the canopy (Table 8). No nests were located in old-growth stands.

In managed stands, ruby-crowned kinglets foraged 60% of the time in Douglas-fir trees (Fig. 5a, Table 9). Other species of trees were used less frequently, although some preference was exhibited for both western larch and grand fir trees (Fig. 5a). Ruby-crowned kinglets foraged predominantly in the upper portions of the canopy, and preferred searching for insects in foliage over 15 m above the ground (Fig. 6). Too few observations of ruby-crowned kinglets were made in old-growth stands to assess foraging preferences.

Dusky Flycatcher. - Dusky flycatchers nested only in managed stands, generally in areas dominated by ponderosa pine trees with relatively high percent cover of ground vegetation (Figs. 4, 3f, Table 4). In addition, nest-sites were frequently near openings, although stem density around the nests was not indicative of this fact. Nests were located in either ponderosa pine or Douglas-fir trees; most (10 nests) were situated in the lower 1/3 of the canopy (Table 8). Due to difficulties in field identification, information on foraging behavior was not analyzed.

Habitat Use by Birds Associated with Old-Growth Forests

Townsend's warblers and golden-crowned kinglets occurred infrequently in managed stands; therefore, only information on habitat use in old-growth stands is presented for these species.

Townsend's Warbler. - In comparison to the average site in old-growth stands, Townsend's warblers generally nested in sites that had high canopy volumes of grand fir and Douglas-fir (CVGF, CVDF), and high percent cover of ground vegetation (PRPGRC) (due primarily to the presence of 2 species of shrubs -- Vaccinium membranaceum and Salix scouleri) (Figs. 1, 3c, Table 3). Of the 3 variables, standardized discriminant function coefficients indicated that the canopy volume of grand fir (CVGF) was most important in separating nest-sites from random-sites (Fig. 1). Nests were generally placed in the lower (11 nests) or middle (4 nests) 1/3 of the canopy in overstory trees (Table 8).

Townsend's warblers foraged most frequently, and to a greater extent than expected in grand fir trees (Fig. 5b, Table 9). Western larch trees also were preferred, while ponderosa pine and Douglas-fir trees were avoided (Fig. 5b). Most foraging (88%) occurred in the upper portions of the canopy, with foliage in the 15-20 m range being used most heavily (Fig. 6).

Golden-crowned Kinglet. - Sites used by the golden-crowned kinglet for nesting were similar to those used by the Townsend's warbler (Fig. 1), with 1 exception. Around golden-crowned kinglet nests, the canopy volume of grand fir trees (CVGF) was positively correlated

(r = 0.75, P < 0.001) with the density of grand fir trees (DGF).
Consequently, stem density, particularly of trees in size class 1,
generally was greater around nests of golden-crowned kinglets than
around nests of Townsend's warblers, or random-sites in old-growth
stands (Fig. 3a, Table 3). Nests most frequently were placed in
overstory trees in the lower (9 nests) or middle (6 nests) 1/3 of the
canopy (Table 8).

Golden-crowned kinglets also were similar to Townsend's warblers
in their selection of tree species when foraging (Fig. 5b, Table 9).
However, kinglets generally foraged lower in the canopy than
Townsend's warblers; foliage in the 5-20 m range was used more than
expected, while foliage in the upper canopy generally was avoided
(Fig. 6).

Red-breasted Nuthatch. - On the average, sites used for nesting by
the red-breasted nuthatch in old-growth stands had greater densities
of large snags (DS34), and trees in size class 2 (DT2) than
random-sites (Fig. 1, Table 3). These results suggested that snags
chosen as nest-sites by the red-breasted nuthatch (Table 8) frequently
were part of a group or patch of snags surrounded by small fir trees
(Fig. 3b). However, the wide distribution of nuthatch nests along the
axis of the discriminant function (Fig. 1), and the associated low
percentage of nests classified correctly (Table 2) indicated that this
species nested in snags in other places as well.

Red-breasted nuthatches also were common in managed stands.
Vegetation around nests located in these stands was separated from
vegetation around random-sites by a linear function of the canopy

volumes of Douglas-fir and ponderosa pine (CVDF, CVPP) (Fig. 4). Because there seemed to be little in common between the structure and composition of vegetation at nest-sites in managed and old-growth stands, we suspect that the main criterion for nest-site selection was the presence of a suitable site for excavation. Snags in all size classes were used as nest-sites, but large snags were preferred (Fig. 7). Heights of nest cavities varied considerably in both managed and old-growth stands (Table 8), and were correlated ($r = 0.89$, $P < 0.001$) with the height of the nest snag. Species of snags were used in approximately the same proportion in which they occurred.

While foraging, the red-breasted nuthatch used the surface of snags 11-12% of the time in both managed and old-growth stands; the remaining time was spent on the foliage and bark of trees. With the exception of Douglas-fir and western larch trees in old-growth stands, species of trees in both habitats were used in approximately the same proportions in which they occurred (Figs. 5a, 5b, Table 9). In old-growth stands, nuthatches preferred to forage in foliage 15-20 m above the ground (Fig. 6). In managed stands, foraging by nuthatches generally tracked the availability of foliage by height class (Fig. 6).

DISCUSSION

Vegetation Characteristics and Avian Populations

Of the vegetation parameters we examined, the density of large trees and snags, the density of small, understory trees, and tree height diversity distinguished old-growth forests from managed forests. Each of these variables could be associated either directly or indirectly with differences in bird populations between managed and old-growth forests. Large snags were particularly important in this regard.

Most species of birds that nest in cavities prefer large snags as nest-sites; woodpeckers also prefer large snags as substrates for foraging (Conner et al. 1975, McClelland and Frissell 1975, Bull and Meslow 1977, Bull 1980, Mannan et al. 1980, Raphael 1980). For these reasons, densities of hole-nesting birds generally are greater in forests with large snags than in forests without them (Haapanen 1965, Balda 1975, Nilsson 1979, Scott 1979, Mannan et al. 1980).

We believe the difference in abundance of large snags between managed and old-growth forests was at least partly responsible for the difference in abundance of hole-nesting birds in the 2 habitats. Those species that apparently required large or specific types of snags, or specific conditions surrounding a snag for foraging or nesting (e.g. pileated woodpecker, Bull and Meslow 1977; brown creeper, Raphael 1980; Vaux's swift, Thomas et al. 1979) occurred infrequently, if at all, in managed stands. Species that nested in

small snags, stumps, or dead branches of living trees, and tolerated a variety of stand conditions (e.g. mountain chickadee, hairy woodpecker, red-breasted nuthatch) were common in both old-growth and managed forests.

Large trees also were indirectly important to hole-nesting birds because they are the source of large snags. In addition, the Townsend's warbler and golden-crowned kinglet generally placed nests in large, overstory trees, but due to the range of sizes of nest trees, we doubt that these sites were required for nesting. One species that apparently requires a grove or patch of large trees for nesting is the goshawk (Reynolds et al. 1982). Goshawks nested in 2 of our old-growth stands, but did not nest in any of the managed stands.

The relatively high density of small trees in old-growth stands was directly related to the abundance of grand fir trees. Both the Townsend's warbler and golden-crowned kinglet demonstrated preference on a within-habitat level for grand fir trees when foraging and nesting. We attribute the low abundance of Townsend's warblers and golden-crowned kinglets in managed stands to the near absence of grand fir trees. We suspect that both species of birds were selecting specifically for grand fir trees, and not the physical structure in which grand fir trees usually occurred (i.e. multi-layered canopies), because patches without grand fir trees, regardless of structure, were used infrequently. Selection for a particular species of tree when foraging (e.g. Balda 1969, Willson 1970, James 1976, Franzreb 1978, Eckhardt 1979, Holmes et al. 1979) may occur because the food resource is greater on the preferred tree species, or because the physical

configuration of needles and branches allows the bird in question to more easily search for and capture prey items (Holmes and Robinson 1981).

Although not quantitatively described, nests of the hermit thrush also were located in patches of small grand fir trees. Most observations of this species occurred in dense thickets. Similarly, Bock and Lynch (1970) found that the hermit thrush was characteristic of only the most shaded and concealed areas of the forest. Kilgore (1971) noted that the hermit thrush disappeared from stands of giant sequoia (Squoiadendron giganteum) after dense thickets of white fir (Abies concolor) and incense cedar (Libocedrus decurrens) were removed from the understory. We suspect that the low abundance of this species in managed stands was due to the absence of dense understory vegetation. The Swainson's thrush also occasionally used dense patches of grand fir in old-growth stands, but this bird is more charcteristic of riparian vegetation than upland forests in this region (Thomas et al. 1979).

The distinguishing characteristics of vegetation in managed forests were converse expressions of those that distinguished old-growth forests; they included low densities of large snags and trees, low density of understory trees, and low tree height diversity (i.e. a single canopy layer). These characteristics, and the uniform spacing between trees combined to produce an overall effect of 'openness' in managed forests (Fig. 3).

Some species of birds that forage on or near the ground prefer open forests for foraging and nesting, presumably because of the

abundance of food associated with ground vegetation (Haapanen 1965, Bock and Lynch 1970, Kilgore 1971, Franzreb and Ohmart 1978, Apfelbaum and Haney 1981, Beedy 1981). In our study, the chipping sparrow demonstrated a within-habitat preference for open areas when nesting and foraging. The more uniform degree of openness in managed versus old-growth forests (Fig. 3) was probably the reason for the difference in abundance of chipping sparrows between the 2 habitats. Several other species that foraged on the ground (e.g. Cassin's finch, dark-eyed junco, mourning dove) also were more abundant in managed stands than in old-growth stands. These species may have been associated with open areas for foraging and nesting as well.

The degree of openness of a forest appears to be important in determining the number of species and individuals of birds that forage for insects in the air. Forests with openings (either man-made or natural) generally support greater densities of flycatchers than forests without such openings (Haapanen 1965, Kilgore 1971, Franzreb and Ohmart 1978, Beedy 1981). Abundance of flying insects, availability of open perch sites, and room for aerial pursuit have been suggested as reasons for the preference of open areas by flycatchers (Kilgore 1971, Franzreb and Ohmart 1978).

In this study, the dusky flycatcher was the most abundant species in managed forests, but did not occur, or occurred infrequently, in old-growth forests. In contrast, the Hammond's flycatcher was approximately equal in abundance in both habitats. Johnson (1963) reported that where the dusky and Hammond's flycatchers occurred together in California, the former used open stands of timber on sunny

slopes, whereas the latter used a variety of habitats, but generally occupied more heavily forested stands. Our results indicated that in managed forests, the dusky flycatcher nested in areas that were dominated by ponderosa pine trees and had relatively high percent cover of ground vegetation -- both parameters suggest open areas with sunlight penetration. Old-growth stands may have been too 'closed' for the dusky flycatcher. We recommend further investigation of the use of habitat by these species, especially in managed stands where both species nest.

Although the slopes of all stands faced west or southwest, topographic irregularities sometimes produced small areas that faced north. In managed stands, these areas were dominated by Douglas-fir trees mixed with small numbers of larch and grand fir trees. Ruby-crowned kinglets used these patches for foraging and nesting.

Given the species of trees preferred by the ruby-crowned kinglet, it seemed unusual that this species was not abundant in old-growth stands. A competitive interaction between ruby-crowned and golden-crowned kinglets might explain the situation, but this seems unlikely as both species occur together in other mixed-coniferous forests (Franzreb and Ohmart 1978). There is some evidence suggesting that ruby-crowned kinglets prefer, or at least tolerate open forests. Beedy (1981) found that this species was present during the breeding season in forests with open canopies, but did not occur in the same type of forests when the canopies were closed. In our study, the few observations of the ruby-crowned kinglet in old-growth stands generally were made in the more open patches. We tentatively conclude

that although the composition of trees in old-growth forests seemed compatible with the preferences of the ruby-crowned kinglet, the structure of the forest where the preferred tree species occured was too 'closed'.

