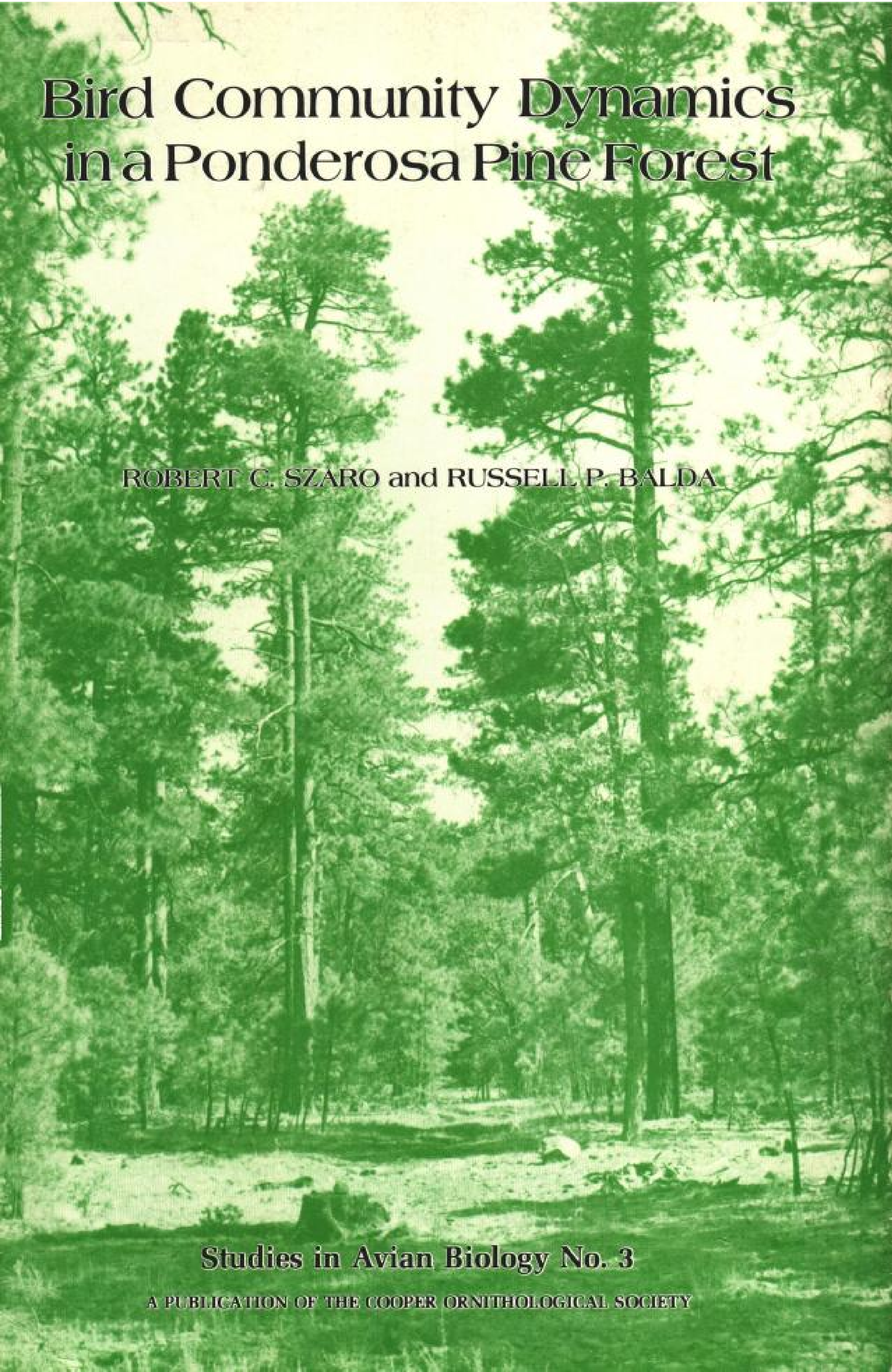

Bird Community Dynamics in a Ponderosa Pine Forest

ROBERT C. SZARO and RUSSELL P. BALDA

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A PUBLICATION OF THE COOPER ORNITHOLOGICAL SOCIETY

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Cover Photograph: Natural ponderosa pine forest in northern Arizona, by Robert C. Szaro.

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CONTENTS

TABLES

FIGURES

Mountain Chickadee (*Parus gambeli*), by Virgil Scott

Studies in Avian Biology No. 3:1–66, 1979.

INTRODUCTION

Bird densities in a particular habitat are believed to be regulated by a vast constellation of factors interacting with one another. This becomes apparent when one examines the breeding bird community of a particular habitat and discovers that it is a dynamic system. Any alteration of that habitat may result in changing the suitability of the habitat for a given species' niche requirements. Subsequently, certain species may be drastically affected by such alterations while others will remain relatively stable. How this system is affected by changes in habitat physiognomy resulting from timber management is the focal point of this study.

The relationship between breeding bird populations and vegetation has interested avian ecologists for quite some time (for example, Johnston and Odum 1956, Bond 1957, Anderson 1970). Much work has been done on correlating the foliage height diversity of the habitat with bird species diversity (MacArthur 1965, Pianka 1966, Orians 1969, Karr 1971, Karr and Roth 1971, Recher 1971). As the structural complexity of a community increases, the number of bird species increases (MacArthur and MacArthur 1961, MacArthur et al. 1966, Karr 1968, Recher 1969, and others). MacArthur (1964) working in succulent desert scrub and montane communities in southeastern Arizona, speculated that birds here were using more than foliage layers for habitat selection in these structurally more complex habitats. A significant relationship was found between physiognomic cover diversity and breeding species diversity (Tomoff 1974). Most of these works, however, had at least four dominant species of plants present, thus offering the birds a wide variety of microhabitats. In contrast, the ponderosa pine (*Pinus ponderosa*) forest, the habitat studied here, is a monoculture with only one other tree species, gambel oak (*Quercus gambelii*) appearing with regularity.

To date, no information has been gathered as to how foliage volume and its pattern of distribution is related to breeding bird densities in a pure coniferous forest. Studies by Balda (1967, 1969) and Pearson (1971) recorded the vertical distributions of the various bird species within mixed forest type communities. Breeding bird densities may be related to the distribution and total volume of tree foliage because of the foraging and nesting habits of the different bird species (Balda 1969, 1970). Moreover, no information has been gathered on how differences in foliage volume affect bird behavior. The population density of Blackburnian Warblers (*Dendroica fusca*) and Myrtle Warblers (*Dendroica coronata*) appears to be closely correlated with foliage volume (MacArthur 1958). Foliage volume may also be an important factor in limiting the densities of Parula Warblers (*Parula americana*) and nuthatches (Morse 1967, Balda 1969). Data by Balda (1969) strongly suggest that the removal of tall ponderosa pines (12 to 21 m) may have a negative effect on the density of Grace's Warblers (*Dendroica graciae*), while removal of the understory may reduce the populations of the Gray-headed Junco (*Junco caniceps*) and the Chipping Sparrow (*Spizella passerina*).

Since the foliage configuration is probably related to the resource base, that is the food supply, it may be assumed that the bird community may be affected by changes in foliage distribution. Bock and Lynch (1970) and Kilgore (1971) showed that habitat alteration increased bird densities and diversities. The total effect on the bird community will be influenced by the magnitude of the logging operation and the method of tree removal. Therefore, it is necessary to know not only the distribution of the available foliage but how the birds use the trees.

Biomass and energy relations of avian communities have proven useful in understanding the evolution of community structure (Karr 1968, Wiens 1969, Karr and Roth 1971, Wiens and Innis 1974, Wiens and Nussbaum 1975). Lasiewski and Dawson (1967) and Zar (1968) calculated the standard metabolic rate of birds from mean body weight. Of greater ecological interest, however, is the energy requirement of normal activities under free-living conditions. Existence energy requirements for birds can be calculated from mean body weight and ambient temperature (Kendeigh 1970, Wiener and Glowacinski 1975). Thus, the total energy flux through a bird community can be examined and related to changes in foliage volume and bird densities.

The present study was undertaken to measure and evaluate 1) the effects on the diversity, density, and behavior patterns of the breeding birds of the ponderosa pine forest of such results of habitat manipulation as differing foliage volumes, foliage patterns, and densities of trees, and 2) the standing crop biomass, consuming biomass, and existence energy requirements of the breeding birds on each plot.

METHODS AND MATERIALS

Five study plots were chosen in relatively homogeneous stands of ponderosa pine, each with a 100-m minimum buffer around the periphery. An attempt was made to choose study plots that contained about the same proportions of different size classes of trees and density of gambel oak. All study areas were set up as 15-ha plots except for the clear cut area which encompassed 45 ha.

The study plots were set up with the aid of a compass, steel tape, alidade, plane table, and tripod. A grid pattern was set up by implanting stakes at 60-m intervals and marking trees. Weather data were collected and analyzed by the U.S. Forest Service.

VEGETATION

Tree measurements were made on all plots except the clear cut plot. The plotless point-quarter method of Cottam and Curtis (1956) was utilized to sample trees with a DBH of 7.5 cm or more. A total of 104 points (416 trees) was sampled on each plot and the data were analyzed quantitatively using the standard formulas of Cottam and Curtis (1956) in order to obtain the following: absolute density, relative density, relative dominance, relative frequency, importance value, mean area, and mean distance between trees for each tree species. On each study plot 104 circular plots were measured in order to count seedlings, saplings, and shrubs. Further, the following data were recorded for the four trees sampled at each point: total tree height, height from the ground to the lowest live limb, outer crown diameter, and inner crown diameter at the lowest live limb. Trees were classified as being conical, cylindrical, or hemispherical. These data were then analyzed using the standard volume formulas for the three shapes (Selby 1973). Foliage data are expressed in terms of foliage per tree species per hectare and volume of foliage per 2-m height class per hectare.

BIRDS

Breeding bird counts were made using the spot-map method described by Kendeigh (1944). Territory size was measured on the composite map as the minimum area encompassed by the observations on a particular bird pair. Differences in mean territory size were tested by the t- and F-statistics, depending upon the number of means compared. Comparisons of yearly variations in population densities were made using the coefficient of variation (Sokal and Rohlf 1973).

After each early morning census the remainder of the day was spent observing foliage use behavior using a modification of Sturman's (1968) technique. At each sighting of a bird the following information was recorded: date, time, bird species, time spent in a particular activity, height in tree, position from trunk, substrate being utilized, and tree species. The G-statistic was used to test the association between bird behavior and treatment (Sokal and Rohlf 1973).

Species diversity (H') (Shannon and Weaver 1948) was calculated by

$$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

where p_i is the proportion of the ith species in the population composed of s species.

Evenness (E) was calculated by

$$E = H'/\ln s$$

In order to assess the behavioral similarity between pairs of species on any given study plot we may construct an m-dimensional Euclidean space in which the relative position of the species can be measured. The relationship among pairs of species within an ecological space may be measured by their Euclidean distances, D (Power 1971). Distance between the jth and kth species is given by

$$D_{jk} = \left[\sum_{i=1}^{m} (p_{ij} - p_{ik})^2\right]^{1/2}$$

where p_{ij} is the proportion of the jth species and p_{ik} is the proportion of the kth species in m number of behavioral categories. Euclidean distances between pairs of species were calculated for the following behavioral parameters: activity pattern, foraging method, tree species selection, horizontal tree position, perch selection, stance, and foliage use.

Then to examine the overall relationship among pairs of species we can measure the composite Euclidean distance (CED). The CED between the jth and kth species is given by

$$CED = \left[\sum_{i=1}^{n} (D_{ijk})^2\right]^{1/2}$$

where n is the number of behavioral parameters.

Dendrograms showing hierarchial arrangements of species were obtained by subjecting the matrices of D and CED to cluster analysis. The unweighted pair-group method on arithmetic averages was used (Sokal and Sneath 1963, Rohlf 1970, Power 1971, Cody 1974).

The foliage use index (FUI) was the calculation of the Euclidean distance between a particular bird species and the composite foliage configuration for a particular study plot. Distance between the jth species and the foliage profile is given by

$$FUI = \left[\sum_{i=1}^{n} (p_{ij} - p_{ik})^2\right]^{1/2} \Big/ n$$

where p_{ij} is the proportion of bird observations and p_{ik} is the proportion of the total foliage volume in n number of foliage strata. The FUI has a range of 0 to $\sqrt{2}/n$ where 0 indicates a bird species is using the foliage profile in exact relation to its availability. In contrast a FUI of $\sqrt{2}/n$ indicates the selection of a single stratum in which the proportion of the foliage volume is close to zero. Thus as the FUI becomes smaller the fit with the foliage profile becomes better. That is, an individual bird species or the entire bird community uses the foliage profile in closer relation to its availability.

The correlation coefficient (r) was calculated between foliage volume and bird density or a given behavioral parameter (Sokal and Rohlf 1973).

Consuming biomass (CB) was calculated using fresh dead weights whenever possible (Karr 1968). CB is given by

$$CB = W^{0.633}$$

where W is the mean weight of a given species.

Existence energy (EMR) was calculated as suggested by Kendeigh (1970) and later modified by Weiner and Glowacinski (1975). Thus, the relationship between ambient temperature and body weight in a passerine bird is given by

$$EMR = 1.572W^{0.621} + 0.06514W^{0.3625}(30 - t)$$

where t is ambient temperature in degrees celsius. The above expression was also used for the non-passerines on the study plots as they are undoubtedly closer to the passerines than to the Galliformes, Anseriformes, and Falconiformes on which the non-passerine equation is based.