The degree of openness appeared to be the most important proximate factor influencing the densities of those species that were more abundant in managed forests than in old-growth forests. Crawford et al. (1981) also found that the degree of canopy closure was a powerful variable for predicting habitat preferences by songbirds.

Vegetation Characteristics and Avian Guilds

Avian guilds have been used to assess how groupings of birds respond to differences in structure and composition of vegetation in different habitats, or in the same habitat at different times (Balda 1970, Franzreb and Ohmart 1978, Szaro and Balda 1979, Maurer et al. 1981). In this study, there were differences in the total densities of birds in guilds between managed and old-growth forests. However, with the exception of hole-nesting birds, consistent responses (in terms of density) did not exist for most species within guilds. For example, an examination of the birds that feed in the canopy foliage indicated that the relatively high density of birds in old-growth forests was due primarily to the abundance of only 2 species -- the golden-crowned kinglet and Townsend's warbler. The other 9 species in this guild either were about equal in abundance in the 2 habitats or were greater in managed forests than in old-growth forests. The lack of consistent responses among species within guilds also was apparent

among birds that forage on the ground. The chipping sparrow, Cassin's finch, and dark-eyed junco all were more abundant in managed forests than in old-growth forests, while the reverse was true for the hermit thrush and Swainson's thrush. Even among hole-nesting birds (where most species were more abundant in old-growth forests than in managed forests), variability in habitat requirements appeared to influence the degree of response. In short, species were selecting for nest-sites and substrates for foraging on finer scales than were characterized by the guilds we employed.

Vegetation Characterstics and Avian Communities

Total Density. - In this study, managed forests supported more breeding birds than old-growth forests due primarily to the abundance of the dusky flycatcher, chipping sparrow, Cassin's finch, dark-eyed junco, and ruby-crowned kinglet. Reported effects of forest management on total bird density have varied with the type and age of stands examined, silvicultural treatments employed, and the intensity of application of treatments (Haapanen 1965, Nilsson 1979, Szaro and Balda 1979). Also, the degree of response to habitat alterations varies among bird species; thus, the effects of a particular alteration on total bird density depends, in part, upon the assemblage of species that occupies the area being perturbed. For these reasons, generalizations about the effects of forest management on total bird density are difficult to make. Furthermore, values of total density alone have little meaning from a wildlife management perspective. As in this study, a managed forest may support a high total density of

birds, and still be poor habitat for an entire group of birds (e.g. hole-nesting birds).

Species Diversity. - Bird species diversity was lower in managed forests than in old-growth forests due primarily to the absence of members of the thrush (Turdidae) and woodpecker (Picidae) families, and to the numerical dominance of the dusky and Hammond's flycatchers, chipping sparrow, and Cassin's finch. MacArthur and MacArthur (1961), Karr (1968), Recher (1969), Karr and Roth (1971), and others have found positive correlations between bird species diversity and measures of vertical diversity of vegetation (i.e. foliage height diversity). Similarly, Roth (1976) found that horizontal diversity of vegetation is frequently correlated with the diversity of birds. However, these relationships are not universal (e.g. Balda 1969, Tomoff 1974, Wiens 1974, Willson 1974, Franzreb and Ohmart 1978, Szaro and Balda 1979), and factors other than 'patchiness' of vegetation also influence avian diversity (e.g. historial patterns of vegetation and bird distribution, number of food sources and nest-sites, competitive interactions, plant species composition). In our study, vegetation in managed forests was low in measures of both vertical and horizontal diversity. Thus, our results support the contention that patchiness of vegetation is a predictor of bird species diversity.

Variation Among Years. - The magnitude of annual fluctuations in total density and diversity of birds found in this study are not uncommon (e.g. Franzreb and Ohmart 1978, Szaro and Balda 1979). Factors that potentially cause annual fluctuations in these parameters include events or conditions that affect food, shelter, or nest-sites

during the breeding season (Franzreb and Ohmart 1978), and those that affect required resources during migration and winter (Fretwell 1972). On our study areas, little change among years was apparent in weather conditions or plant phenology during the breeding seasons. Therefore, we suspect that the observed fluctuations in bird density and diversity were due, in part, to events or conditions that occurred outside the breeding season. Even though these fluctuations occurred, the relationships between densities of the same bird species in managed and old-growth forests remained approximately the same throughout the study.

MANAGEMENT IMPLICATIONS

Although the 'managed' (i.e. thinned) stands we examined approximated the structure of managed forests at rotation age, certain structural aspects of these stands may differ from managed forests of the future. These differences influence the management implications of our study. For example, in several instances, the presence of nesting woodpeckers in managed stands was directly dependent upon the presence of large 'remnant' snags (Cline et al. 1980) -- those few that remained standing after the thinning operation. Such snags will not be present in future, more intensively managed forests (unless management plans dictate their presence), and densities of most woodpeckers (and some other hole-nesting birds) probably will be lower than those observed in the managed stands in this study. Also, silvicultural perscriptions for managed forests of the future call for thinning at an earlier age than was accomplished in the stands we examined. When the canopy begins to close following the early thinning operation, densities of birds associated with 'open' stands (e.g. chipping sparrow, dusky flycatcher, ruby-crowned kinglet) may decline.

Another limitation of our study was that we examined birds and vegetation structure only on west- or southwest-facing slopes. Managed stands on these slopes were nearly devoid of grand fir trees, and consequently, supported low densities of species such as the Townsend's warbler, golden-crowned kinglet, and hermit thrush. We suspect that north-facing slopes in the Abies grandis zone may produce

enough grand fir, even under timber management regimes, to support golden-crowned kinglets and Townsend's warblers, while shrubs and small trees in early seral stages and riparian buffer strips probably will support hermit thrushes.

With the above limitations of our study in mind, we conclude that if old-growth forests are eliminated from areas under intensive management for timber in the Abies grandis zone in northeastern Oregon, some species of birds probably will increase in density (e.g. chipping sparrow, ruby-crowned kinglet, dusky flycatcher, dark-eyed junco, Cassin's finch), some will decrease (e.g. Townsend's warbler, golden-crowned kinglet, hermit thrush, and most hole-nesting birds), and a few may be extirpated on a region-wide basis (e.g. goshawk, Vaux's swift, pileated woodpecker and its associated secondary cavity users). These conclusions generally should apply in forests with similar tree species composition in the Abies grandis zone throughout the Pacific Northwest. However, with the possible exception of information on hole-nesting birds, our results should not be applied beyond these limits.

If the objective of wildlife management in forest ecosystems is to maintain viable populations of all native species, then clearly, management efforts should focus on those birds (and other animals) that will be negatively impacted by the liquidation of old-growth forests. One strategy that may be effective for managing some of these birds is to incorporate important components of old-growth forests into managed forests. An example of such a component is large snags. Specific sizes and numbers of snags required for most

hole-nesting birds have been calculated (Thomas et al. 1979).
However, under intensive management regimes for timber, methods for
maintaining large snags are complex, and require careful, long-term
planning. Furthermore, providing snags without regard for stand
conditions around the snag may be sufficient for some species, but not
for others (Bull 1980, Raphael 1980).

Perhaps the best way to insure the availability of habitat for
birds associated with old-growth forests is to maintain patches of
undisturbed old-growth habitat in managed forest systems. Although we
avoided the complicating factor of riparian zones in this study, one
place old-growth forests could be maintained is in riparian buffer
strips (Cline et al. 1980). If old-growth forests are maintained in
managed forests, practical questions that confront timber and wildlife
managers include: (1) how much old-growth habitat is needed? (2)
what are the required sizes, shapes, and distribution of patches of
old-growth habitat? and (3) how should the distribution of patches of
old-growth habitat be managed over time? (Mannan 1980). Answers to
the above questions require, in part, species-specific information on
nest-site requirements, foraging ecology, size of territory or home
range, dispersal capabilities of the young, and viable population size.

Community parameters such as total density and species diversity,
or correlations between these measures and vegetation parameters, do
not alone provide the basis for management of birds associated with
old-growth forests. For example, in our study, bird species diversity
was high where vegetation patchiness was high. But this association
provided little insight into the components of vegetation that were

important to birds. For instance, some species of birds associated with multi-layered canopies (e.g. Townsend's warbler, golden-crowned kinglet) appeared to be selecting for a specific species of tree (i.e. grand fir), and not for the physical structure of the forest. In addition, neither measure of vegetation patchiness (vertical or horizontal) was strongly influenced by the density of large snags, and yet large snags seemed to play an important role in determining avian diversity on our study areas.

Even the use of guilds in developing management programs for birds in old-growth forests may prove inadequate unless the guilds are formulated from species-specific information on habitat-use. Clearly, detailed information at the species level is important to the development of management programs for old-growth forests. Judging from the results of this study and others, such management programs will need to address both the structural and compositional elements of forest vegetation.

Table 1. Description of variables characterizing the structure and composition of vegetation at random-sites, and nest-sites of selected species of birds in managed and old-growth mixed-coniferous forests, northeastern Oregon.

Mnemonic	Description
DS34	Density[a] of snags in size classes 3 and 4 (31+ cm dbh[b])
DT1	Density[c] of trees in size class 1 (2.5-10 cm dbh)
DT2	Density[c] of trees in size class 2 (11-30 cm dbh)
DT3	Density[c] of trees in size class 3 (31-50 cm dbh)
DT4	Density[c] of trees in size class 4 (51+ cm dbh)
DDF	Density[c] of Douglas-fir trees
DPP	Density[c] of ponderosa pine trees
DGF	Density[c] of grand fir trees
DWL	Density[c] of western larch trees
CVDF	Canopy volume[d] of Douglas-fir trees
CVPP	Canopy volume of ponderosa pine trees
CVGF	Canopy volume of grand fir trees
CVWL	Canopy volume of western larch trees
THD	Tree height diversity[e]
PRPCC	Proportion of canopy cover
PRPGRC	Proportion of ground vegetation cover

[a] Number per 0.5 ha.
[b] dbh = diameter at breast height.
[c] Number per 0.05 ha.
[d] Cubic meters per 0.05 ha.
[e] Calculated using Shannon's function (Shannon and Weaver 1949,

$$H' = -\sum_{i=1}^{s} p_i \log_e p_i,$$ where p_i is the proportion of total density

in the ith height class, and s is the number of classes.

Table 2. Summary of discriminant function anlayses of habitat variables between random-sites in managed and old-growth forests, and between random-aites and nest-sites of selected species of birds.

Group 1 versus group 2	α required for entry of variables	Eigenvalue	Canonical Correlation	Chi-square[a] value (df, significance)	Classification[b] N correctly classified in group 1 (total)	N correctly classified in group 2 (total)
Old-growth vs managed	0.005	2.33	0.84	139.74[c] (4, P < 0.00001)	59 (60)	53 (60)
Townsend's warbler vs old-growth	0.05	0.86	0.68	44.47 (2, P < 0.0001)	12 (15)	53 (60)
Golden-crowned kinglet vs old-growth	0.005	0.52	0.59	31.19 (2, P < 0.0001)	13 (17)	49 (60)
Red-breasted nuthatch vs old-growth	0.005	0.49	0.58	32.92[c] (2, P < 0.0001)	16 (25)	46 (60)
Red-breasted nuthatch vs managed	0.05	0.37	0.52	23.00 (2, P < 0.0001)	13 (17)	50 (60)
Ruby-crowned kinglet vs managed	0.005	0.61	0.62	36.93[c] (3, P < 0.0001)	14 (21)	51 (60)
Chipping sparrow vs managed	0.005	0.56	0.60	40.63[c] (3, P < 0.0001)	24 (34)	48 (60)
Dusky flycatcher vs managed	0.01	0.47	0.56	27.19[c] (2, P < 0.0001)	9 (13)	50 (60)

[a] Test of separation of groups by the discriminant function.

[b] Classification derived from the 'jackknife' procedure (Biomedical Statistical Program P Series, Dixon and Brown 1979).

[c] Variance-covariance matrices were different (Box's M Test, P ≤ 0.05)

Table 3. Descriptive statistics of vegetation at random-sites, and nest-sites of selected species of birds in old-growth mixed-coniferous forests, northeastern Oregon.

Variable[a]	Old-growth forests (n = 60) $\bar{x} \pm$ SD (range)	Red-breasted nuthatch (n = 25) $\bar{x} \pm$ SD (range)	Golden-crowned kinglet (n = 17) $\bar{x} \pm$ SD (range)	Townsend's warbler (n = 15) $\bar{x} \pm$ SD (range)	Chipping sparrow (n = 8) $\bar{x} \pm$ SD (range)
DS34	4.2 ± 4.3 (0-25)	11.3 ± 8.4 (1-30)	5.2 ± 3.3 (2-12)	2.9 ± 2.7 (0-9)	2.1 ± 1.7 (0-5)
DT1	14.5 ± 23.3 (0-156)	26.2 ± 28.7 (0-87)	35.9 ± 39.0 (2-156)	17.7 ± 14.1 (1-41)	4.5 ± 3.7 (0-10)
DT2	8.5 ± 6.9 (0-32)	15.8 ± 15.9 (1-54)	16.5 ± 11.3 (1-38)	12.8 ± 6.8 (4-26)	5.4 ± 4.0 (1-12)
DT3	2.6 ± 2.4 (0-11)	2.6 ± 2.1 (0-7)	4.2 ± 2.2 (1-7)	3.3 ± 1.6 (1-7)	1.9 ± 2.6 (0-8)
DT4	2.4 ± 1.9 (0-9)	2.5 ± 2.0 (0-8)	2.4 ± 1.5 (0-5)	2.3 ± 1.7 (0-5)	2.3 ± 2.1 (0-6)
DDF	8.7 ± 11.4 (0-63)	9.9 ± 16.5 (0-62)	7.2 ± 5.0 (0-18)	6.5 ± 4.8 (0-17)	6.0 ± 4.4 (0-13)
DPP	3.8 ± 3.5 (0-15)	2.6 ± 3.9 (0-15)	1.4 ± 1.8 (0-7)	1.7 ± 3.3 (0-13)	4.1 ± 4.5 (0-13)
DGF	14.4 ± 3.0 (0-148)	29.6 ± 6.8 (0-121)	44.6 ± 9.1 (0-148)	26.9 ± 4.7 (1-60)	3.1 ± 1.2 (0-10)

[a] For description of mnemonics see Table 1.

Table 3. Continued

Variable[a]	Old-growth forests (n = 60)	Red-breasted nuthatch (n = 25)	Golden-crowned kinglet (n = 17)	Townsend's warbler (n = 15)	Chipping sparrow (n = 8)
	$\bar{x}$ ± SD (range)	$\bar{x}$ ± SD (range)	$\bar{x}$ ± SD (range)	$\bar{x}$ ± SD (range)	$\bar{x}$ ± SD (range)
DWL	1.0 ± 0.4 (0-18)	3.2 ± 1.1 (0-23)	3.4 ± 1.6 (0-23)	1.1 ± 0.5 (0-6)	0.6 ± 0.4 (0-3)
CVDF	516.8 ± 486.2 (0-1871)	624.0 ± 724.7 (0-2940)	952.5 ± 895.3 (0-2732)	827.8 ± 1179.3 (0-4305)	888.1 ± 1189.3 (0-3699)
CVPP	287.4 ± 323.0 (0-1482)	378.4 ± 832.2 (0-4000)	230.6 ± 612.1 (0-2414)	260.8 ± 407.0 (0-1351)	451.9 ± 457.5 (0-1257)
CVGF	348.2 ± 456.8 (0-2196)	751.9 ± 673.5 (0-2571)	1137.0 ± 652.8 (0-2766)	1093.8 ± 788.1 (17-2636)	249.9 ± 739.1 (0-2122)
CVWL	30.9 ± 104.5 (0-645)	113.2 ± 222.3 (0-1021)	64.1 ± 124.7 (0-417)	81.9 ± 193.3 (0-610)	47.3 ± 76.1 (0-185)
PRPCC	0.59 ± 0.22 (0.01-0.93)	0.57 ± 0.24 (0.09-0.99)	0.68 ± 0.16 (0.38-0.97)	0.63 ± 0.17 (0.26-0.86)	0.44 ± 0.13 (0.23-0.59)
PRPGRC	0.17 ± 0.10 (0.01-0.57)	0.25 ± 0.15 (0.01-0.57)	0.15 ± 0.11 (0.03-0.40)	0.32 ± 0.17 (0.08-0.61)	0.22 ± 0.08 (0.10-0.30)
THD	1.44 ± 0.29 (0.69-2.00)	1.49 ± 0.17 (1.16-1.81)	1.59 ± 0.22 (0.88-1.82)	1.57 ± 0.20 (1.27-2.01)	1.38 ± 0.34 (0.69-1.83)

[a] For description of mnemonics see Table 1.

Table 4. Descriptive statistics of vegetation at random-sites, and nest-sites of selected species of birds in managed mixed-coniferous forests, northeastern Oregon.

Variable[a]	Managed forests (n = 60) $\bar{x} \pm$ SD (range)	Dusky flycatcher (n = 13) $\bar{x} \pm$ SD (range)	Red-breasted nuthatch (n = 17) $\bar{x} \pm$ SD (range)	Ruby-crowned kinglet (n = 21) $\bar{x} \pm$ SD (range)	Chipping sparrow (n = 34) $\bar{x} \pm$ SD (range)
DS34	0.7 ± 0.9 (0-4)	0.2 ± 0.4 (0-1)	1.0 ± 1.2 (0-4)	1.2 ± 1.4 (0-5)	0.6 ± 0.8 (0-3)
DT1	0.4 ± 0.7 (0-3)	0.5 ± 0.8 (0-2)	0.6 ± 0.8 (0-3)	1.4 ± 1.9 (0-6)	0.8 ± 1.0 (0-4)
DT2	9.0 ± 5.7 (1-28)	7.5 ± 4.5 (2-15)	9.1 ± 5.8 (3-21)	6.6 ± 3.5 (2-14)	5.4 ± 4.2 (0-15)
DT3	3.7 ± 2.5 (0-12)	4.5 ± 4.1 (0-11)	4.0 ± 2.3 (0-8)	5.5 ± 3.5 (0-16)	3.4 ± 2.7 (0-12)
DT4	0.1 ± 0.3 (0-1)	0.3 ± 0.6 (0-2)	0.1 ± 0.3 (0-1)	0.3 ± 0.6 (0-2)	0.6 ± 1.0 (0-4)
DDF	4.5 ± 4.9 (0-25)	3.4 ± 3.9 (0-13)	6.3 ± 6.5 (0-24)	4.8 ± 3.2 (0-12)	2.3 ± 2.5 (0-10)
DPP	8.0 ± 7.2 (0-35)	9.5 ± 7.4 (2-25)	7.2 ± 5.2 (1-19)	4.1 ± 3.3 (0-13)	7.3 ± 6.4 (1-29)
DGF	0.4 ± 0.2 (0-10)	0.0 ± 0.0 (0-0)	0.0 ± 0.0 (0-0)	3.0 ± 1.1 (0-18)	0.2 ± 0.2 (0-6)

[a] For description of mnemonics see Table 1.

Table 4. Continued

Variable[a]	Managed forests (n = 60) $\bar{x} \pm$ SD (range)	Dusky flycatcher (n = 13) $\bar{x} \pm$ SD (range)	Red-breasted nuthatch (n = 17) $\bar{x} \pm$ SD (range)	Ruby-crowned kinglet (n = 21) $\bar{x} \pm$ SD (range)	Chipping sparrow (n = 34) $\bar{x} \pm$ SD (range)
DWL	0.3 ± 0.1 (0-6)	0.0 ± 0.0 (0-0)	0.2 ± 0.2 (0-4)	2.0 ± 0.8 (0-12)	0.3 ± 0.3 (0-9)
CVDF	302.7 ± 322.4 (0-1395)	359.1 ± 398.7 (0-1215)	538.1 ± 374.2 (0-1166)	545.9 ± 434.8 (0-1756)	287.9 ± 291.0 (0-920)
CVPP	227.8 ± 207.6 (0-953)	512.7 ± 472.6 (34-1414)	414.4 ± 380.9 (13-1406)	262.8 ± 230.5 (0-699)	451.4 ± 404.6 (5-1558)
CVGF	24.9 ± 107.5 (0-761)	0.0 ± 0.0 (0-0)	0.0 ± 0.0 (0-0)	306.5 ± 563.4 (0-2046)	45.2 ± 242.3 (0-1411)
CVWL	7.8 ± 27.6 (0-170)	0.0 ± 0.0 (0-0)	29.4 ± 121.3 (0-500)	154.0 ± 283.5 (0-1137)	23.6 ± 120.9 (0-701)
PRPCC	0.40 ± 0.15 (0.11-0.76)	0.39 ± 0.18 (0.12-0.63)	0.48 ± 0.12 (0.17-0.66)	0.43 ± 0.16 (0.09-0.69)	0.36 ± 0.15 (0.05-0.71)
PRPGRC	0.20 ± 0.09 (0.03-0.42)	0.36 ± 0.15 (0.13-0.63)	0.28 ± 0.10 (0.04-0.41)	0.27 ± 0.15 (0.05-0.41)	0.34 ± 0.16 (0.05-0.72)
THD	1.04 ± 0.35 (0-1.71)	0.92 ± 0.36 (0.41-1.49)	1.01 ± 0.27 (0.69-1.46)	1.20 ± 0.33 (0.38-1.73)	1.06 ± 0.29 (0.50-1.55)

[a]For description of mnemonics see Table 1.

Table 5. Densities of breeding birds in managed and old-growth mixed-coniferous forests, northeastern Oregon.