DESCRIPTION OF STUDY AREAS

The five study areas are in the Coconino National Forest, Coconino County, Arizona (Fig. 1). All the areas are located within a 21-km radius on the Beaver Creek Watershed. The areas included a clear cut, a uniformly thinned, a strip cut, a silviculturally cut, and a control plot. All study sites were cut before the

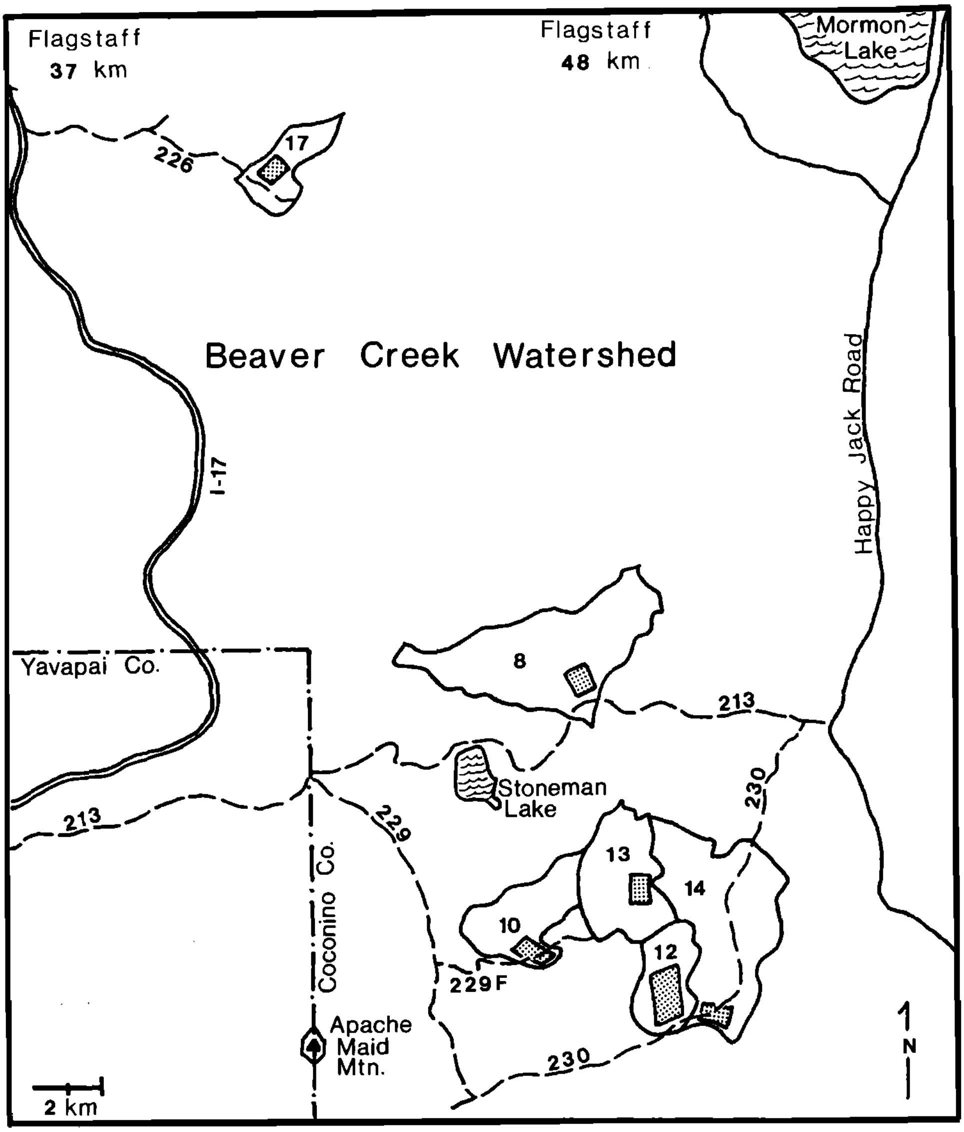

FIGURE 1. Map of Beaver Creek Watershed, Coconino National Forest, Arizona. Stippled areas represent the study areas. Areas enclosed by solid lines are numbered watersheds. Dashed lines represent numbered Forest Service roads.

study began except for the silviculturally cut area which was cut during the spring of 1974.

The ponderosa pine vegetation type, which was found on all study areas before treatment, is found primarily in areas of brolliar, siesta, and sponsellar soils (Williams and Anderson 1967).

Control Plot

The control is located on watershed 13 approximately 66 km southeast of Flagstaff on FS-230 (Forest Service road 230) at an elevation of 2195 m and at

TABLE 1
COMPOSITION OF TREES ON ALL STUDY PLOTS

Species	Relative density	Relative dominance	Relative frequency	Importance value	Absolute density[a]
		Control plot			
P. ponderosa	90.1	85.7	77.0	252.8	582.5
Q. gambelii	8.4	8.3	19.3	36.0	54.3
J. deppeana	1.5	6.0	3.7	11.2	9.3
		Silviculturally cut plot			
P. ponderosa	92.3	93.6	81.3	267.2	271.4
Q. gambelii	7.7	6.4	18.7	32.8	22.6
		Silviculturally cut plot			
P. ponderosa	91.5	92.5	79.4	263.4	216.1
Q. gambelii	8.5	7.5	20.6	36.6	20.1
		Strip cut plot			
P. ponderosa	79.1	82.0	67.1	228.2	145.4
Q. gambelii	20.4	15.7	31.5	67.6	34.4
J. deppeana	0.5	2.3	1.4	4.2	0.8
		Severely thinned plot			
P. ponderosa	86.8	91.9	74.3	253.0	59.7
Q. gambelii	13.2	8.1	25.7	47.0	9.0

[a] Trees/ha.

34°29′00″N, 110°45′21″W (Fig. 1). The study area is on a southwest-facing slope of about 17° in the west-central portion of the 149-ha watershed.

Watershed 13 was left untreated as the control area. Ponderosa pine was the major dominant tree species with an importance value of 252.8 (Table 1, Fig. 2). There were approximately 646 trees/ha with a canopy volume of 19,370 m^3/ha and a total basal area of 26.7 m^2/ha. The mean tree height was 15.5 m and the lower live limb height was 8.7 m. The bulge area, specifically that region of the foliage profile that encompasses at least 70% of the foliage, was between 4 and 18 m and included 82.1% of the foliage volume on the study area.

SILVICULTURALLY CUT PLOT

The silviculturally cut plot is located on watershed 8, approximately 64 km southeast of Flagstaff on FS-213 near Stoneman Lake at an elevation of 2256 m and at 34°29′37″N, 111°47′52″W (Fig. 1). The study area is on a west-facing slope of about 13° in the southwest corner of the 729-ha watershed.

Stands made up of trees less than 25.4 cm DBH were thinned to a growing stock level of 13.8 m^2 of basal area per ha (F. R. Larson, unpublished data). Stands consisting of trees 30.5 cm in DBH and larger were thinned to an actual 16.1 m^2 of basal area per ha. Trees were cut so as to upgrade the stand rather than to obtain uniform spacing. In most cases gambel oak were left intact.

Prior to treatment, ponderosa pine was the major dominant tree species with an importance value of 267.2 (Table 1). There were approximately 294 trees/ha with a canopy volume of 23,976 m^3/ha and a total basal area of 28.9 m^2/ha. The mean height of the trees was 14.1 m and the mean lower live limb height was 7.4

FIGURE 2. Control plot. Note the large trees and dense thickets.

m. The bulge area, between 4 and 20 m, encompassed 76.6% of the foliage volume on the study area.

The treatment in April 1974 reduced ponderosa pine by 55 trees/ha of 20% whereas gambel oak was reduced by 2 trees/ha or 10% (Table 1, Fig. 3). There were approximately 236 trees/ha with a canopy volume of 17,039 m^3/ha. This

FIGURE 3. Silviculturally cut plot. Note the openings created by treatment.

amounted to a reduction of 28.9% in the available foliage. The total basal area for all tree species was 23.3 m^2/ha. The mean tree height was 13.2 m, with a mean lower live limb height of 7.1 m. The bulge area, between 4 and 20 m, included 76.9% of the foliage volume on the study area.

Strip Cut Plot

The strip cut plot is located on watershed 14, approximately 68 km southeast of Flagstaff on FS-230 at an elevation of 2149 m and at 34°27′44″N, 111°44′54″W (Fig. 1). The study area is on a south-facing slope of about 9° in the southeast corner of the 221-ha watershed.

The objective of the treatment was to increase water yield while at the same time providing good timber production and pleasing aesthetics (H. E. Brown, unpublished data). Clear cut strips were designed primarily to increase streamflow. The alternative "leave" strips were thinned in a manner to improve production.

The pattern was one of alternate cut and leave strips. The cut and leave strips averaged 18 and 36 m in width respectively. Spacers of uncut trees were left in the cut strips at intervals to break up the visual continuity of the strips. These were of irregular shapes, 15–21 m long, at intervals of about 122 m. Most of the gambel oak were left in the cut strips and where there was enough oak to break up the continuity of the strips it was not necessary to use spacers. Width of the clear cut areas within any strip varied as much as 50% (i.e., 36 ± 18 m) in order to provide an aesthetically pleasing, irregular pattern of elongated openings.

The treatment was completed in the spring of 1970. Ponderosa pine was the major dominant tree species with an importance value of 228.2 (Table 1, Fig. 4). There were approximately 181 trees/ha with a canopy volume of 6526 m^3/ha and a total basal area of 12.4 m^2/ha. The mean tree height was 11.5 m and the lower live limb height was 6.0 m. The bulge area, between 2 and 14 m, encompassed 75.8% of the foliage volume on the study area.

Severely Thinned Plot

The severely thinned plot is located on watershed 17, approximately 43 km south of Flagstaff off I-17 on FS-226 at an elevation of 2091 m and at 34°34′25″N, 111°53′56″W (Fig. 1). The study area is on a southwest-facing slope of about 8° in the southwest corner of the 49-ha watershed.

The treatment was intended to provide a reasonable opportunity for increased water yield while leaving a light stocked timber stand that could be subjected to even-aged management (H. E. Brown, unpublished data). Slash was piled in strategically arranged windrows. Windrows were piled as high and narrow as possible in order to maximize snow trapping and retention. Windrows were arranged with 10-m breaks at intervals of 60 m or less in order to reduce possible fire spreading.

The treatment was completed in the spring of 1969. Ponderosa pine was the major dominant tree species with an importance value of 253.0 (Table 1, Fig. 5). There were approximately 69 trees/ha with a canopy volume of 3990 m^3/ha and a total basal area of 7.9 m^2/ha. The mean tree height was 11.0 m and the mean lower live limb height was 6.2 m. The bulge area, between 4 and 16 m, encompassed 70.9% of the foliage on the study area.

FIGURE 4. Strip cut plot. Note the open strip area.

Clear Cut Plot

The clear cut plot is located on watershed 12, approximately 69 km southeast of Flagstaff on FS-230 at an elevation of 2146 m and at 34°28′35″N, 111°44′25″W (Fig. 1). The study area is on a southwest-facing slope of about 10° in the southeast corner of the 80-ha watershed.

The treatment was designed to test the effects of clear cutting all the woody

FIGURE 5. Severely thinned plot. Note the slash windrows and uniform thinning of this area.

FIGURE 6. Clear cut plot. Note the growth of gambel oak sprouts which obscure the windrows.

vegetation on the watershed and windrowing the resultant slash (H. E. Brown, unpublished data). All wood products that could be sold were removed from the watershed. The remaining slash and debris were machine windrowed in such a way as to trap and retain snow, reduce evapotranspiration losses, and increase the drainage efficiency of the watershed. In areas of heavy slash the windrows were at least 1.5 m high and were spaced about 30 m apart. In areas of lighter slash the windrows were spaced further apart in order to achieve the minimum height. Windrows were placed in either an east-west or northeast-southwest direction.

The treatment was completed during the spring of 1967. Since that time there has been a considerable amount of shrubby growth by gambel oak next to the slash windrows (Fig. 6).

Weather

Total winter and early spring precipitation (Oct.–Apr.) was 106.5 cm in 1972–1973, 28.8 cm in 1973–1974, and 48.6 cm in 1974–1975 on the silviculturally cut area. The winter and early spring of 1973–1974 had 73% less accumulated precipitation than the same period of 1972–1973. The precipitation during the winter and early spring of 1974–1975 amounted to 69% more than 1973–1974 but was still 54% less than in 1972–1973. Most of the precipitation during each of the three winters came in the form of snow.

The mean maximum temperature during the period of November to April rose from 5°C in 1972–1973 to 8.5°C in 1973–1974 and decreased to 6.3°C in 1974–1975. The mean minimum temperature remained approximately the same at −9.3° to −9.4°C.