Species	Foraging Guild[a]	Nesting Guild[b]	Managed 1978	Managed 1979	Managed 1980	Old-growth 1978	Old-growth 1979	Old-growth 1980
Goshawk (Accipiter gentilis)	V	C				+[c]	+	0.5
Cooper's hawk (Accipiter cooperii)	V	C			+			
Sharp-shinned hawk (Accipiter striatus)	V	C	+					+
Red-tailed hawk (Buteo jamaicensis)	V	C	+		0.5			0.5
Blue grouse (Dendragapus obscurus)	CF	G	0.5	1	1	0.5	1	1
Ruffed grouse (Bonasa umbellus)	CF	G	0.5	0.5	+	+	0.5	0.5
Mourning dove (Zenaida macroura)	G	C	0.5	0.5	0.5	+		
Great-horned owl (Bubo virginianus)	V	C		P[d]	P		P	P
Saw-whet owl (Aegolius acadicus)	V	H		P	P		PP[e]	PP
Flammulated owl (Otus flammeolus)	V	H					P	P
Common nighthawk (Chordeiles minor)	A	G	0.5	+	0.5	+	+	
Vaux's swift (Chaetura vauxi)	A	H			+	+	0.5	1
Calliope hummingbird (Stellula calliope)	G	C	+	+	+			+
Common flicker (Colaptes auratus)	V	H	+	+	0.5	1	0.5	0.5
Pileated woodpecker (Dryocopus pileatus)	B	H	+	+	+	0.5	0.5	0.5
White-headed woodpecker (Picoides albolarvatus)	B	H	0.5	0.5		1	1	
Yellow-bellied sapsucker (Sphyrapicus varius)	B	H	0.5			0.5	+	0.5
Williamson's sapsucker (Sphyrapicus thyroideus)	B	H	+	+	+	0.5	0.5	0.5
Hairy woodpecker (Picoides villosus)	B	H	1	1	2	1	2	3
Black-backed three-toed woodpecker (Picoides arcticus)	B	H	+	0.5	1	0.5		+
Hammond's flycather (Empidonax hammondii)	A	C	38	48	41	35	37	36
Dusky flycatcher (Empidonax oberholseri)	A	C	47	58	50			
Steller's jay (Cyanocitta stelleri)	V	C		+		+	+	+

Table 5. Continued

Species	Foraging Guild[a]	Nesting Guild[b]	Managed			Old-growth		
			1978	1979	1980	1978	1979	1980
Gray jay (Perisoreus canadensis)	V	C			+	0.5	+	1
Common raven (Corvus corax)	G	C	+	+	0.5	+		0.5
Mountain chickadee (Parus gambeli)	CF	H	7	6	14	7	8	16
White-breasted nuthatch (Sitta carolinensis)	B	H	1	1	2	0.5	0.5	1
Red-breasted nuthatch (Sitta canadensis)	B	H	3	7	7	10	15	17
Brown creeper (Certhia familiaris)	B	H	0.5	0.5	0.5	17	16	19
American robin (Turdus migratorius)	G	C	3	2	2	2	3	2
Varied thrush (Ixoreus naevius)[f]	G	C				0.5	+	0.5
Townsend's solitaire (Myadestes townsendi)	G	G	1	2	1	1	1	1
Hermit thrush (Catharus guttatus)	G	C	1	2	2	14	11	10
Swainson's thrush (Catharus ustulatus)	G	C				0.5	1	1
Golden-crowned kinglet (Regulus satrapa)	CF	C	0.5		0.5	31	25	25
Ruby-crowned kinglet (Regulus calendula)	CF	C	8	9	11	2	0.5	1
Solitary vireo (Vireo solitarius)	CF	C	9	11	7	7	6	4
Yellow-rumped warbler (Dendroica coronata)	CF	C	22	24	19	15	20	18
Townsend's warbler (Dendroica townsendi)	CF	C	0.5	2	2	11	15	18
MacGillivray's Warbler (Oporornis tolmiei)	G	C	+	+		2	1	
Brown-headed cowbird (Molothrus ater)	G	C	4	4	3	0.5		
Western tanager (Piranga ludoviciana)	CF	C	11	8	12	13	11	13
Evening grosbeak (Hesperiphona vespertina)	CF	C			1			1
Cassin's finch (Carpodacus cassinii)	G	C	16	20	30	6	5	14

Table 5. Continued

Species	Foraging Guild[a]	Nesting Guild[b]	Managed			Old-growth		
			1978	1979	1980	1978	1979	1980
Pine siskin (Carduelis pinus)	G	C	15	2	10	10	0.5	8
Red crossbill (Loxia curvirostra)	CF	C	7	2	6	5	0.5	6
Dark-eyed junco (Junco hyemalis)	G	G	19	16	23	12	8	16
Chipping sparrow (Spizella passerina)	G	C	27	35	35	13	15	12
Total density[g]			244.5	263.5	285.5	221.0	206.5	249.5
Species diversity (H')[h]			2.57	2.44	2.63	2.81	2.68	2.86
Species richness			28	26	30	32	29	34
Evenness (J)[i]			0.77	0.75	0.77	0.81	0.80	0.85

[a] A = air, B = bark, CF = canopy foliage, G = ground or low foliage, V = various substrates.

[b] C = canopy of trees and other vegetation, G = ground, H = holes in snags.

[c] Species with less than 0.1 singing males per 40.5 ha.

[d] Detected in 2 stands during call-censuses in 1979 and 1980. Call censuses were initiated after sunset and consisted of playing tape-recorded calls of all endemic species of owls every 3rd station 2 times per year.

[e] Detected in 4 stands during call-censuses (see d) in 1979 and 1980.

[f] Detected only in late-May.

[g] We calculated a mean of the 5 values generated for each stand per year. Split-plot-in-time analysis of variance (Snedecor and Cochran 1956) was then used to evaluate differences between grand means (i.e. 3-year-averages). Grand means differed ($P < 0.05$) between managed and old-growth forests. Variation among years was different (1-way-analysis of variance, $P < 0.05$) in and old-growth forests, but not managed forests.

[h] H' = Shannon's function (Shannon and Weaver 1949). Three-year-average differed (split-plot-in-time analysis of variances, see g, $P < 0.05$) between managed and old-growth forests. Variation among years was different (1-way-analysis of variance, $P < 0.05$) in both managed and old-growth forests.

[i] J = H' observed/H' maximum for a given number of species.

Table 6. Density[a] and species richness of breeding birds in guilds based on general location of foraging and nesting in managed and old-growth mixed-coniferous forests, northeastern Oregon.

	Managed Forests	Old-Growth Forests
Nesting		
Hole		
Density (% total birds)	19.0 (7)	47.7 (21) **
Species richness (% total species)	7 (25)	10 (31) **
Canopy		
Density (% total birds)	223.3 (84)	163.8 (73) **
Species richness (% total species)	17 (61)	18 (56)
Ground		
Density (% total birds)	22.2 (8)	14.2 (6) **
Species richness (% total species)	4 (14)	4 (13)
Foraging[b]		
Canopy foliage		
Density (% total birds)	67.7 (26)	94.2 (42) *
Species richness (% total species)	10 (36)	10 (31)
Ground - low foliage		
Density (% total birds)	92.2 (35)	57.2 (25) **
Species richness (% total species)	9 (32)	10 (31)
Bark		
Density (% total birds)	9.8 (4)	36.2 (16) **
Species richness (% total species)	6 (21)	8 (25) **
Air		
Density (% total birds)	94.3 (36)	36.5 (16) **
Species richness (% total species)	3 (11)	2 (6) **

[a] Number per 40.5 ha averaged over 3 years. Split-plot-in-time analysis of variance was used to evaluate differences in density and species richness.

[b] Species that used a variety of substrates when foraging were not included.

* $P < 0.05$, ** $P < 0.01$

Table 7. Density and proporton of snags with cavities or evidence of woodpecker foraging by size class in managed and old-growth mixed-coniferous forests, northeastern Oregon.

Forest[a/]	Size class[b/]	(A) Total snags Sampled	(B) Total snags per hectare	Snags with cavities		Snags with evidence of woodpecker foraging	
				(C) Percent of total snags sampled (%A)[c/]	N per hectare (B)x(C)	(D) Percent total snags sampled (%A)[d/]	N per hectare (B)x(D)
Managed	2	230	7.6	2.6	0.2	71.7	5.5
	3	29	1.0	17.2	0.2	79.3	0.8
	4	15	0.5	40.0	0.2	100.0	0.5
	Total	274	9.1	6.2	0.6	74.1	6.7
Old-growth	2	182	6.0	1.1	0.1	67.0	4.0
	3	114	3.8	7.9	0.3	94.7	3.6
	4	137	4.6	32.1	1.5	93.4	4.3
	Total	433	14.4	12.7	1.8	82.7	11.9

[a/] Chi-square tests indicated differences in the number of snags with cavities ($P < 0.01$, $X^2 = 7.75$, 1 df), and with evidence of woodpecker foraging ($P < 0.01$, $X^2 = 7.56$, 1 df) in managed and old-growth forests.

[b/] Size classes of snags are based on diameter (dbh): 2 = 11-30 cm, 3 = 31-50 cm, 4 = 51+ cm.

[c/] Chi-square tests indicated differences among numbers of snags with cavities in the 3 size classes in both old-growth ($P < 0.01$, $X^2 = 71.04$, 2 df) and managed ($P < 0.01$, $X^2 = 40.62$, 2 df) forests.

[d/] Chi-square tests indicated differences among numbers of snags with evidence of woodpecker foraging in the 3 size classes in both old-growth ($P < 0.01$, $X^2 = 53.74$, 2 df) and managed ($P < 0.05$, $X^2 = 6.32$, 2 df) forests.

Table 8. Characteristics of nests and nest trees (or snags) of selected species of birds in managed and old-growth mixed-coniferous forests, northeastern Oregon.

Forest	Bird Species	N	Nest height (m)		Species[a] (n)				Height (m)		Diameter (cm)	
			$\overline{x}$	Range	DF	PP	GF	WL	$\overline{x}$	Range	$\overline{x}$	Range
Old-growth	Red-breasted nuthatch[b]	25	20.4	8.2-33.2	8	7	4	6	24.2	5.2-40.8	64.0	25.4-104.9
	Golden-crowned kinglet[c]	17	16.3	7.9-28.4	7		9		28.0	22.0-34.4	51.8	30.5-78.2
	Townsend's warbler[d]	15	11.0	4.6-20.7	5		9		27.3	20.1-34.1	54.6	33.3-78.2
	Chipping Sparrow	8	7.7	2.4-18.9	5	2	1		27.9	15.2-37.8	65.8	24.9-110.0
Managed	Dusky flycatcher[e]	13	5.3	2.1-11.3	5	8			16.6	9.1-22.6	31.2	19.1-60.5
	Red-breasted nuthatch[f]	17	8.1	3.7-14.3	5	12			12.3	5.2-31.7	32.2	14.0-54.6
	Ruby-crowned kinglet	21	11.8	2.1-20.2	15	1	5		22.0	12.2-30.5	39.5	25.4-63.0
	Chipping sparrow	34	4.4	1.2-13.4	11	23			17.1	4.0-26.8	36.7	9.4-65.8

[a] DF = Douglas-fir, PP = ponderosa pine, GF = grand fir, and WL = western larch.

[b] Twenty-two of 25 nuthatch nests in old-growth stands were in completely dead trees; 3 were in dead-topped trees.

[c] One golden-crowned kinglet nest was located in an Engelmann spruce (Picea engelmannii) tree.

[d] One Townsend's warbler nest was located in an Engelmann spruce tree.

[e] Identified by collecting birds at nest in late July 1980.

[f] Thirteen nuthatch nests in managed stands were in completely dead trees; 4 were in dead parts of living trees.

Table 9. Descriptions of samples of information on behavior of selected bird species in managed and old-growth mixed-coniferous forests, northeastern Oregon.

Forest	Species	Sets of observations	Observations per set x ± SD	Total observations	Observations of foraging
Old-growth	Golden-crowned kinglet	40	9.8 ± 6.7	392	334
	Townsend's warbler	95	11.3 ± 6.6	1074	545
	Red-breasted nuthatch	29	8.9 ± 5.0	259	211
Managed	Red-breasted nuthatch	15	13.1 ± 6.3	197	175
	Ruby-crowned kinglet	92	14.7 ± 6.3	1356	700
	Chipping sparrow	26	16.9 ± 5.2	439	212

Figure 1. Discriminant functions of habitat variables that separated the vegetation around random-sites in old-growth forests from vegetation around random-sites in managed forests, or from vegetation around nest-sites of selected species of birds. Standardized discriminant function coefficients are listed to the right of the variables composing the linear functions. Arrows mark group means.