During the breeding season (May-July) the mean daily temperature rose from 14.1°C in 1973 to 15.2°C in 1974 and then dropped to 12.6°C in 1975. Precipitation

TABLE 2

BREEDING DENSITIES (prs/40 ha) OF SPECIES AND FORAGING AND NESTING GUILDS IN 1973

	Study plots[a]				
	C. cut	S. Thn.	Strip	Cntrl.	Silv. (PT)
Species (guilds)					
Mountain Chickadee (PG,CD)	—	1.5	—	—	—
Pygmy Nuthatch (PG,CD)	—	—	—	13.5	7.5
House Wren (PG,CD)	—	—	2.3	—	2.3
Solitary Vireo (PG,FN)	—	3.8	6.0	1.5	—
Yellow-rumped Warbler (PG,FN)	—	—	3.0	—	—
Grace's Warbler (PG,FN)	—	3.8	7.5	7.5	11.2
Red-faced Warbler (PG,GN)	—	—	—	2.3	3.0
Western Tanager (PG,FN)	—	1.5	3.0	—	3.0
Rock Wren (GF,GN)	5.0	5.2	3.8	—	—
Robin (GF,FN)	—	6.8	5.2	—	—
Hermit Thrush (GF,GN)	—	—	—	0.8	—
Gray-headed junco (GF,GN)	2.0	9.8	6.0	9.0	12.7
Rufous-sided Towhee (GF,FN)	5.5	—	—	—	—
Chipping Sparrow (GF,FN)	—	6.0	4.5	—	3.0
Common Flicker (HT,CD)	—	3.0	2.3	3.0	3.0
Hairy Woodpecker (HT,CD)	—	2.3	2.3	3.0	3.0
Steller's Jay (HT,FN)	—	—	3.0	—	3.0
White-br. Nuthatch (HT,CD)	—	5.2	4.5	3.0	3.0
Black-headed Grosbeak (HT,FN)	—	—	—	—	1.5
Broad-td. Hummingbird (AF,FN)	—	—	3.0	—	—
Western Flycatcher (AF,CD)	—	—	—	6.0	3.0
Western Wood Pewee (AF,FN)	—	3.0	8.2	—	2.3
Violet-green Swallow (AF,CD)	—	—	—	9.0	6.0
Western Bluebird (AF,CD)	—	6.0	6.7	4.5	5.2
Foraging guilds					
Pickers and gleaners (PG)	—	10.5	20.8	24.8	27.0
Ground feeders (GF)	12.5	27.8	19.5	9.8	15.8
Hammerers and tearers (HT)	—	10.5	12.0	9.0	13.5
Aerial feeders (AF)	—	9.0	18.0	19.5	16.5
Nesting guilds					
Cavity and depression (CD)	—	18.0	18.0	42.0	33.0
Foliage nesters (FN)	5.5	24.8	43.5	9.0	24.0
Ground nesters (GN)	7.0	15.0	9.8	12.0	15.8
Totals	12.5	57.8	71.3	63.0	72.8

[a] C. cut = clear cut plot; S. Thn. = severely thinned plot; Strip = strip cut plot; Cntrl. = control plot; Silv. (PT) = silviculturally cut plot (pre-treatment).

during the months of May and June amounted to 3.1 cm in 1973, 0.0 cm in 1974, and 0.8 cm in 1975. Precipitation during the breeding season (May–July) was 7.3 cm in 1973 and 1974, 8.2 cm in 1975.

RESULTS

BREEDING SEASON CENSUSES

Densities.—There was a tremendous amount of variability in breeding bird densities between study plots (Tables 2–4). The densities in pairs per 40 ha varied from 12.5 to 72.8 in 1973 with the lowest densities on the clear cut plot and the

TABLE 3
BREEDING DENSITIES (prs/40 ha) OF SPECIES AND FORAGING AND NESTING GUILDS IN 1974

	Study plots[a]				
	C. cut	S. Thn.	Strip	Silv.	Cntrl.
Species (guilds)					
Mountain Chickadee (PG,CD)	—	—	9.0	6.0	7.5
Pygmy Nuthatch (PG,CD)	—	2.3	3.0	15.0	15.0
Solitary Vireo (PG,FN)	—	6.0	12.0	6.0	3.0
Yellow-rumped Warbler (PG,FN)	—	—	3.0	15.0	3.0
Grace's Warbler (PG,FN)	—	6.0	18.7	18.7	12.0
Red-faced Warbler (PG,GN)	—	—	—	—	4.5
Western Tanager (PG,FN)	—	—	3.0	6.7	—
Hepatic Tanager (PG,FN)	—	—	3.0	—	—
Mourning Dove (GF,FN)	—	6.0	—	—	3.0
Rock Wren (GF,GN)	5.5	3.0	8.3	—	—
Robin (GF,FN)	—	4.5	7.5	3.0	—
Hermit Thrush (GF,GN)	—	—	—	0.8	1.5
Gray-headed Junco (GF,GN)	2.0	6.7	10.5	22.5	18.0
Rufous-sided Towhee (GF,FN)	6.5	—	—	—	—
Chipping Sparrow (GF,FN)	—	6.0	12.0	7.5	1.5
Common Flicker (HT,CD)	—	3.0	3.8	3.0	3.0
Hairy Woodpecker (HT,CD)	—	3.0	6.0	3.0	3.0
Steller's Jay (HT,FN)	—	7.5	7.5	6.0	9.0
White-br. Nuthatch (HT,CD)	—	9.0	9.0	7.5	10.5
Black-headed Grosbeak (HT,FN)	—	—	1.5	3.0	4.5
Common Nighthawk (AF,GN)	—	3.0	3.0	—	3.0
Broad-td. Hummingbird (AF,FN)	—	10.5	15.0	5.2	9.0
Say's Phoebe (AF,FN)	—	—	3.0	—	—
Western Flycatcher (AF,CD)	—	—	—	5.3	6.8
Western Wood Pewee (AF,FN)	—	3.0	9.0	3.0	—
Violet-green Swallow (AF,CD)	—	—	3.0	9.0	9.0
Mountain Bluebird (AF,CD)	1.0	—	—	—	—
Western Bluebird (AF,CD)	—	8.3	12.0	8.3	6.0
Foraging guilds					
Pickers and gleaners (PG)	—	14.3	51.7	67.5	45.0
Ground feeders (GF)	14.0	26.2	38.3	33.8	24.0
Hammerers and tearers (HT)	—	22.5	27.8	22.5	30.0
Aerial feeders (AF)	1.0	24.8	45.0	30.7	33.8
Nesting Guilds					
Cavity and depression (CD)	1.0	22.5	45.8	57.0	60.8
Foliage nesters (FN)	6.5	49.5	95.2	74.2	45.0
Ground nesters (GN)	7.5	12.8	21.8	23.3	27.0
Totals	15.0	87.8	162.8	154.5	132.8

[a] See footnote Table 2.

highest densities on the silviculturally cut plot. In 1974 the lowest and highest densities were on the clear cut and strip cut plots with bird densities on the forested watersheds nearly double that of their 1973 values. In 1975 densities decreased on all forested watersheds while on the clear cut plot bird densities remained stable. The decreases varied from 10% on the silviculturally cut plot to 34% on the control plot.

The density data were subdivided into foraging and nesting guilds after Root

TABLE 4
BREEDING DENSITIES (prs/40 ha) OF SPECIES AND FORAGING AND NESTING GUILDS IN 1975

	Study plots[a]				
	C. cut	S. Thn.	Strip	Silv.	Cntrl.
Species (guilds)					
Mountain Chickadee (PG,CD)	—	1.5	—	4.5	3.0
Pygmy Nuthatch (PG,CD)	—	1.5	9.0	18.0	13.5
House Wren (PG,CD)	—	—	3.0	—	—
Solitary Vireo (PG,FN)	—	6.0	6.0	6.0	3.0
Yellow-rumped Warbler (PG,FN)	—	3.0	3.0	9.0	—
Grace's Warbler (PG,FN)	—	7.5	9.8	19.5	6.0
Red-faced Warbler (PG,GN)	—	—	—	—	1.5
Western Tanager (PG,FN)	—	—	3.0	4.5	3.0
Mourning Dove (GF,FN)	—	4.5	—	3.0	3.0
Rock Wren (GF,GN)	4.5	6.0	6.0	—	—
Robin (GF,FN)	1.0	3.0	3.0	3.0	—
Hermit Thrush (GF,GN)	—	—	—	—	2.3
Gray-headed Junco (GF,GN)	1.5	6.0	12.0	15.0	12.0
Rufous-sided Towhee (GF,FN)	7.3	—	—	—	—
Chipping Sparrow (GF,FN)	—	3.0	6.0	4.5	3.0
Common Flicker (HT,CD)	1.5	3.0	3.0	3.0	3.0
Acorn Woodpecker (HT,CD)	—	3.0	—	—	—
Hairy Woodpecker (HT,CD)	—	1.5	3.0	3.0	3.0
Steller's Jay (HT,CD)	—	3.0	3.0	3.0	6.0
White-br. Nuthatch (HT,CD)	—	6.0	12.0	15.0	3.0
Black-headed Grosbeak (HT,FN)	—	—	1.5	3.0	3.0
Common Nighthawk (AF,GN)	—	3.0	3.0	3.0	3.0
Broad-td. Hummingbird (AF,FN)	—	9.0	9.0	3.0	3.0
Western Flycatcher (AF,CD)	—	—	—	3.0	3.0
Western Wood Pewee (AF,FN)	—	3.0	9.0	1.5	—
Violet-green Swallow (AF,CD)	—	—	3.0	7.5	7.5
Western Bluebird (AF,CD)	—	3.0	15.0	7.5	3.0
Foraging guilds					
Pickers and gleaners (PG)	—	19.5	33.8	61.5	30.0
Ground feeders (GF)	14.3	22.5	27.0	25.5	20.3
Hammerers and tearers (HT)	1.5	16.5	22.5	27.0	18.0
Aerial feeders (AF)	—	18.0	39.0	25.5	19.5
Nesting guilds					
Cavity and depression (CD)	1.5	19.5	48.0	61.5	39.0
Foliage nesters (FN)	8.3	42.0	53.3	60.0	30.0
Ground nesters (GN)	6.0	15.0	21.0	18.0	18.8
Totals	15.8	76.5	122.3	139.5	87.8

[a] See footnote Table 2.

(1967). In 1973 the pickers and gleaners exhibited a positive correlation with increasing foliage volume across the different watersheds (r = 0.91). However, in 1974 and 1975 they reached their highest densities on the silviculturally cut plot and declined in density on the control plot. The densities of the other foraging guilds fluctuated in response to foliage volume throughout the study (Tables 2–4). Nesting guild densities fluctuated with foliage volume with no real trends present except in 1974, when ground nester densities were positively correlated with increasing foliage volume (r = 0.89) and cavity and depression nester densities (r = 0.90) with increasing foliage volume.

Individual species also showed varying patterns with increasing foliage volume. Six species (Common Flicker, *Colaptes auratus*; Hairy Woodpecker, *Picoides villosus*; White-breasted Nuthatch, *Sitta carolinensis*; Grace's Warbler, *Dendroica graciae*; Gray-headed Junco; Western Bluebird, *Sialia maxicana*) were present on all forested areas throughout the study. The Common Flicker and Hairy Woodpecker had stable densities with increasing foliage volume in all years. In 1973 the Grace's Warbler (r = 0.87) and Gray-headed Junco (r = 0.70) increased in density with increasing foliage volume, whereas the White-breasted Nuthatch showed a negative correlation (r = −0.98) between density and foliage volume. The Western Bluebird fluctuated in density. In addition, five species (Pygmy Nuthatch, *Sitta pygmaea*; Steller's Jay, *Cyanocitta stelleri*; Chipping Sparrow, *Spizella passerina*; Broad-tailed Hummingbird, *Selasphorus platycercus*; Solitary Vireo, *Vireo solitarius*) were present on all the forested study plots in 1974 and 1975. In 1975 one other species, the Common Nighthawk (*Chordeiles minor*) was present on all the forested study areas. Three species (Robin, *Turdus migratorius*; Rock Wren, *Salpinctes obsoletus*; Rufous-sided Towhee, *Pipilo erythrophthalmus*) failed to occur in areas of denser foliage. In contrast, three species (Violet-green Swallow, *Tachycineta thalassina*; Red-faced Warbler, *Cardellina rubrifrons*; Western Flycatcher, *Empidonax difficilis*) were not present below a certain threshold of foliage volume.

The breeding bird communities on all the forested areas experienced similar patterns of density change during the study. They were most dense in 1974, had their lowest densities in 1973, and had intermediate densities in 1975 (Tables 2–4). However, the magnitude of density change varied between study plots. Similarly, most individual species followed this same pattern of density fluctuations. Coefficients of variation indicated that the variability in densities was very similar on the control, silviculturally cut and strip cut plots (37, 36, and 39% respectively) but that it was much lower on the severely thinned plot (21%) during the three-year study period. Coefficients of variation for the two-year period (1974 and 1975) showed that there was much less density variability on the silviculturally cut (7%) and severely thinned plots (10%) than on the strip cut (21%) and control (29%) plots.

The foraging guilds exhibited a large amount of variation in their yearly density fluctuations. The pickers and gleaners on the severely thinned (31%) and control (32%) plots exhibited less variation than the same guild on the strip cut (41%) and silviculturally cut (42%) plots. The ground feeders on the severely thinned plot (11%) showed much less variation than the ground feeders on the strip cut (35%), silviculturally cut (36%), and control (41%) plots. Density variations in the hammerers and tearers were much lower on the severely thinned (36%) and control (33%) plots than on the strip cut (48%) and silviculturally improved (56%) plots. The aerial feeders had their greatest variability in densities on the severely thinned (46%) and strip cut (42%) plots and their least variability on the silviculturally cut (30%) and control (34%) plots.

The nesting guilds showed differing amounts of variability in their yearly densities. The cavity and depression nesters exhibited their least variation on the severely thinned plot (12%) and their greatest variation on the strip cut plot (45%). This guild exhibited similar variations on the silviculturally cut (30%) and control

TABLE 5
SPECIES RICHNESS, DIVERSITY, AND EVENNESS FOR THE BIRD COMMUNITIES ON ALL STUDY PLOTS

Plots	Number of species			Diversity (H')			Evenness (E)		
	1973	1974	1975	1973	1974	1975	1973	1974	1975
Clear cut	3	4	5	1.02	1.18	1.34	0.93	0.85	0.83
Severely thinned	13	16	19	2.44	2.67	2.82	0.95	0.96	0.96
Strip cut	16	22	20	2.68	2.89	2.83	0.97	0.94	0.95
Silviculturally cut	—	20	21	—	2.76	2.77	—	0.92	0.91
Control	12	20	20	2.23	2.78	2.81	0.90	0.93	0.94
Silviculturally cut (pre-treat.)	16	—	—	2.57	—	—	0.93	—	—

(25%) plots. The foliage nesters varied from a low of 33% on the severely thinned plot to a high of 65% on the control plot. On the strip cut and silviculturally cut plots, the foliage nesters exhibited variations of 44 and 49% respectively. The ground nesters on the severely thinned plot showed very little variation (9%). Ground nester variation was much greater on the strip cut (38%), silviculturally cut (20%), and control (39%) plots than on the severely thinned plot.