Figure 1.

MANAGED AND OLD GROWTH FORESTS

```
                                                      M
                                                      M
                                                      M
                                                      M
                                                      M
                                                      MMMM  M
                                                   M  MMM  M
                O                 O                 MMM  MMMMM MM
          O  O  O  O    O       O O              MMMMMMMMMMMMM MM  M
          OO  O  O OOOO O    O  OO  O   OMM   M  MMMMMMMMMMMMMM MM M  M
  O  O  O   OO   O OO OOOOOOOOOO  O  OOOOOO O  OOO M OO  OOMMMMMMMOMMMMMMMM  M  MM
```
```
-5        -4        -3        -2        -1         O         1         2         3
```

HIGH

DENSITY OF TREES 51+ CM DBH	-0.60	
DENSITY OF TREES 2.5 - 10 CM DBH	-0.50	LOW
TREE HEIGHT DIVERSITY	-0.39	
DENSITY OF SNAGS 31+ CM DBH, 3+ M TALL	-0.34	
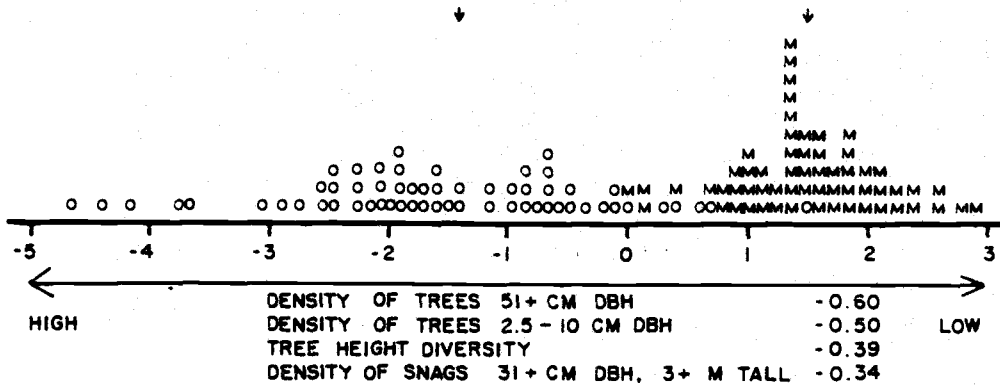
TOWNSEND'S WARBLER NESTS AND OLD-GROWTH FORESTS

```
                                                  O
                                                  O
                               O      OO   O OOO  O
                      TT        T  OT   OOO O OOO  OOO OOO O   OO
            TT  T     O  TTOT   TO   TTO OOTOOOOOOOOO OOOOOO OOO OO   OOOOOO    O
```
```
-5        -4        -3        -2        -1         O         1         2         3
```

HIGH

CANOPY VOLUME OF GRAND FIR	-0.94	
PROPORTION OF GROUND COVER	-0.77	LOW
CANOPY VOLUME OF DOUGLAS-FIR	-0.41	

GOLDEN-CROWNED KINGLET NESTS AND OLD-GROWTH FORESTS

```
                                                      O
                                  G         O  O   O  O
                  G               O  O  G   O  O  O  O  GOO
            G  G     G            O  O GGOOOOO O OO OO OOOOO   O
         O  GGO  GGGGO    OGG  OOOOOO OO OOOOOO  OOOOOOOOOOOO
```
```
-5        -4        -3        -2        -1         O         1         2         3
```

HIGH

CANOPY VOLUME OF GRAND FIR	-1.00	
CANOPY VOLUME OF DOUGLAS-FIR	-0.59	LOW

RED-BREASTED NUTHATCH NESTS AND OLD-GROWTH FORESTS

```
                                              R
                                              O
                               RR     OR R O  O
                               ORO  ROOOOOOO O
                  R            OOOOR ROOOOOOOOO   OO OOO O
         R     RRR    RROOORRORRR  ROOOOOO OOOOOOOOOOR  OO OOOOO
```
```
-5        -4        -3        -2        -1         O         1         2         3
```

HIGH

DENSITY OF SNAGS 31+ CM DBH, 3+ M TALL	-0.95	
DENSITY OF TREES 11-30 CM DBH	-0.61	LOW

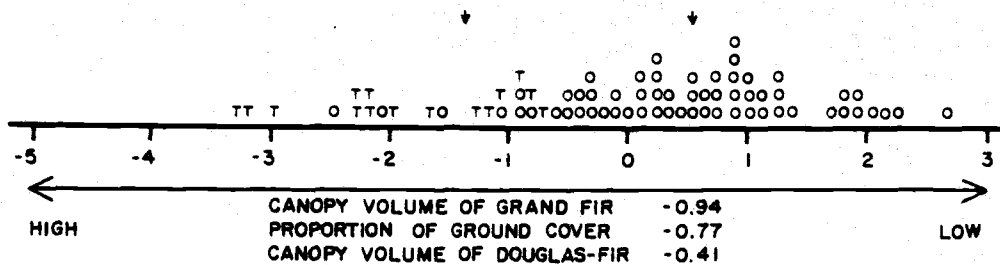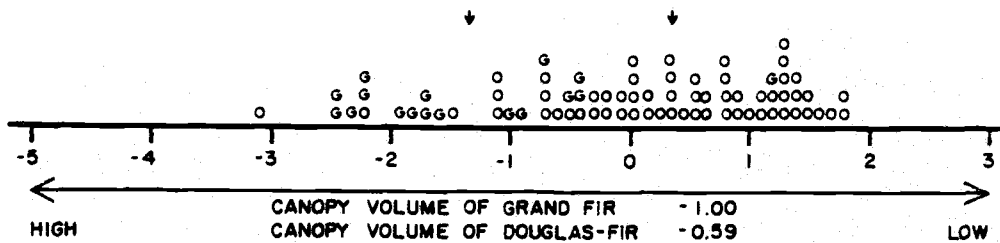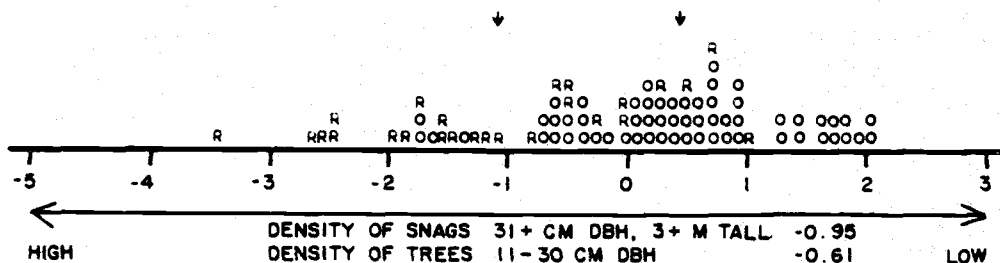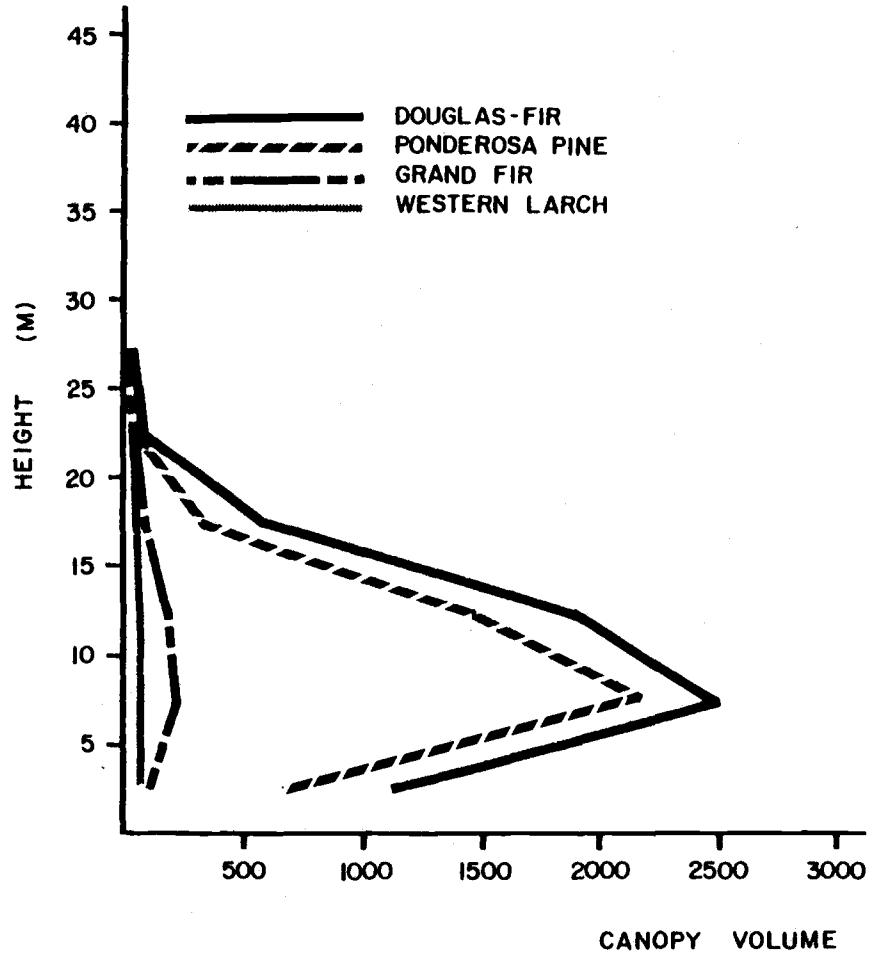Figure 2. Profiles of canopy volume of managed and old-growth mixed-coniferous forests, northeastern Oregon.

Figure 2.   MANAGED FORESTS   OLD-GROWTH FORESTS

Legend:
- DOUGLAS-FIR
- PONDEROSA PINE
- GRAND FIR
- WESTERN LARCH

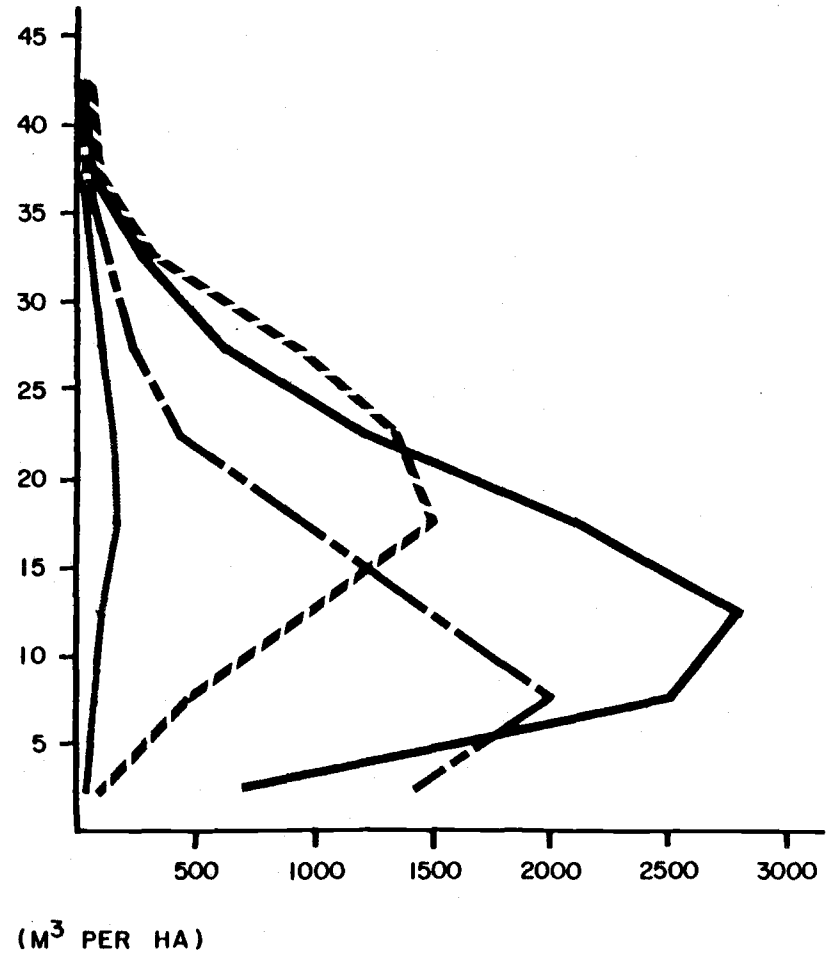HEIGHT (M)

CANOPY VOLUME (M³ PER HA)

Figure 3. Schematic of the structure and composition of vegetation in managed and old-growth mixed-coniferous forests, northeastern Oregon. Triangular-shaped canopies represent fir trees (primarily Douglas-fir in the overstory and grand fir in the understory), oval-shaped canopies represent ponderosa pine trees, and vertical lines without canopies represent snags. Numbers of trees and snags per line segment are approximately equivalent to the number of trees and snags per 0.02 ha.

Figure 3.

OLD-GROWTH FORESTS
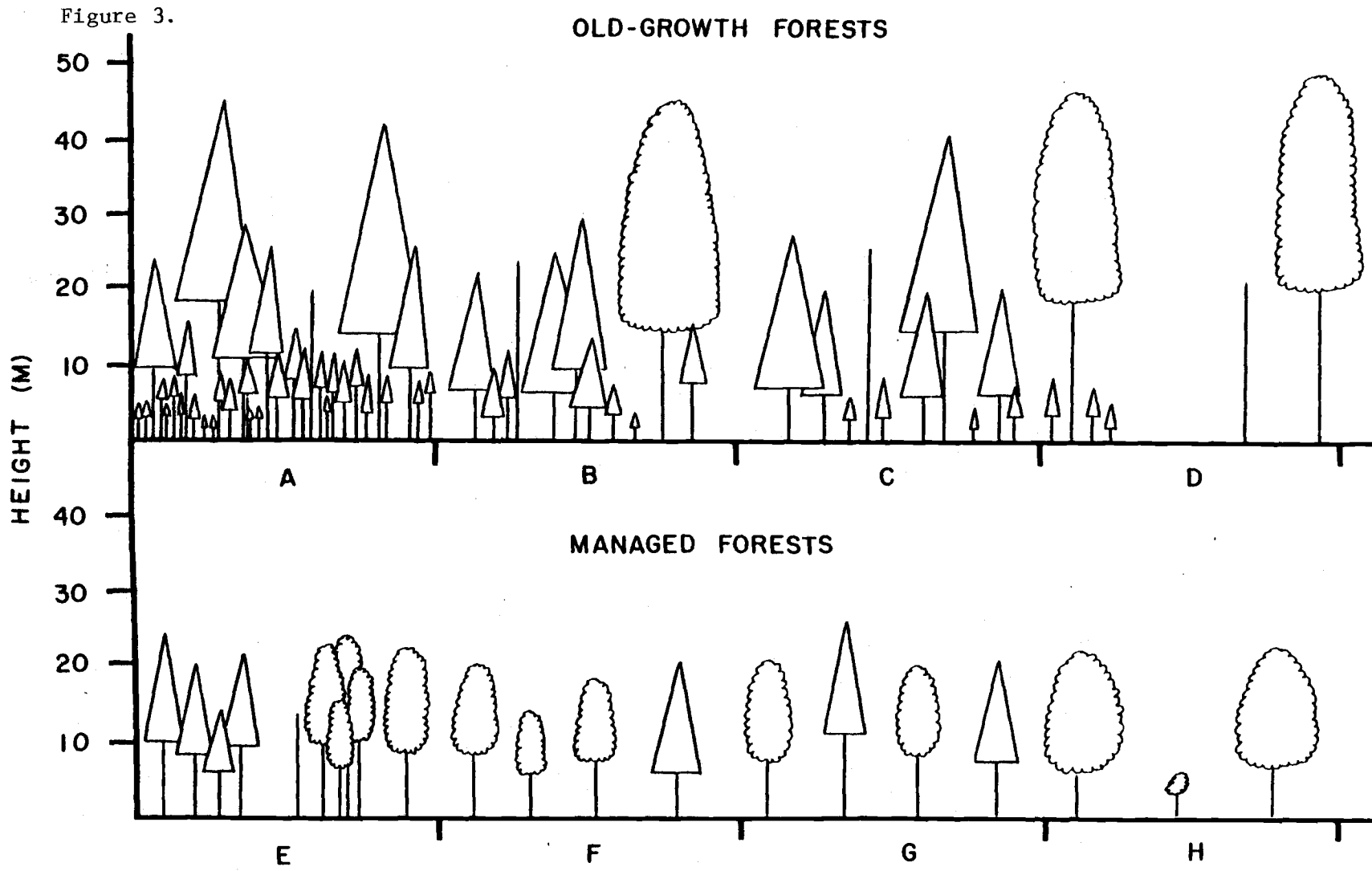
MANAGED FORESTS

HEIGHT (M)

Figure 4. Discriminant functions of habitat variables that separated the vegetation around random-sites in managed forests from vegetation around nest-sites of selected species of birds. Standardized discriminant function coefficients are listed to the right of the variables composing the linear functions. Arrows mark group means.

Figure 4.

CHIPPING SPARROW NESTS AND MANAGED FORESTS

RUBY-CROWNED KINGLET NESTS AND MANAGED FORESTS

DUSKY FLYCATCHER NESTS AND MANAGED FORESTS

RED-BREASTED NUTHATCH NESTS AND MANAGED FORESTS

Figure 5. Availability (based on canopy volume) and use of tree species by selected species of birds when foraging in managed (a) and old-growth (b) mixed-coniferous forests, northeastern Oregon. Chi-square values were generated from tests for goodness of fit (Sokal and Rohlf 1969). Confidence intervals were calculated following Neu et al. (1974).

Figure 5a.

Figure 5a.

PERCENT - MANAGED FORESTS

AVAILABLE

USED

CHIPPING
SPARROW
(N = 83)
(χ^2 = 31.56, 3 d.f.,
P < 0.01)

RUBY-CROWNED
KINGLET
(N = 700)
(χ^2 = 2330.11, 3 d.f.,
P < 0.01)

RED-BREASTED
NUTHATCH
(N = 156)
(χ^2 = 12.12, 3 d.f.,
P < 0.01)

DOUGLAS-FIR   PONDEROSA   GRAND FIR   WESTERN
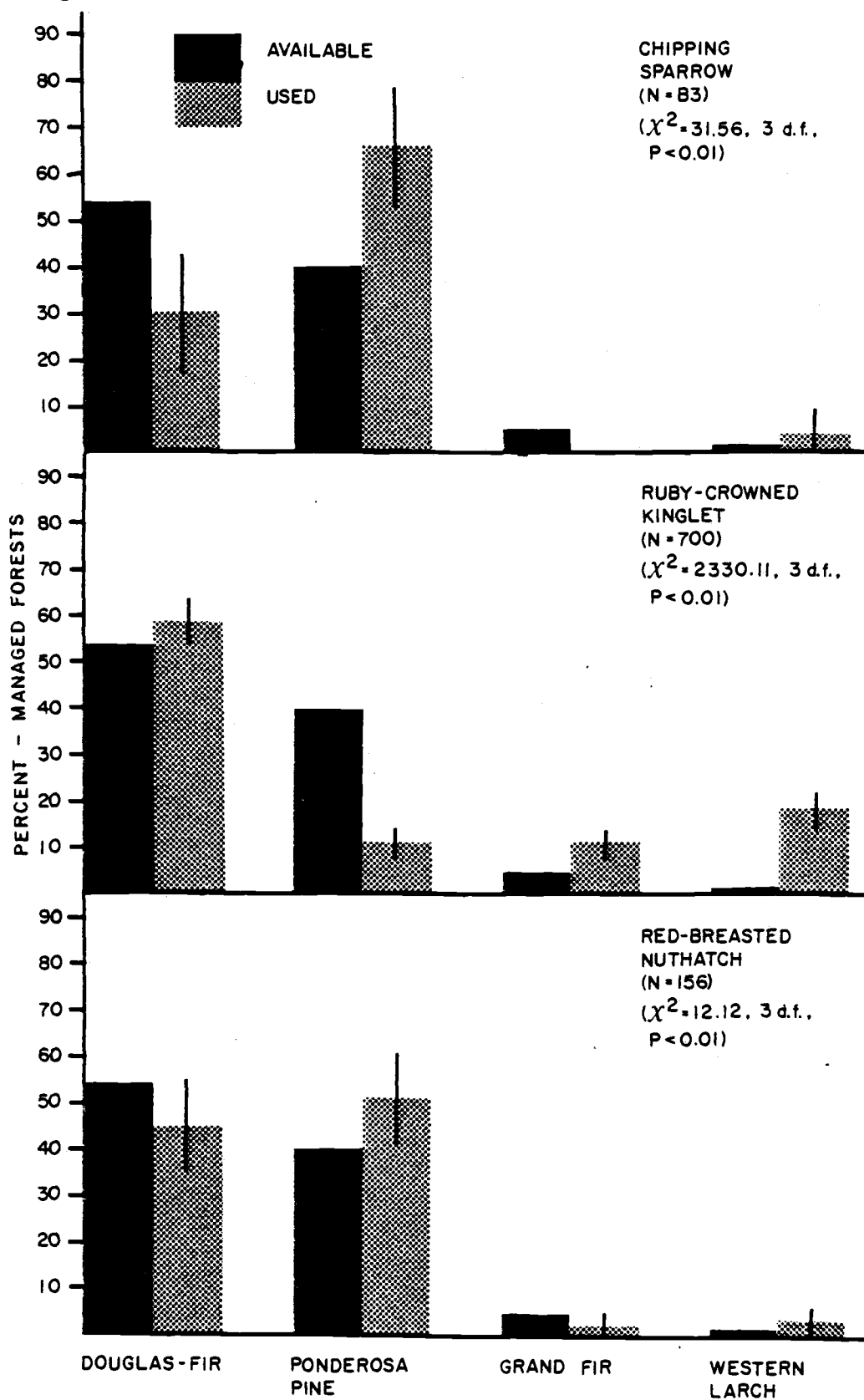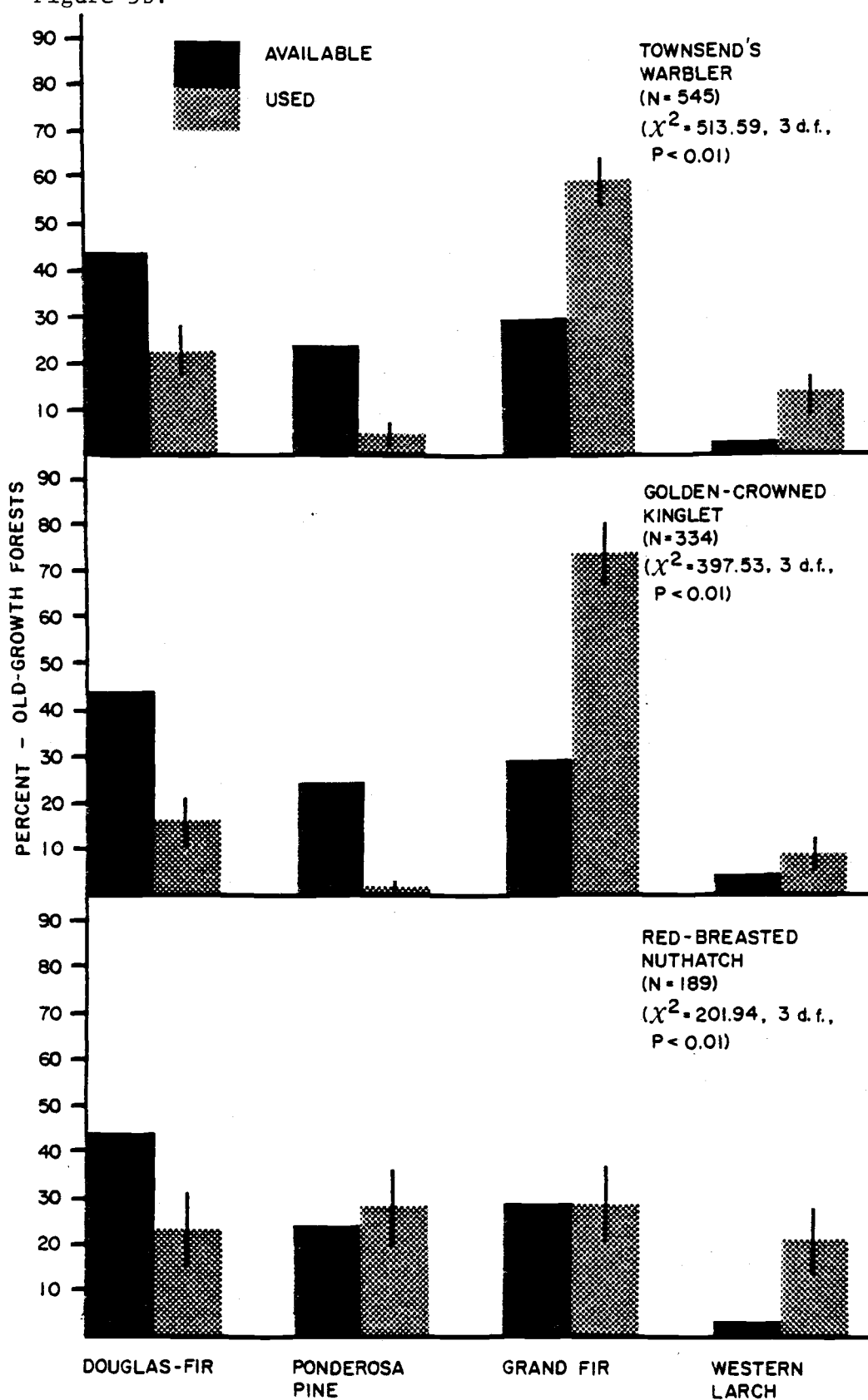   PINE   LARCH