Species richness.—The study plot with the highest number of breeding species changed during the three years (Table 5). In 1973 the highest number of breeding species (16) was found on the silviculturally cut and strip cut plots. In 1974 the number of species on the strip cut plot (22) was greater than the 20 species on the silviculturally cut and control plots. Twenty-one species were found on the silviculturally cut plot whereas 20 species were found on the strip cut and control plots in 1975.

Species number and composition changed on all areas between years. The number of species on the clear cut plot increased by one each year from three in 1973 to five in 1975 (Table 5). In 1974 the additional species was the Mountain Bluebird, while in 1975 it did not breed on the area and the Robin and Common Flicker became breeding species.

The avian community on the severely thinned plot added three species each year to a high of 19 species in 1975. In 1974 there were five additions (Common Nighthawk, Pygmy Nuthatch, Steller's Jay, Mourning Dove (*Zenaida macroura*), Broad-tailed Hummingbird) as well as two subtractions (Western Tanager, *Piranga ludoviciana*; Mountain Chickadee, *Parus gambelii*). In 1975 the Mountain Chickadee again bred on the area and the Yellow-rumped Warbler (*Dendroica coronata*) and Acorn Woodpecker (*Melanerpes formicivorous*) were breeding species on the severely thinned plot for the first time.

Changes in species number and composition in the breeding bird community on the strip cut plot consisted of an increase of six species from 1973 to 1974. In 1973 there was a total of 16 species, whereas in 1974 there were 22 species present on the study site. Twenty species were found on the plot in 1975. The House Wren (*Troglodytes aedon*) was a breeding species on the study area in 1973 and 1975 but not in 1974. Seven new species (Pygmy Nuthatch; Say's Phoebe, *Sayornis saya*; Hepatic Tanager, *Piranga flava*; Black-headed Grosbeak, *Pheucticus melanocephalus*; Common Nighthawk; Mountain Chickadee; and Violet-green

TABLE 6
BEHAVIORAL RESPONSES TO HABITAT ALTERATION

Guilds and Species	No. changes	Activity pattern	Foraging method	Tree species	Tree position	Perch	Stance	Mean height
Pickers and gleaners								
Mountain Chickadee	5	A[a]	–	A	A	A	–	A
Pgymy Nuthatch	5	–	–	A	A	A	A	A
Solitary Vireo	6	A	–	A	A	A	A	A
Yellow-rd. Warbler	5	A	A	A	–	A	–	A
Grace's Warbler	5	–	–	A	A	A	A	A
Ground feeders								
Rock Wren	3	A	–	A	–	A	–	–
Gray-headed Junco	6	A	A	A	A	A	–	A
Chipping Sparrow	5	A	–	A	A	A	–	A
Aerial feeders								
Broad-td. Hummingbird	3	–	–	A	A	A	–	–
Western Wood Pewee	5	A	–	A	A	A	–	A
Violet-gr. Swallow	3	A	–	–	–	A	–	A
Western Bluebird	6	A	A	A	A	A	–	A
Hammerers and tearers								
Common Flicker	7	A	A	A	A	A	A	A
Hairy Woodpecker	5	A	–	–	A	A	A	A
White-br. Nuthatch	7	A	A	A	A	A	A	A
Total		13	5	13	12	15	6	13

[a] Behavioral response associated with treatment by G-test, $P \leq 0.05$.

Swallow) bred on the strip cut plot in 1974. In 1975 Say's Phoebe, Hepatic Tanager, and Mountain Chickadee were again missing from the breeding bird community.

The breeding bird community on the control plot showed a large increase in species from 12 in 1973 to 20 in 1974 and 1975. There were eight additional species (Common Nighthawk, Broad-tailed Hummingbird, Steller's Jay, Yellow-rumped Warbler, Chipping Sparrow, Black-headed Grosbeak, Mourning Dove, Western Flycatcher) breeding in 1974. However, in 1975, even though species numbers remained the same, the Yellow-rumped Warbler left the area and the Western Tanager became a breeding species for the first time.

The difference between the breeding bird community on the control plot in 1973 and on the silviculturally cut plot in 1974 was an increase of four species. Six additional species (Yellow-rumped Warbler; Solitary Vireo; Mountain Chickadee; Broad-tailed Hummingbird; Hermit Thrush, *Catharus guttatus*; Robin) were present in the breeding community while two species (Red-faced Warbler, House Wren) did not utilize the area.

Diversities.—Bird species diversities varied on the study sites with the changing densities and species numbers (Table 5). Breeding bird diversity increased each year on the clear cut plot from 1.02 to 1.34 in 1975. Similarly, diversity increased each year on the severely thinned plot from 2.44 in 1973 to 2.82 in 1975. The breeding bird community on the strip cut plot had its highest diversity in 1974 whereas the avian communities on the silviculturally cut and control plots had their highest diversities in 1975. The breeding bird community on the strip cut had the highest diversity each year of the study.

TABLE 7
ACTIVITY PATTERN ALTERATIONS BY FOUR SELECTED BIRD SPECIES

Species	Plot	n	% total observations: Singing-calling	Foraging	Resting-preening
Solitary Vireo[a]	S. Thn.	245	69.8	29.4	0.8
	Strip	260	66.2	33.5	0.3
	Silv.	149	47.2	48.9	3.4
	Cntrl.	222	70.3	23.8	5.9
Gray-headed Junco[a]	S. Thn.	139	33.8	38.1	28.1
	Strip	125	37.6	48.8	13.6
	Silv.	178	69.1	20.2	10.7
	Cntrl.	199	60.3	33.2	6.5
Western Wood Pewee[a]	S. Thn.	68	30.9	47.1	22.0
	Strip	308	34.1	47.4	18.5
	Silv.	72	51.4	40.3	8.3
Common Flicker[a]	S. Thn.	64	17.2	34.4	48.4
	Strip	88	22.7	35.2	42.1
	Silv.	24	29.2	45.8	25.0
	Cntrl.	35	17.1	20.0	62.9

[a] Activity pattern associated with treatment by G-test, $P \leq 0.05$.

BEHAVIOR

Activity patterns.—The observations in a particular activity by foraging guilds were divided into three categories: 1) singing and calling, 2) foraging, and 3) resting and preening. A composite community activity pattern was calculated by summing all the observations regardless of species. The composite community activity pattern was associated with treatment (G-test, $P \leq 0.05$) as were the activity patterns for 12 out of the 15 species (Table 6).

The activity patterns of four species which altered their behavior in response to treatment are illustrated in Table 7. The Solitary Vireo did more resting on the control and silviculturally cut plots than on either of the heavily treated areas. Moreover, that species foraged more on the silviculturally cut plot than any of the other study sties. The Gray-headed Junco spent more time foraging on the severely thinned and strip cut plots than it did on the silviculturally cut and control plots. The amount of time the junco spent resting and preening was inversely correlated with foliage volume ($r = 0.91$). The Western Wood Pewee (*Contopus sordidulus*) was the only aerial feeder to do a substantial amount of calling. In fact, the proportion of the pewee's time spent calling was directly correlated with foliage volume ($r = 0.99$) while the amount of time it spent resting and preening was inversely correlated with foliage volume ($r = -1.00$). The Common Flicker did much more resting than any of the other hammerers and tearers.

A cluster analysis of the activity patterns was performed on the coefficient matrix of Euclidean distances. The species on all study plots clustered into groups representing similarities in activity patterns. For example, on the severely thinned plot the species clustered into two main groups: 1) Yellow-rumped Warbler, Western Wood Pewee, Gray-headed Junco, Western Bluebird, Common Flicker, Grace's Warbler, Chipping Sparrow, Solitary Vireo, and Rock Wren, and 2) Violet-green Swallow, Hairy Woodpecker, Mountain Chickadee, White-breasted

TABLE 8
FORAGING METHOD ALTERATIONS BY FOUR SELECTED BIRD SPECIES

Species	Plot	n	% total observations: Picking-gleaning	Aerial feeding	Hammering-tearing	Probing-walking
Yellow-rumped Warbler[a]	S. Thn.	34	55.9	11.7	0.0	32.4
	Strip	32	68.8	25.0	0.0	6.2
	Silv.	110	95.5	0.9	0.0	3.6
Gray-headed Junco[a]	S. Thn.	53	15.1	0.0	0.0	84.9
	Strip	61	27.9	0.0	0.0	72.1
	Silv.	36	0.0	0.0	0.0	100.0
	Cntrl.	84	10.7	0.0	0.0	89.3
Western Bluebird[a]	S. Thn.	69	0.0	0.0	81.2	18.8
	Strip	84	6.0	0.0	69.0	25.0
	Silv.	46	0.0	0.0	91.3	8.7
	Cntrl.	36	0.0	0.0	97.2	2.8
White-breasted Nuthatch[a]	S. Thn.	81	1.2	0.0	98.8	0.0
	Strip	177	2.8	0.0	93.2	4.0
	Silv.	103	15.5	0.0	84.5	0.0
	Cntrl.	72	9.7	0.0	90.3	0.0

[a] Foraging method associated with treatment by G-test, $P \leq 0.05$.

Nuthatch, and Broad-tailed Hummingbird. The first group consists of those species that spent 9–47% of their time foraging whereas the second group spent over 94% of their time foraging. On the other study sites the species split into two basic groups: 1) those species that spent less than 60% of their time foraging, and 2) those species that spent more than 60% of their time foraging. The most consistent members of group 2 were the Hairy Woodpecker, Broad-tailed Hummingbird, Mountain Chickadee, White-breasted Nuthatch, and Pygmy Nuthatch.

Foraging methods.—Observations of foraging methods were divided into four categories: 1) picking and gleaning, 2) aerial feeding, 3) hammering and tearing, and 4) probing and walking. Foraging methods of the community composite were independent of treatment ($P \leq 0.05$).

The foraging methods of only five species (Yellow-rumped Warbler, Gray-headed Junco, Western Bluebird, Common Flicker, White-breasted Nuthatch) were associated with treatment ($P \leq 0.05$) (Tables 6 and 8). The amount of time the Yellow-rumped Warbler spent picking and gleaning was positively correlated with foliage volume ($r = 0.99$) (Table 8). The Western Bluebird spent a larger part of its time on the ground on the heavily treated study plots. The Common Flicker spent 39–64% of its time probing on the heavily treated plots but spent no time probing on the silviculturally cut and control plots. The White-breasted Nuthatch was the only species in the hammerer and tearer guild that picked and gleaned, which it did in greater proportion on the natural and silviculturally cut areas than on the heavily treated areas.

A clustering of the foraging methods on the four study plots indicates that the species cluster on the basis of foraging guilds. The four clusters on all areas were: 1) pickers and gleaners (Yellow-rumped Warbler, Grace's Warbler, Solitary Vireo, Mountain Chickadee, Pygmy Nuthatch), 2) ground feeders (Rock Wren, Chip-

TABLE 9
ALTERATIONS IN TREE SPECIES SELECTION BY FIVE BIRD SPECIES

Species	Plot	n	% total observations: Ponderosa pine	Gambel oak
Yellow-rumped Warbler[a]	S. Thn.	34	35.3	61.7
	Strip	64	73.4	26.6
	Silv.	186	87.1	12.9
Grace's Warbler[a]	S. Thn.	165	72.7	27.3
	Strip	185	83.8	16.2
	Silv.	253	97.2	2.7
	Cntrl.	200	88.5	11.5
Gray-headed Junco[a]	S. Thn.	55	92.7	7.3
	Strip	59	62.7	37.3
	Silv.	131	96.9	3.1
	Cntrl.	123	97.6	3.4
Western Bluebird[a]	S. Thn.	79	86.1	13.9
	Strip	120	86.7	13.3
	Silv.	46	100.0	0.0
	Cntrl.	45	97.8	2.2
White-breasted Nuthatch[a]	S. Thn.	82	67.1	32.9
	Strip	164	80.5	19.5
	Silv.	94	79.8	20.2
	Cntrl.	74	85.1	14.9
% foliage	S. Thn.	—	85.0	15.0
	Strip	—	67.2	32.5
	Silv.	—	83.2	16.8
	Cntrl.	—	84.9	10.4

[a] Tree species selection associated with treatment by *G*-test, $P \leq 0.05$.

ping Sparrow, Gray-headed Junco), 3) aerial feeders (Violet-green Swallow, Western Wood Pewee, Broad-tailed Hummingbird, Western Bluebird), and 4) hammerers and tearers (Hairy Woodpecker and White-breasted Nuthatch). The only species which switched from one foraging cluster to another was the Common Flicker.

Tree species selection.—The selection of tree species by the birds was divided into three categories: 1) ponderosa pine, 2) gambel oak, and 3) alligator juniper (*Juniperus deppeana*). However, as no birds were observed in the juniper, it was not considered in the following analysis. Tree species selection by the community composite was associated with treatment ($P \leq 0.05$). Moreover, the tree species selections of 13 of the 15 species were influenced by treatment (Table 6).

The amount of available foliage volume varied from watershed to watershed but was lowest on the severely thinned plot (3968 m^3/ha) and highest on the control plot (19,370 m^3/ha). Yet, because of selective cutting practices, the proportion of gambel oak on the treated areas (15.0% on the severely thinned plot, 16.8% on the silviculturally cut plot and 32.5% on the strip cut plot) was greater than on the control plot (10.4%). Gambel oak foliage was not used in proportion to its availability by any of the 15 species examined but in general was used in greater proportion on the more open sites (the severely thinned and strip cut plots) than on the denser areas (silviculturally cut and control plots). For example, the Gray-headed Junco, Western Bluebird, Yellow-rumped Warbler, and Grace's Warbler spent more time in gambel oak on the severely thinned and strip cut plots than on the denser areas (Table 9). The White-breasted Nuthatch, however, overused gambel oak on all plots except the strip cut plot where it used oak 20% of the time compared with its 33% availability.