Figure 5b.

Figure 6. Availability (based on canopy volume) and use of foliage by height class by selected species of birds when foraging in managed and old-growth mixed-coniferous forests, northeastern Oregon. Shaded areas represent the percent of canopy volume available by height class (all tree species combined); solid lines denote percent use by birds. Chi-square values were generated from tests for goodness of fit (Sokal and Rohlf 1969). Confidence intervals were calculated following Neu et al. (1974).

Figure 6.

TOWNSEND'S WARBLER (N = 545) (x^2 = 158.58, 6 d.f., P < 0.01)

GOLDEN-CROWNED KINGLET (N = 334) (x^2 = 45.47, 6 d.f., P < 0.01)

RED-BREASTED NUTHATCH (N = 189) (x^2 = 128.08, 6 d.f., P < 0.01)

CHIPPING SPARROW (N = 83) (x^2 = 84.42, 4 d.f., P < 0.01)

RUBY-CROWNED KINGLET (N = 700) (x^2 = 735.55, 4 d.f., P < 0.01)

RED-BREASTED NUTHATCH (N = 156) (x^2 = 15.45, 4 d.f., P < 0.01)

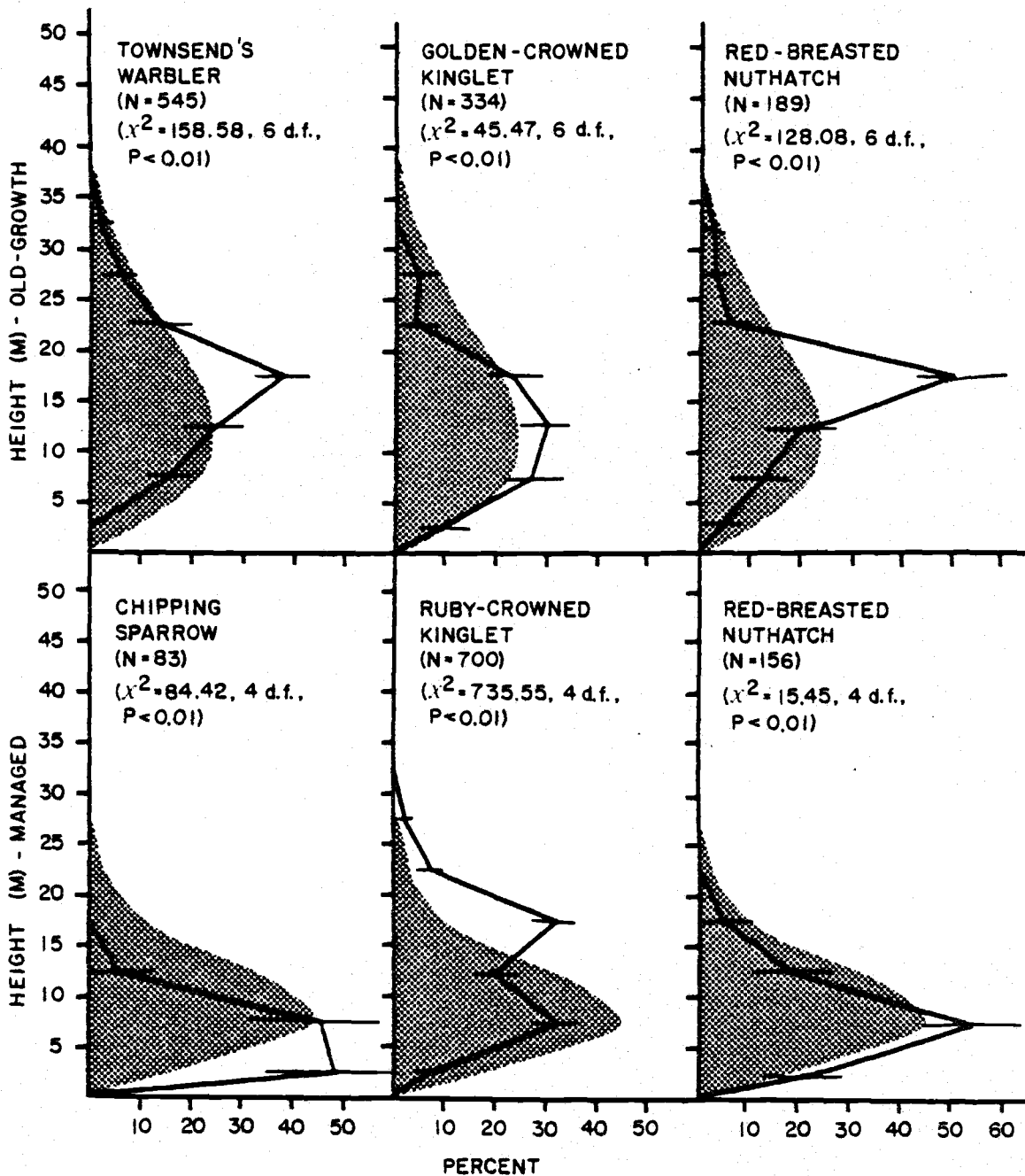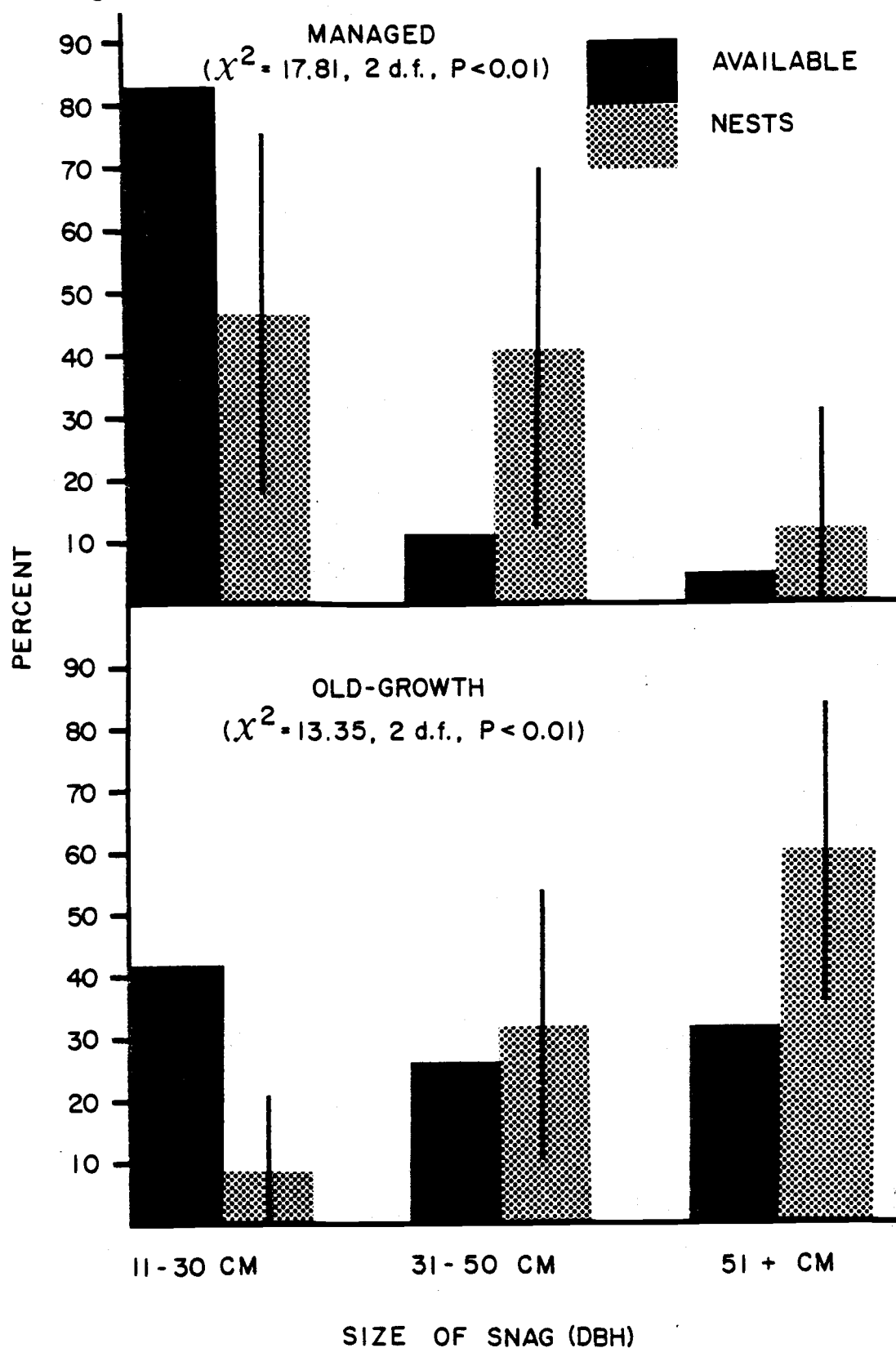HEIGHT (M) - OLD-GROWTH

HEIGHT (M) - MANAGED

PERCENT

Figure 7. Availability and use of snags as nest-sites by the red-breasted nuthatch in managed and old-growth mixed-coniferous forests, northeastern Oregon. Chi-square values were generated from tests for goodness of fit (Sokal and Rohlf 1969). Confidence intervals were calculated following Neu et al. (1974).

Figure 7.

MANAGED
$(\chi^2 = 17.81, 2 \text{ d.f.}, P < 0.01)$

AVAILABLE

NESTS

OLD-GROWTH
$(\chi^2 = 13.35, 2 \text{ d.f.}, P < 0.01)$

PERCENT

11 - 30 CM   31 - 50 CM   51 + CM

SIZE OF SNAG (DBH)

LITERATURE CITED

Apfelbaum, S., and A. Haney. 1981. Bird populations before and after wildfire in a Great Lakes pine forest. Condor 83:347-354.

Balda, R. P. 1969. Foliage use by birds of the oak-juniper woodland and ponderosa pine forest in southeastern Arizona. Condor 71:399-412.

_____. 1970. Effects of spring leaf-fall on composition and density of breeding birds in two southern Arizona woodlands. Condor 72:325-331.

_____. 1975. The relationship of secondary cavity nesters to snag densities in western coniferous forests. U.S. Dep. Agric. For. Serv. Southwest Reg. Wildl. Habitat Tech. Bull. 1. 37pp.

Beedy, E. C. 1981. Bird communities and forest structure in the Sierra Nevada of California. Condor 83:97-105.

Beuter, J. H., K. N. Johnson, and H. L. Scheurman. 1976. Timber for Oregon's tomorrow: an analysis of reasonably possible occurrences. Oreg. State Univ. Sch. For., For. Res. Lab. Res. Bull. 19. 111pp.

Bock, C. E., and J. F. Lynch. 1970. Breeding bird populations of burned and unburned conifer forests in the Sierra Nevada. Condor 72:182-189.

Bull, E. L. 1980. Resource partitioning among woodpeckers in northeastern Oregon, Ph. D. Thesis. Univ. Idaho, Moscow. 109pp.

_____, and E. C. Meslow. 1977. Habitat requirements of the pileated woodpecker in northeastern Oregon. J. For. 75:335-337.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. J. For. 39:388-394.

Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44:773-786.

Conner, R. N., R. G. Hooper, H. S. Crawford, and H. S. Mosby. 1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. J. Wildl. Manage. 39:144-150.

Crawford, H. S., R. G. Hooper, and R. W. Titterington. 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. J. Wildl. Manage. 45:680-692.

Dixon, W. J., and M. B. Brown. 1970. Biomedical computer programs P series. Univ. Calif. Press, Berkeley. 880pp.

Eckhardt, R. C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. Ecol. Monogr. 49:129-149.

Emlen, J. T. 1967. A rapid method for measuring arboreal canopy cover. Ecology 48:158-159.

_____. 1971. Population densities of birds derived from transect counts. Auk 88:323-342.

Forsman, E. D. 1976. A preliminary investigation of the spotted owl in Oregon. M. S. Thesis. Oregon State Univ., Corvallis. 127pp.

_____. 1980. Habitat utilization by spotted owls in the west-central Cascades of Oregon. Ph. D. dissertation. Oregon State Univ., Corvallis. 95pp.

_____, E. C. Meslow, and M. J. Strub. 1977. Spotted owl abundance in young versus old-growth forests, Oregon. Wildl. Soc. Bull. 5:43-47.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U. S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-8. 417pp.

_____, K. Cromack, Jr., W. Denison, A. Mckee, C. Maser, J. Sedell, F. Swanson, and G. Juday. 1981. Ecological characteristics of old-growth Douglas-fir forests. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-118. 48pp.

Franzreb, K. E. 1976. Comparison of variable strip transect and spot-map methods for censusing avian populations in a mixed-coniferous forest. Condor 78:260-262.

_____. 1978. Tree species used by birds in logged and unlogged mixed-coniferous forests. Wilson Bull. 90:221-238.

_____, and R. D. Ohmart. 1978. The effects of timber harvesting on breeding birds in a mixed-coniferous forest. Condor 80:431-441.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton Univ. Press, Princeton, N. J. 217pp.

Haapanen, A. 1965. Bird fauna of the Finnish forests in relation to forest succession I. Ann. Zool. Fenn. 2:153-196.

Hagar, D. C. 1960. The interrelationships of logging, birds, and timber regeneration in the Douglas-fir region of northwestern California. Ecology 41:116-125.

Hilden, O. 1965. Habitat selection in birds: a review. Ann. Zool. Fenn. 2:53-75.

Holmes, R. T., R. E. Bonney, Jr., and S. W. Pacala. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. Ecology 60:512-520.

_____, and S. K. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia 48:31-35.

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83:215-236.

James, R. D. 1976. Foraging behavior and habitat selection of three species of vireos in southern Ontario. Wilson Bull. 88:62-75.

Johnson, D. H. 1981. The use and misuse of statistics in wildlife habitat studies. Pages 11-19 in D. E. Capen, ed. The use of multivariate statistics in studies of wildlife habitat. U. S. Dep. Agric. For. Serv. Gen. Tech. Rep. RM-87.

Johnson, N. K. 1963. Biosystematics of sibling species of flycatchers in the Empidonax hammondii- oberholseri- wrightii complex. Univ. Calif. Publ. Zool. 66:79-238.

Karr, J. R. 1968. Habitat and avian diversity on strip-mined land in east-central Illinois. Condor 70:348-357.

_____, and R. R. Roth. 1971. Vegetation structure and avian diversity in several new world areas. Am. Nat. 105:423-435.

Kilgore, B. M. 1971. Response of breeding bird populations to habitat changes in a giant sequoia forest. Am. Midl. Nat. 85:135-152.

Klecka, W. R. 1975. Discriminant analysis. Pages 434-467 in N. H. Nie, C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent, eds. SPSS Statistical package for the social sciences. 2nd ed. McGraw Hill Book Co., New York, N. Y.

Lachenbruck, P. A. 1975. Discriminant analysis. Hafner Press, New York, N. Y. 128pp.

Landres, P. B., and J. A. MacMahon. 1980. Guilds and community organization: analysis of an oak woodland avifauna in Sonora, Mexico. Auk 97:351-365.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

Mannan, R. W. 1980. Assemblages of bird species in western coniferous old-growth forests. Pages 357-368 in R. M. DeGraff, tech. ed. Proc. management of western forests and grasslands for nongame birds. U. S. Dep. Agric. For. Serv. Gen. Tech. Rep. INT-86.

_____, E. C. Meslow, and H. M. Wight. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44:787-797.

Maurer, B. A., L. B. McArthur, and R. C. Whitmore. 1981. Effect of logging on guild structure of a forest bird community in West Virginia. Am. Birds. 35:11-13.

McClelland, B. R., and S. S. Frissell. 1975. Identifying forest snags useful for hole-nesting birds. J. For. 73:414-417.

_____, _____, W. C. Fischer, and C. H. Halvorson. 1979. Habitat management for hole-nesting birds in forests of western larch and Douglas-fir. J. For. 77:480-483.

Meslow, E. C., and H. M. Wight. 1975. Avifauna and succession in Douglas-fir forests of the Pacific Northwest. Pages 266-271 in D. R. Smith, tech. coord. Proc. symposium on management of forest and range habitats for nongame birds. U. S. Dep. Agric. For. Serv. Gen. Tech. Rep. WO-1.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, Inc. New York, N. Y. 547pp.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541-545.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. SPSS Statistical package for the social sciences. 2nd ed. McGraw-Hill Book Co., New York, N. Y. 675pp.

Nilsson, S. G. 1979. Effect of forest management on the breeding bird community in southern Sweden. Biol. Conserv. 16:135-143.

Noon, B. R. 1981. The distribution of an avian guild along a temperate elevational gradient: the importance and expression of competition. Ecol. Monogr. 51:105-124.

Pimentel, R. A., and D. F. Frey. 1978. Multivariate analysis of variance and discriminant analysis. Pages 247-274 in P. W. Colgan, ed. Quantitative ethology. John Wiley and Sons, New York, N. Y.

Ramsey, F. L., and J. M. Scott. 1978. Use of circular plot surveys in estimating the density of a population with poisson scattering. Tech. Rep. 60. Dep. Stat. Oreg. State Univ., Corvallis. 34pp.

Raphael, M. G. 1980. Utilization of standing dead trees by breeding birds at Sagehen Creek, California. Ph. D. Thesis. Univ. California, Berkeley. 195pp.

_____. 1981. Interspecific differences in nesting habitat of sympatric woodpeckers and nuthatches. Pages 142-151 in D. E. Capen, ed. The use of multivariate statistics in studies of wildlife habitat. U. S. Dep. Agric. For. Serv. Gen. Tech. Rep. RM-87.

Recher, H. F. 1969. Bird species diversity and habitat diversity in Australia and North America. Am. Nat. 103:75-80.

Reynolds, R. T., E. C. Meslow, and H. W. Wight. 1982. Nesting habitat of coexisting _Accipiter_ in Oregon. J. Wildl. Manage. 46:124-138.

_____, J. M. Scott, and R. A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. Condor 82:309-313.

Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher Ecol. Monogr. 37:317-350.

Roth, R. R. 1976. Spatial heterogeneity and bird species diversity. Ecology 57:773-782.

Scott, V. E. 1979. Bird response to snag removal in ponderosa pine. J. For. 77:26-28.

Shannon, C. E., and W. Weaver. 1949. The mathematical theory of communication. Univ. Illinois Press, Urbana. 117pp.

Snedecor, G. W., and W. G. Cochran. 1956. Statistical methods. The Iowa State Univ. Press, Ames. 534pp.

Sokal, R. R., and S. S. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco, Calif. 776pp.

Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc., New York, N. Y. 481pp.

Sturnam, W. A. 1968. Description and anlaysis of breeding habitats of the chickadees, _Parus atricapillus_ and _P. rufescens_. Ecology 49:418-431.

Szaro, R. C., and R. P. Balda. 1979. Bird community dynamics in a ponderosa pine forest. Stud. Avian. Biol. 3. 66pp.

Thomas, J. W. ed. 1979. Wildlife habitats in managed forests the Blue Mountains of Oregon and Washington. U. S. Dep. Agric. For. Serv. Agric. Handbk. 553. 512pp.

_____, R. G. Anderson, C. Maser, and E. L. Bull. 1979. Snags. Pages 60-77 in J. W. Thomas, ed. Wildlife habitats in managed forests the Blue Mountains of Oregon and Washington. U. S. Dep. Agric. For. Serv. Agric. Handbk. 553.

Titus, K., and J. A. Mosher. 1981. Nest-site habitat selected by woodland hawks in the central Appalachians. Auk 98:270-281.

Tomoff, C. S. 1974. Avian species diversity in desert scrub. Ecology 55:396-403.

Tramer, E. J. 1969. Bird species diversity: components of Shannon's formula. Ecology 50:927-929.

Webb, W. L., D. F. Behrend, and B. Saisorn. 1977. Effect of logging on songbird populations in a northern hardwood forest. Wildl. Monogr. 55. 35pp.

Wiens, J. A. 1974. Habitat heterogeneity and avian community structure in North American grasslands. Am. Midl. Nat. 91:195-213.

Willson, M. F. 1970. Foraging behavior of some winter birds of deciduous woods. Condor 72:169-174.

_____. 1974. Avian community organization and habitat structure. Ecology 55:1017-1029.