Cluster analyses of tree species selection indicate that the bird species segregated on the basis of the proportion of their time spent in ponderosa pine. For example, on the severely thinned plot the bird species clustered into three groups: 1) Yellow-rumped Warbler, Western Wood Pewee, and Broad-tailed Hummingbird (13–54%), 2) Grace's Warbler, Solitary Vireo, White-breasted Nuthatch, Rock Wren, and Chipping Sparrow (67–82%), and 3) Western Bluebird, Common Flicker, Gray-headed Junco, Hairy Woodpecker, and Mountain Chickadee (86–100%). On the strip cut plot the clusters were 1) Rock Wren, Gray-headed Junco, Western Wood Pewee, and Chipping Sparrow (44–67%), 2) Yellow-rumped Warbler, Pygmy Nuthatch, Grace's Warbler, Western Bluebird, Solitary Vireo, and White-breasted Nuthatch (73–87%), and 3) Violet-green Swallow, Mountain Chickadee, Common Flicker, and Hairy Woodpecker (93–100%). On the silviculturally cut and control areas there were two main clusters, with those spending less than 97% of their time in ponderosa pine in the first cluster and those spending more than 97% of their time in ponderosa pine in the second. The latter group consisted of the Violet-green Swallow, Chipping Sparrow, Common Flicker, Hairy Woodpecker, Western Bluebird, Pygmy Nuthatch, and Gray-headed Junco. Grace's Warbler was in the second group only on the silviculturally cut area.

Horizontal tree position.—Observations on the position from the trunk were divided into two categories: 1) trunks and inner branches, and 2) outer foliage. The horizontal tree positions of the entire breeding bird community were associated with treatment ($P \leq 0.05$). Moreover, the trunk positions of 11 species were affected by treatment ($P \leq 0.05$) (Table 6).

There was a general dichotomy in tree position selection between the four guilds. The pickers and gleaners and the ground feeders spent most of their time in the outer foliage whereas the hammerers and tearers and the aerial feeders spent most of their time on the trunks and inner branches. For example, the Solitary Vireo used the inner branch space the heaviest on the strip cut plot (36%) where it was the least available (5.6%) (Table 10). In contrast, the Gray-headed Junco made greater use of the inner branch space on the silviculturally cut plot than on the other study plots. The Western Wood Pewee which spent 66% of its time in the outer foliage on the severely thinned plot, by dramatic contrast spent none of its time in the outer foliage on the silviculturally cut plot. The White-breasted Nuthatch spent at least 82% of its time on the trunks and inner branches on all areas (Table 10).

The bird communities on all four study plots separate into two clusters: 1) those species mainly using the foliage, and 2) those species mainly using the trunks and inner branches. For example, the clusters on the severly thinned area were: 1) Yellow-rumped Warbler, Grace's Warbler, Mountain Chickadee, Rock Wren, Chipping Sparrow, Gray-headed Junco, Western Wood Pewee, Solitary Vireo, and Broad-tailed Hummingbird (65–100% outer foliage use), and 2) White-breasted Nuthatch, Western Bluebird, Common Flicker, and Hairy Woodpecker (68–100% trunk and inner branch use). The pine use clusters on the other three

TABLE 10
ALTERATIONS IN HORIZONTAL TREE POSITIONS BY FOUR BIRD SPECIES

Species	Plot	n	% total observations: Outer foliage	% total observations: Trunks-branches
Solitary Vireo[a]	S. Thn.	245	86.9	13.1
	Strip	260	64.2	35.8
	Silv.	149	71.1	28.9
	Cntrl.	222	86.9	13.1
Gray-headed Junco[a]	S. Thn.	55	92.7	7.3
	Strip	59	78.0	22.0
	Silv.	131	49.6	50.4
	Cntrl.	123	74.0	26.0
Western Wood Pewee[a]	S. Thn.	35	65.7	34.3
	Strip	157	45.2	54.8
	Silv.	36	0.0	100.0
White-breasted Nuthatch[a]	S. Thn.	82	18.3	81.7
	Strip	164	3.7	96.3
	Silv.	94	4.3	95.7
	Cntrl.	74	8.1	91.7
% foliage	S. Thn.	—	85.9	14.1
	Strip	—	94.4	5.6
	Silv.	—	87.7	12.3
	Cntrl.	—	81.7	18.3

[a] Horizontal tree position associated with treatment by G-test, $P \leq 0.05$.

plots were the same as above except that the Pygmy Nuthatch was in the first cluster and the Violet-green Swallow and Western Wood Pewee were in the second cluster.

Perch selection.—Observations on perch selection were divided into six categories: 1) trunk, 2) branches, 3) twigs, 4) foliage (needles and leaves), 5) ground, and 6) air. The composite bird community perch selection was associated with treatment ($P \leq 0.05$), as was that of each of the 15 individual species ($P \leq 0.05$) (Table 6).

Members of a foraging guild exhibited similar preferences for a particular foraging substrate. The pickers and gleaners were found primarily on twigs. For example, the Pygmy Nuthatch and Grace's Warbler spent more than 60% of their time on twigs (Table 11). The ground feeders foraged primarily on the ground but utilized the twigs and branches as song posts. The aerial feeders obviously foraged in the air more than any other guild but primarily used branches as both song and foraging posts. The Western Bluebird was the only member of this guild to use the ground as a foraging substrate (Table 11). The hammerers and tearers spent most of their time on the trunks and branches except for the Common Flicker which spent much of its time on the ground on the severely thinned and strip cut plots but little or no time on the ground on the silviculturally cut and control plots (Table 11).

The perch selection of individual species cluster into foraging guilds or combinations of foraging guilds. For example, on the severely thinned plot the clusters were: 1) Yellow-rumped Warbler, Chipping Sparrow, Grace's Warbler, Solitary

TABLE 11
PERCH SELECTION ALTERATIONS BY FIVE SELECTED BIRD SPECIES

Species	Plot	*n*	% total observations: Trunk	Branch	Twig	Foliage	Ground	Air
Pygmy Nuthatch[a]	Strip	48	2.1	0.0	83.3	14.6	0.0	0.0
	Silv.	144	9.0	5.6	59.7	20.1	5.6	0.0
	Cntrl.	358	3.4	8.7	60.9	22.9	3.6	0.5
Grace's Warbler[a]	S. Thn.	165	0.0	3.6	88.5	6.7	0.0	1.2
	Strip	187	0.0	1.1	90.4	5.3	0.5	2.7
	Silv.	253	0.0	1.6	89.3	5.9	2.0	1.2
	Cntrl.	209	0.0	6.2	84.8	3.8	3.8	1.4
Gray-headed Junco[a]	S. Thn.	139	0.0	38.8	23.0	0.7	37.5	0.0
	Strip	125	0.0	3.2	36.8	4.0	56.0	0.0
	Silv.	178	0.0	43.3	25.3	0.0	31.4	0.0
	Cntrl.	199	0.0	23.1	36.7	2.5	37.7	0.0
Western Bluebird[a]	S. Thn.	152	0.0	38.2	13.7	0.0	9.9	38.2
	Strip	206	2.4	47.6	6.8	0.0	10.7	32.5
	Silv.	95	0.0	50.5	0.0	0.0	6.3	43.2
	Cntrl.	81	0.0	53.1	2.5	0.0	3.7	40.7
Common Flicker[a]	S. Thn.	64	14.1	54.6	0.0	0.0	31.3	0.0
	Strip	88	27.3	37.5	0.0	0.0	35.2	0.0
	Silv.	24	45.8	45.8	0.0	0.0	8.3	0.0
	Cntrl.	35	45.7	54.3	0.0	0.0	0.0	0.0

[a] Perch selection associated with treatment by *G*-test, $P \leq 0.05$.

Vireo, and Mountain Chickadee (58–89% twigs), 2) Rock Wren, Common Flicker, and Gray-headed Junco (31–85% ground), 3) Violet-green Swallow, Broad-tailed Hummingbird, Western Bluebird, and Western Wood Pewee (38–88% air), and 4) Hairy Woodpecker and White-breasted Nuthatch (71–100% trunk). The Chipping Sparrow was the only species that did not cluster according to foraging guild on the severely thinned plot. The clustering was the same on the strip cut plot except for the addition of the Pygmy Nuthatch into the first cluster. On the silviculturally cut plot the pickers and gleaners and the hammerers and tearers cluster into separate groups whereas the ground feeders and aerial feeders cluster together

TABLE 12
CHANGES IN STANCE BY THE PYGMY NUTHATCH AND WHITE-BREASTED NUTHATCH

Species	Plot	*n*	% total observations: Standing upright	Hanging	Head up	Head down
Pygmy Nuthatch[a]	Strip	48	85.4	12.5	2.1	0.0
	Silv.	144	71.5	20.2	8.3	0.0
	Cntrl.	356	72.5	23.3	2.2	2.0
White-breasted Nuthatch[a]	S. Thn.	82	9.8	12.2	42.7	35.3
	Strip	196	32.1	14.3	30.6	23.0
	Silv.	94	0.0	2.1	53.2	44.7
	Cntrl.	74	17.6	9.5	40.5	32.4

[a] Stance associated with treatment by *G*-test, $P \leq 0.05$.

TABLE 13
MEAN HEIGHTS AND USE RANGES FOR SEVEN SELECTED BIRD SPECIES

Species	Plot	n	Mean	SD	Range
Pygmy Nuthatch[a]	Strip	48	9.5	3.7	2–14
	Silv.	134	13.3	6.7	0–26
	Cntrl.	340	17.0	6.1	0–28
Solitary Vireo[a]	S. Thn.	245	13.1	5.1	2–22
	Strip	260	7.7	3.0	0–14
	Silv.	149	8.8	4.3	2–20
	Cntrl.	222	3.9	2.8	0–14
Gray-headed Junco[a]	S. Thn.	55	12.7	6.9	0–20
	Strip	59	7.0	4.2	0–14
	Silv.	131	8.2	5.4	0–20
	Cntrl.	123	6.2	5.0	0–18
Chipping Sparrow[a]	S. Thn.	54	7.1	3.5	2–14
	Strip	79	6.4	3.7	0–14
	Silv.	60	8.8	2.1	2–12
	Cntrl.	18	8.4	2.8	4–12
Western Wood Pewee[a]	Strip	35	7.5	3.5	0–14
	Silv.	157	6.1	3.1	0–12
	Cntrl.	36	5.3	2.9	2–12
Violet-green Swallow[a]	Strip	51	7.3	2.1	6–12
	Silv.	57	14.1	3.9	12–18
	Cntrl.	83	17.4	4.4	14–20
White-breasted Nuthatch[a]	S. Thn.	82	6.4	2.8	0–14
	Strip	164	7.6	3.2	0–20
	Silv.	94	7.8	5.0	0–16
	Cntrl.	74	8.2	4.4	0–18

[a] Difference in mean height between study plots significant ($P \leq 0.05$) by F-test.

because of their heavy branch use. On the control area the ground feeders clustered with the pickers and gleaners plus the Broad-tailed Hummingbird.

Stance.—Observations on stance were divided into four categories: 1) standing upright, 2) hanging, 3) head up, and 4) head down. The stance selection of only six of the species were associated ($P \leq 0.05$) with treatment (Table 6).

All pickers and gleaners, ground feeders, and aerial feeders spent the majority of their time standing upright (72–100%). In addition, the Common Flicker spent much of its time standing upright on all study areas. The other hammerers and tearers, the Hairy Woodpecker and White-breasted Nuthatch primarily used the trunks and therefore were positioned with their heads up or down. However, the White-breasted Nuthatch was the only species consistently to move vertically down the trunk whereas the Pygmy Nuthatch was the only non-hammerer and tearer to utilize the head-up posture (Table 12).

A clustering of the species on the basis of stance shows that most species on all study plots stood upright. The only exceptions were the Hairy Woodpecker and White-breasted Nuthatch which spent the majority of their time in a vertical position. The only switch that occurred was by the Common Flicker on silviculturally cut plot where it switched from standing upright 88–99% of the time to standing upright only 54% of the time. Furthermore, while the flicker spent less

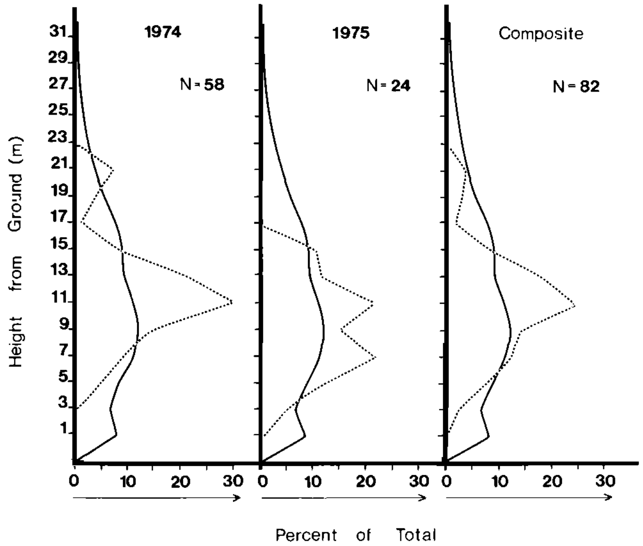

FIGURE 7. Mountain Chickadee use (dotted line) of the available foliage volume (solid line) by height on the silviculturally cut plot. The composite combines all observations for 1974 and 1975.

than 13% of its time vertically upward on the severely thinned, strip cut, and control plots, it was vertically upward 46% of the time in the silviculturally cut plot.

Foliage Utilization

Foliage use both on an individual and community basis was examined over the three-year study period. Observations were classed into 2-m height intervals. Foliage use was examined on a species basis as sexes were not separated.

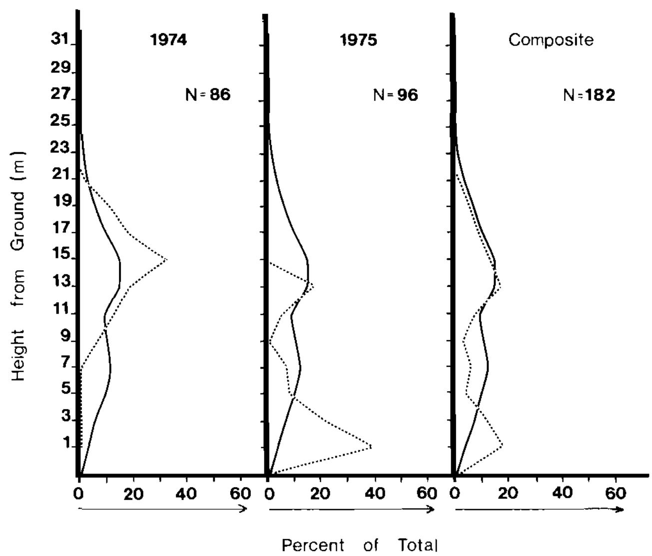

FIGURE 8. Mountain Chickadee use (dotted line) of the available foliage volume (solid line) by height on the control plot. The composite combines all observations for 1974 and 1975.

Mean height and use range.—Differences in use range and mean height in the tree were examined in order to determine the effects of treatment. Only the Rock Wren and Broad-tailed Hummingbird were not influenced by increasing foliage volume (Table 6). There were basically three trends exhibited by the other 13 species: 1) negative correlation, or 2) positive correlation with increasing foliage volume, or 3) change in foliage height selection with no obvious pattern. Of the pickers and gleaners, for example, the Pygmy Nuthatch's mean height in the trees was positively correlated with increasing foliage volume ($r = 0.94$), while that of the Solitary Vireo suggested a negative trend (Table 13). Amongst the ground feeders, the Gray-headed Junco exhibited a negative correlation ($r = 0.70$) between mean height and foliage volume. The Chipping Sparrow fluctuated in height but was consistently higher in the trees on the denser areas. The Western Wood Pewee, an aerial feeder, showed a negative correlation ($r = 0.88$) whereas another aerial feeder, the Violet-green Swallow showed a positive correlation ($r = 0.99$) between mean height and foliage. The White-breasted Nuthatch, a hammerer and tearer, exhibited a positive correlation ($r = 0.81$) between mean height and increasing foliage volume.

Foliage profiles.—Differences in foliage use profiles were examined in order to determine yearly fluctuations and the impact of treatment. The Mountain Chickadee exhibited differing use profile trends on the silviculturally cut and control plots. On the silviculturally cut plot, the chickadee shifted downward from the spire into the bulge (the bulge specifically is that region of the foliage profile which includes approximately 70% of the foliage) from 1974 to 1975 (Fig. 7). Overall, the Mountain Chickadee overused the 7- to 13-m range. Similarly, the Mountain Chickadee shifted down from the spire on the control plot in 1975 and overused the 1- to 4-m region (Fig. 8). The composite profile of the Mountain Chickadee approximated the foliage profile except for the overuse of the 1- to 3-m region and an underuse of the 5- to 11-m region.

Even though the White-breasted Nuthatch moved higher into the trees on all study plots in 1974, its use profiles markedly differed between plots and years. The White-breasted Nuthatch had a statistically significant drop in mean height in 1975 ($P \leq 0.05$) on the severely thinned plot (Fig. 9). The composite profile of the White-breasted Nuthatch showed an underuse of the 11-m and up region and an overuse of the 3- to 7-m region. In contrast, on the strip cut plot the White-breasted Nuthatch expanded its use range by 14 m in 1974 over what it used in 1973 while increasing its mean height by 7 m ($P \leq 0.05$) (Fig. 10). The tremendous overuse of the 3-m height class by the White-breasted Nuthatch in 1973 was dramatically reduced in 1974 with a corresponding overuse of the 17- to 19-m region. In 1975 the White-breasted Nuthatch contracted its use range by 10 m with a marked overuse at 1-m. The White-breasted Nuthatch's composite profile approximated the foliage profile. On the silviculturally cut plot, the White-breasted Nuthatch overused the 5- to 9-m range in 1973 (Fig. 11). In 1974 and 1975, after treatment, the use profile of the White-breasted Nuthatch closely approximated the foliage profile. The use profiles of the White-breasted Nuthatch on the control plot showed over-utilization at different height classes each year (Fig. 12). The nuthatch's composite profile showed a slight overuse of 13-m and below and an underuse above 13-m.

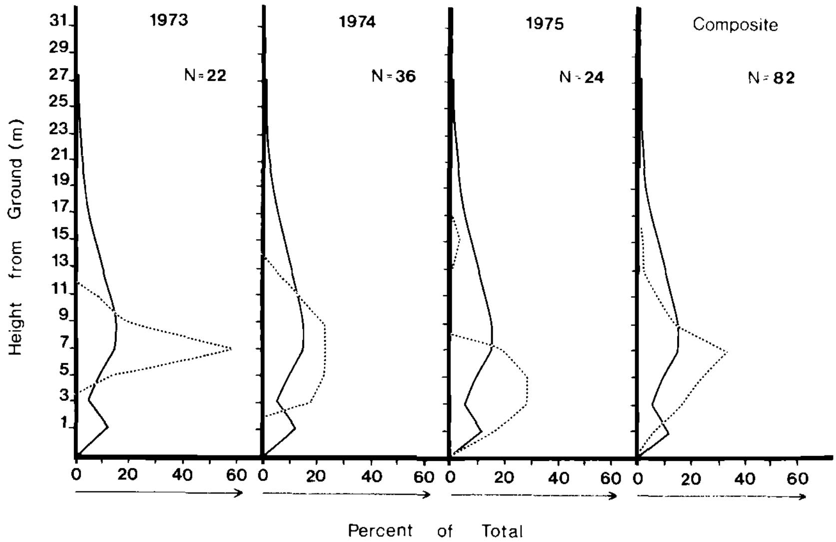

FIGURE 9. White-breasted Nuthatch use (dotted line) of the available foliage volume (solid line) by height on the severely thinned plot. The composite combines all observations for the study.

The Pygmy Nuthatch exhibited similar foliage use profiles on the silviculturally cut and control plots (Figs. 13, 14). On both plots the Pygmy Nuthatch overused the upper portions of the trees in 1974 and then shifted downward from the spire into the bulge region in 1975. Differences emerged in the Pygmy Nuthatch's composite profiles, with an overuse of the 21- to 29-m region on the control plot

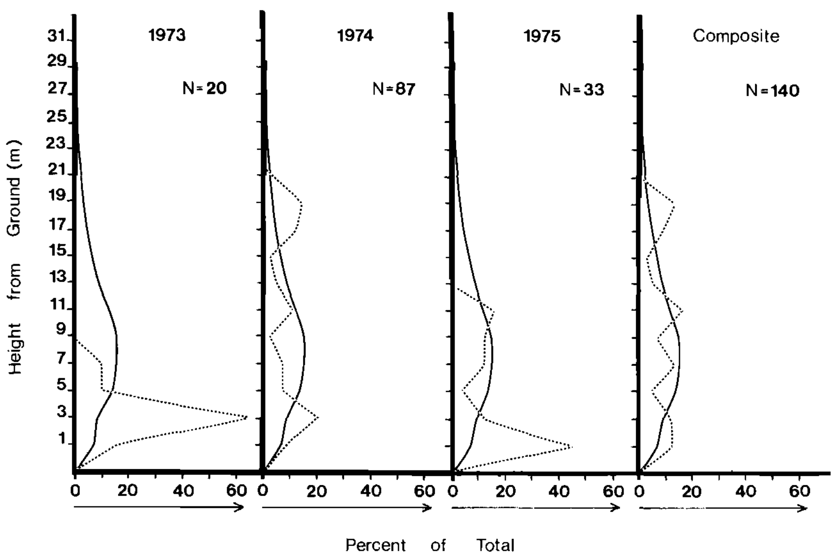

FIGURE 10. White-breasted Nuthatch use (dotted line) of the available foliage volume (solid line) by height on the strip cut plot. The composite combines all observations for the study.

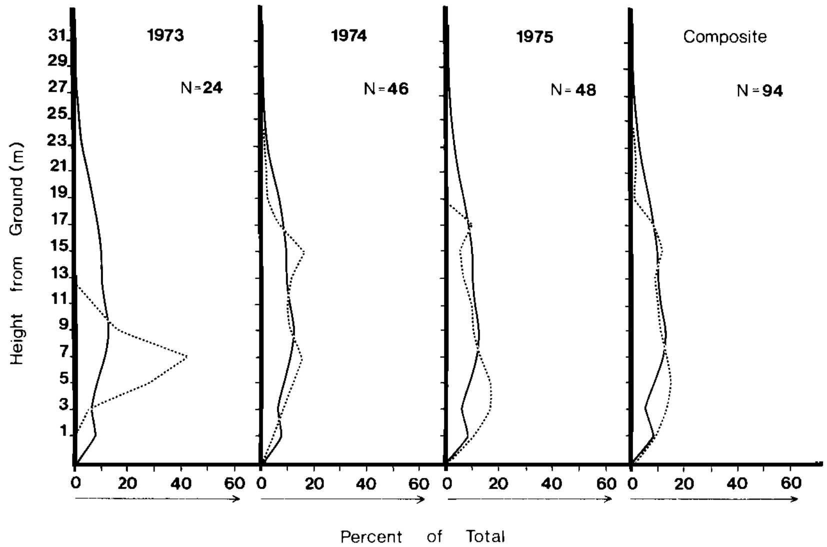

FIGURE 11. White-breasted Nuthatch use (dotted line) of the available foliage volume (solid line) by height on the silviculturally cut plot. The composite combines all observations for 1974 and 1975.

and a close similarity of the use profile and foliage profile on the silviculturally cut plot.

The Western Bluebird overused the lower height classes on all study plots. On the severely thinned plot the Western Bluebird exhibited a dichotomous use profile in 1975 (Fig. 15). Similarly, on the strip cut plot the Western Bluebird exhib-

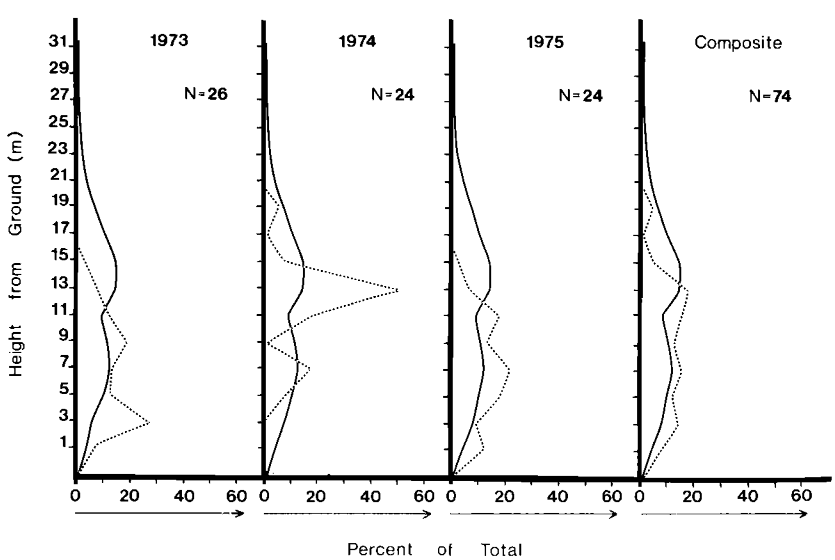

FIGURE 12. White-breasted Nuthatch use (dotted line) of the available foliage volume (solid line) by height on the control plot. The composite combines all observations for the study.

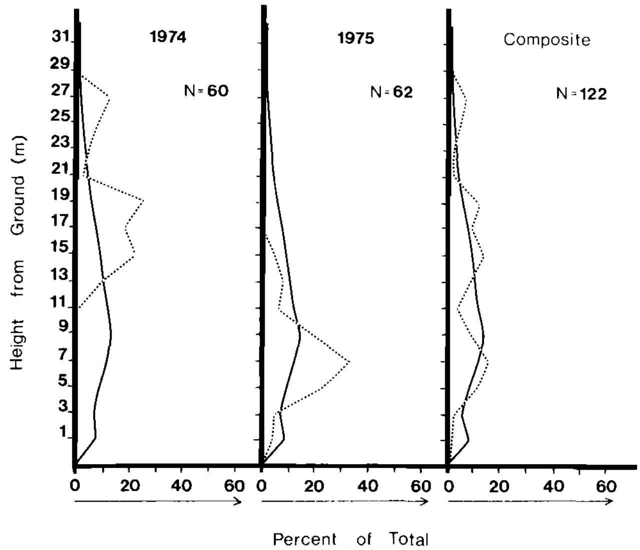

FIGURE 13. Pygmy Nuthatch use (dotted line) of the available foliage volume (solid line) by height on the silviculturally cut plot. The composite combines all observations for 1974 and 1975.

ited a tendency towards a dichotomous use profile in 1974 and 1975 (Fig. 16). In 1973 on the silviculturally cut plot (before treatment) the Western Bluebird had a dichotomous use profile which was not observed on the silviculturally cut plot in 1974 and 1975 (Fig. 17).

The use profiles of the Solitary Vireo on the four study plots showed marked variations. In 1975 the Solitary Vireo on the severely thinned plot contracted its

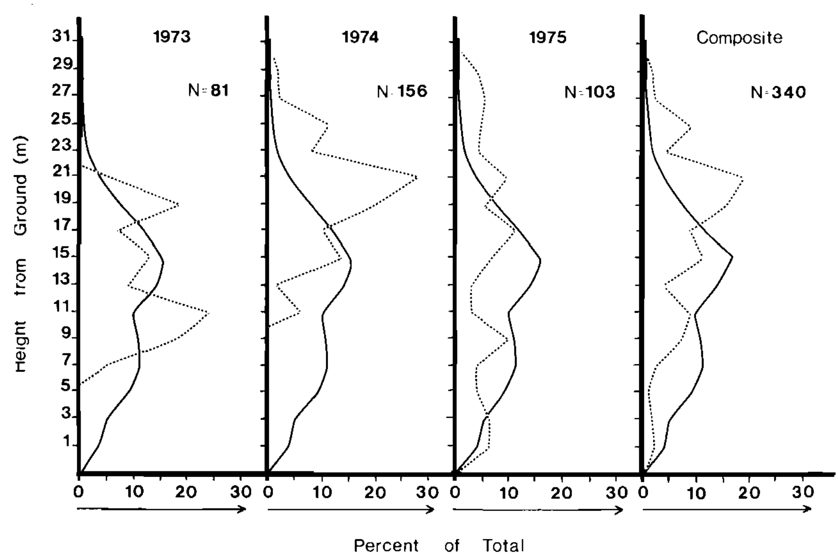

FIGURE 14. Pygmy Nuthatch use (dotted line) of the available foliage volume (solid line) by height on the control plot. The composite combines all observations for the study.

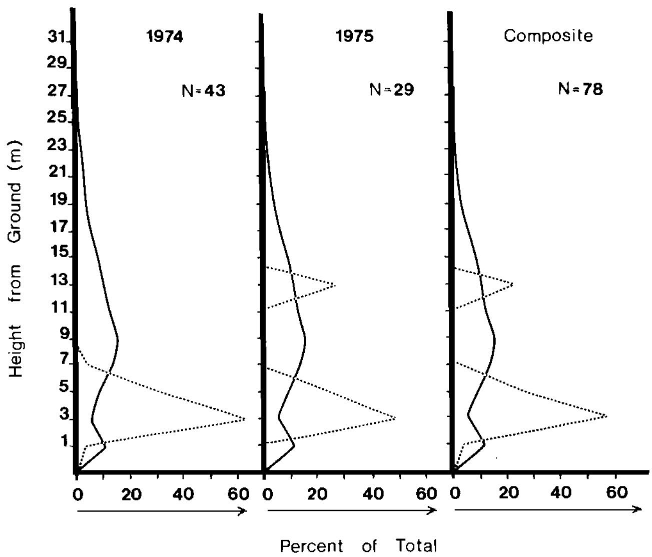

FIGURE 15. Western Bluebird use (dotted line) of the available foliage volume (solid line) by height on the severely thinned plot. The composite combines all observations for 1974 and 1975.

use range and overutilized the 11- to 15-m area which the previous year was grossly underused (Fig. 18). In contrast, in 1974 the Solitary Vireo overutilized the 17- to 23-m area. The Solitary Vireo's overall use profile indicated an overuse of the upper spire. On the strip cut plot the Solitary Vireo remained between 0 to 16 m but overutilized a different height class each year (Fig. 19). On the silviculturally cut plot the vireo heavily used the bulge region in 1974 whereas in

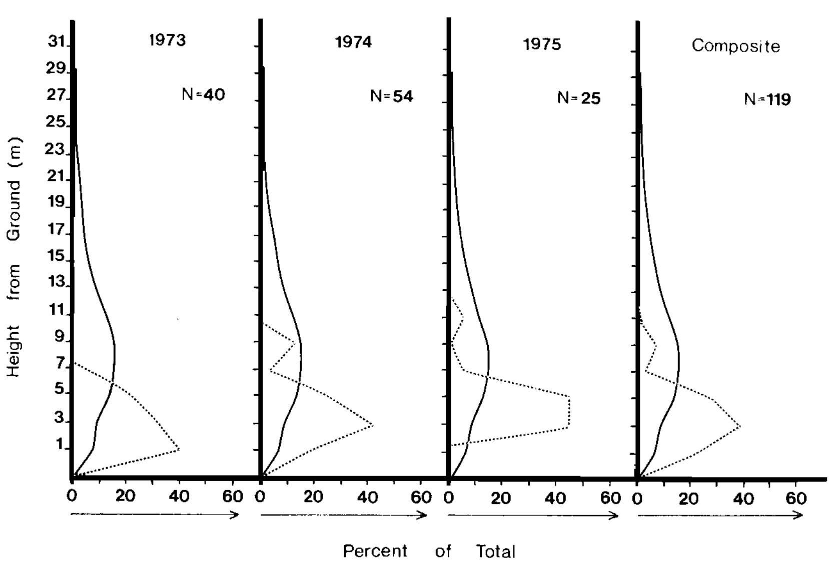

FIGURE 16. Western Bluebird use (dotted line) of the available foliage volume (solid line) by height on the strip cut plot. The composite combines all observations for the study.

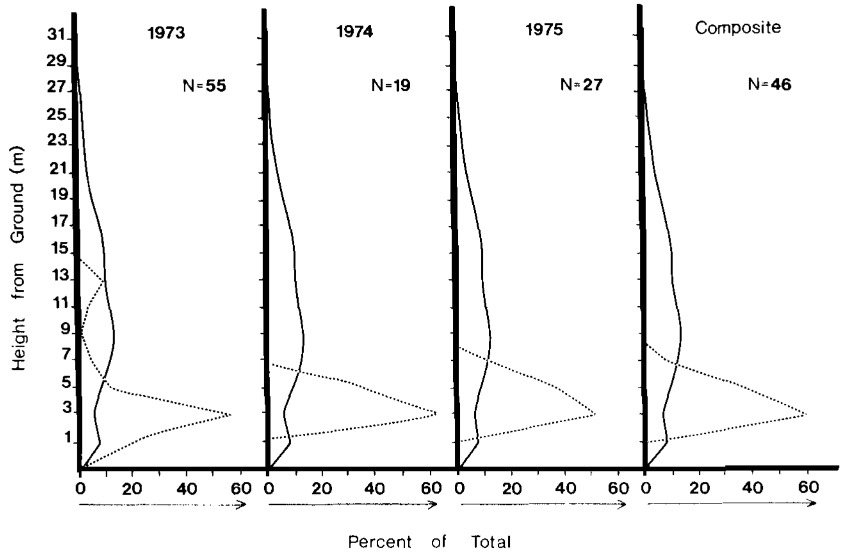

FIGURE 17. Western Bluebird use (dotted line) of the available foliage volume (solid line) by height on the silviculturally cut plot. The composite combines all observations for 1974 and 1975.

1975 it expanded its use range upward and downward with no use of the 13- to 15-m region (Fig. 20). The Solitary Vireo on the control plot remained close to the ground with no difference in mean height between years (Fig. 21). The Solitary Vireo's mean heights showed an inverse relationship with increasing foliage volume ($r = 0.71$).

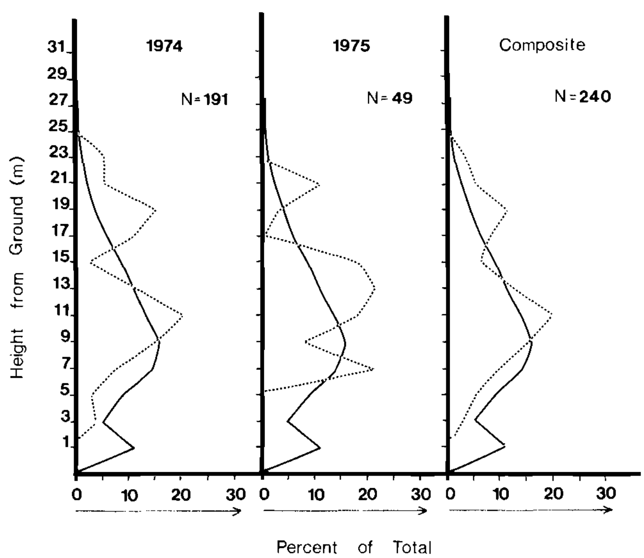

FIGURE 18. Solitary Vireo use (dotted line) of the available foliage volume (solid line) by height on the severely thinned plot. The composite combines all observations for 1974 and 1975.

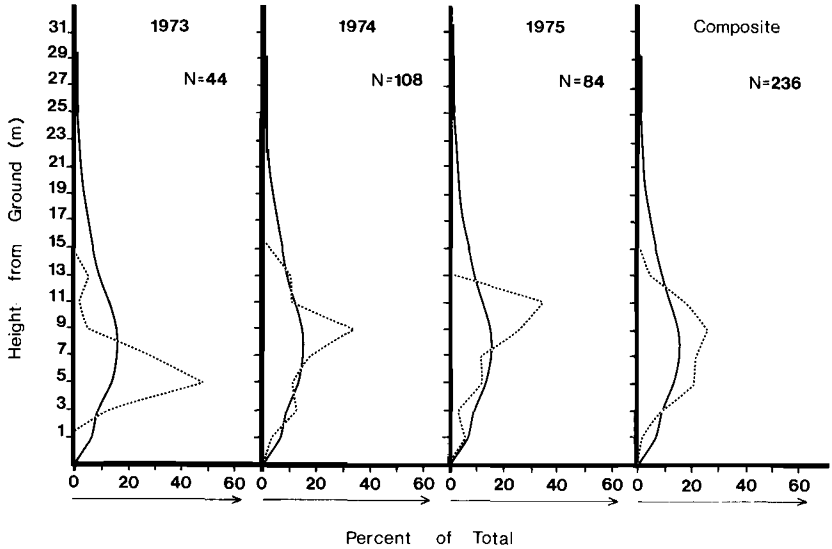

FIGURE 19. Solitary Vireo use (dotted line) of the available foliage volume (solid line) by height on the strip cut plot. The composite combines all observations for the study.

The use profiles of the Yellow-rumped Warbler indicated an overuse of the lower reaches and lower bulge on the silviculturally cut plot (Fig. 22). In 1974 the Yellow-rumped Warbler greatly overused the foliage at 5-m but was not observed at this height in 1975. The Yellow-rumped Warbler's composite profile showed an overuse of the lower reaches and no use of the spire.

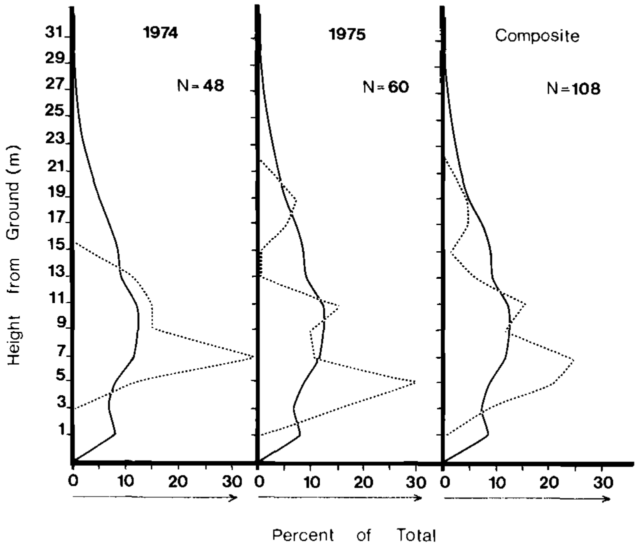

FIGURE 20. Solitary Vireo use (dotted line) of the available foliage volume (solid line) by height on the silviculturally cut plot. The composite combines all observations for 1974 and 1975.

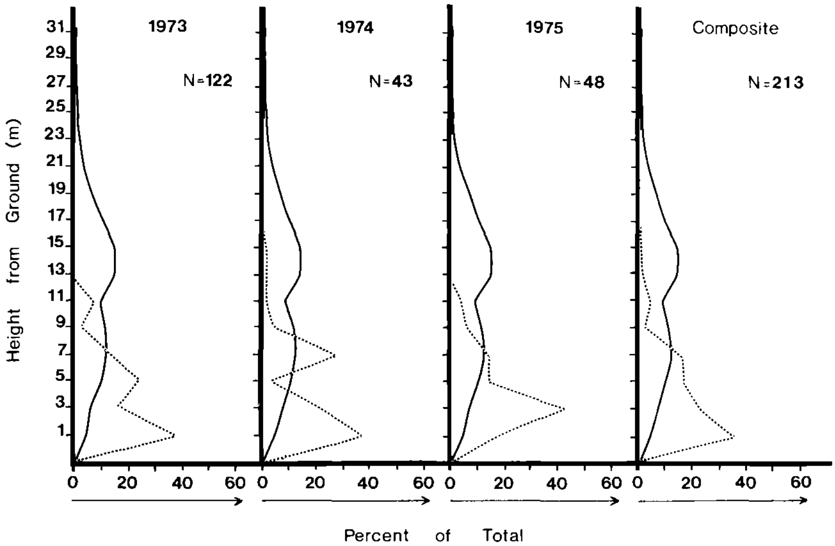

FIGURE 21. Solitary Vireo use (dotted line) of the available foliage volume (solid line) by height on the control plot. The composite combines all observations for the study.

The use profiles of the Grace's Warbler varied considerably between years and study plots. In 1975 the Grace's Warbler moved 4 m higher in the trees on the severely thinned plot ($P \leq 0.05$) (Fig. 23). The Grace's Warbler's composite profile showed an overuse of the 7- to 13-m range and the 19-m height class. In addition, the Grace's Warbler was not observed in the 0- to 4-m region close to the ground. On the strip cut plot the warbler increased its mean height by 7 m in

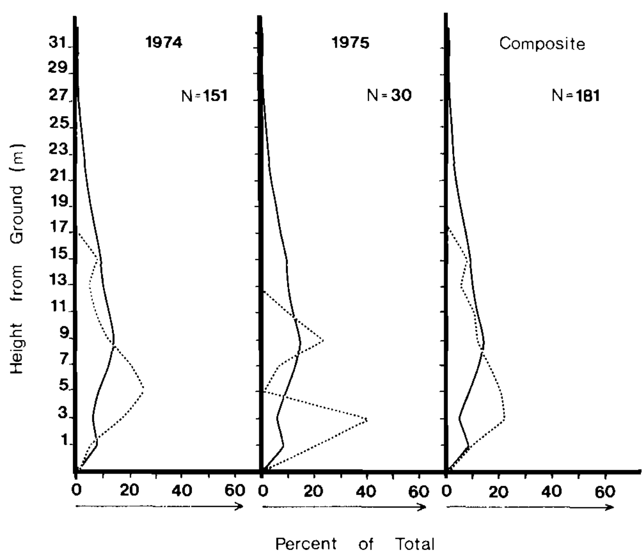

FIGURE 22. Yellow-rumped Warbler use (dotted line) of the available foliage volume (solid line) by height on the silviculturally cut plot. The composite combines all observations for 1974 and 1975.

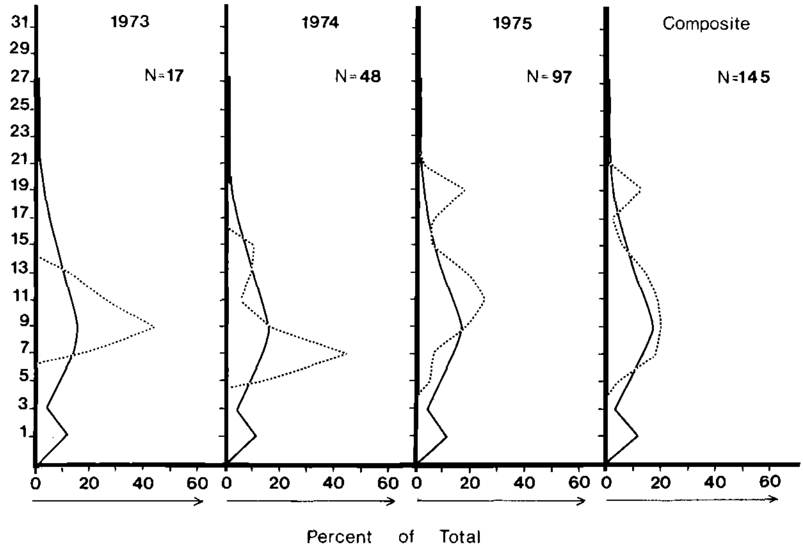

FIGURE 23. Grace's Warbler use (dotted line) of the available foliage volume (solid line) by height on the severely thinned plot. The composite combines all observations for the study.

1974 as compared to 1973 (Fig. 24). The 5- to 7-m range so heavily overused by the Grace's Warbler in 1973 was not used by the warbler in 1974. In 1975 the Grace's Warbler expanded its use range downward, making greater use of the bulge. On the silviculturally cut plot, the Grace's Warbler expanded its use range both higher and lower in the trees while underusing the area that was overused the year before (Fig. 25). In 1975 the Grace's Warbler exhibited a dichotomous

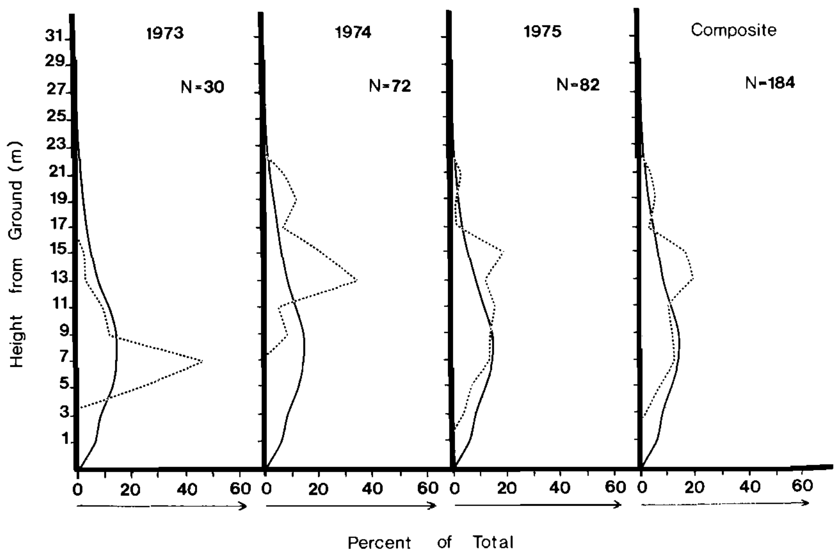

FIGURE 24. Grace's Warbler use (dotted line) of the available foliage volume (solid line) by height on the strip cut plot. The composite combines all observations for the study.

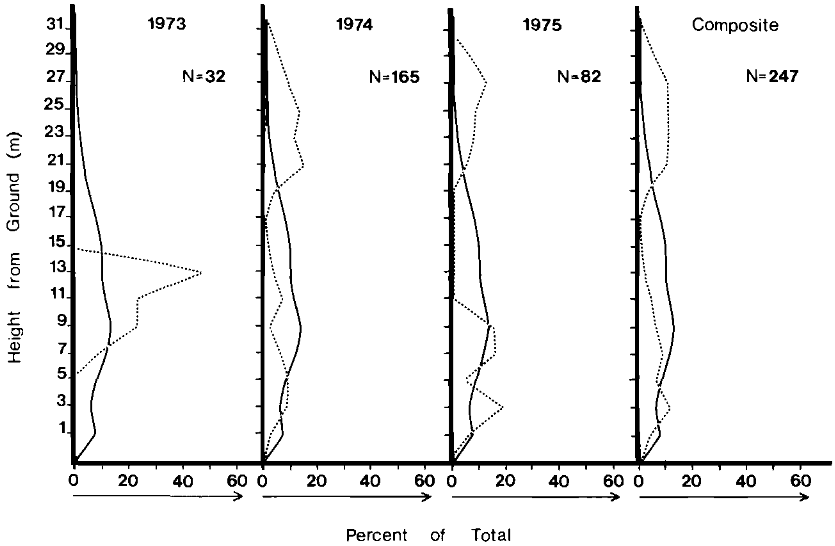

FIGURE 25. Grace's Warbler use (dotted line) of the available foliage volume (solid line) by height on the silviculturally cut plot. The composite combines all observations for 1974 and 1975.

use profile by not using the 11- to 19-m area. The composite bird profile showed that this warbler overused the 21- to 31-m region and underused the 5- to 29-m region. The Grace's Warbler on the control plot shifted its use range upward by 10 m and showed a statistically significant difference in mean height of 6.5 m ($P \leq 0.05$) in 1974 when compared to its profile in 1973 (Fig. 26). In 1975 the Grace's

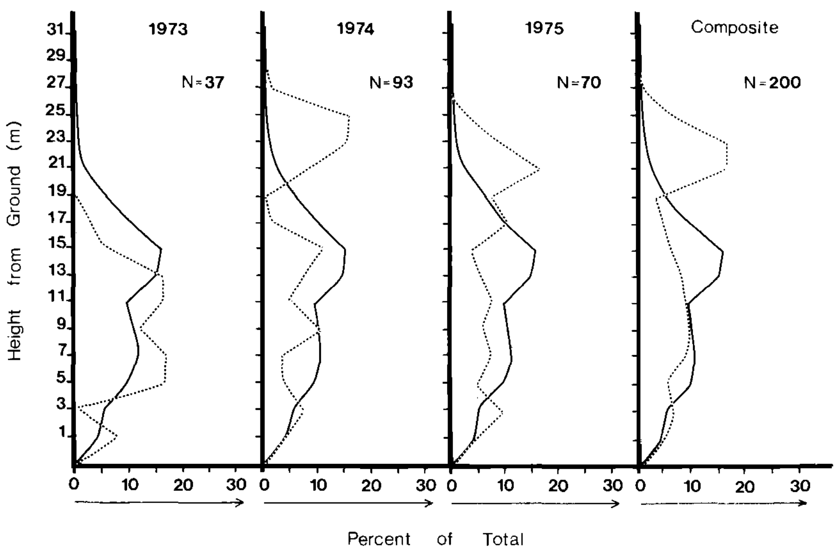

FIGURE 26. Grace's Warbler use (dotted line) of the available foliage volume (solid line) height on the control plot. The composite combines all observations for the study.

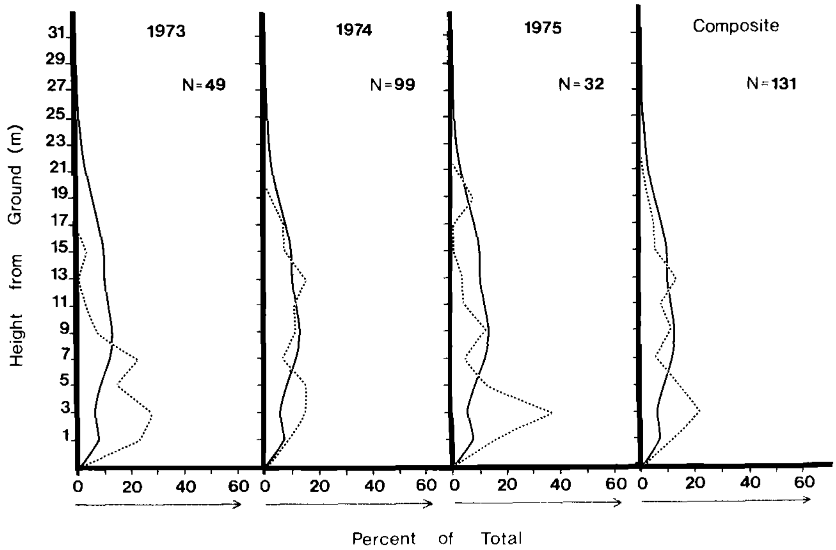

FIGURE 27. Gray-headed Junco use (dotted line) of the available foliage volume (solid line) by height on the silviculturally cut plot. The composite combines all observations for 1974 and 1975.

Warbler's use profile remained similar to its 1974 profile. The Grace's Warbler's three-year composite profile indicated an overuse of the 21- to 27-m region.

There were shifts in foliage use by the Gray-headed Junco between years on the silviculturally cut and control plots. The Gray-headed Junco moved higher in the trees all three years on the silviculturally cut plot (Fig. 27). The composite use pattern of the Gray-headed Junco for the two years after treament showed

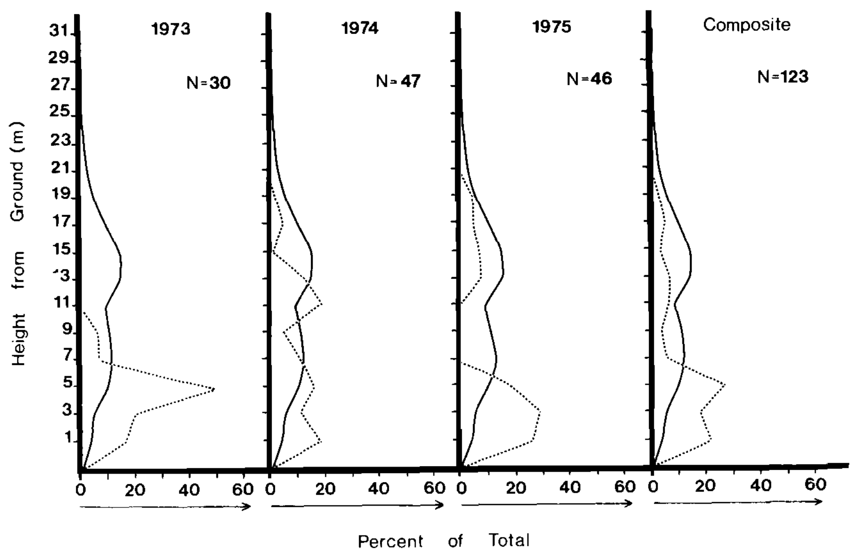

FIGURE 28. Gray-headed Junco use (dotted line) of the available foliage volume (solid line) by height on the control plot. The composite combines all observations for the study.

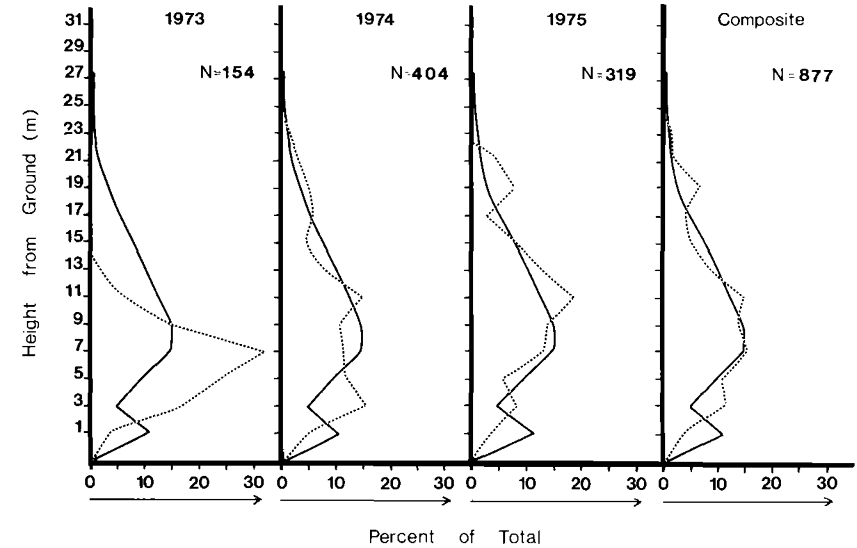

FIGURE 29. Total bird use (dotted line) of the available foliage volume (solid line) by height on the severely thinned plot. The composite combines all observations for the study.

that the Junco overused the 1- to 5-m height range. In 1974 on the control plot, the Gray-headed Junco moved higher in the trees whereas in 1975 it overused the 1- to 5-m region and made no use of the 7- to 11-m area (Fig. 28). The Gray-headed Junco consistently overused the 1- to 5-m region during the study.

The entire bird communities on the four study plots exhibited shifts in foliage utilization. During the study there were dramatic shifts in how the avian com-

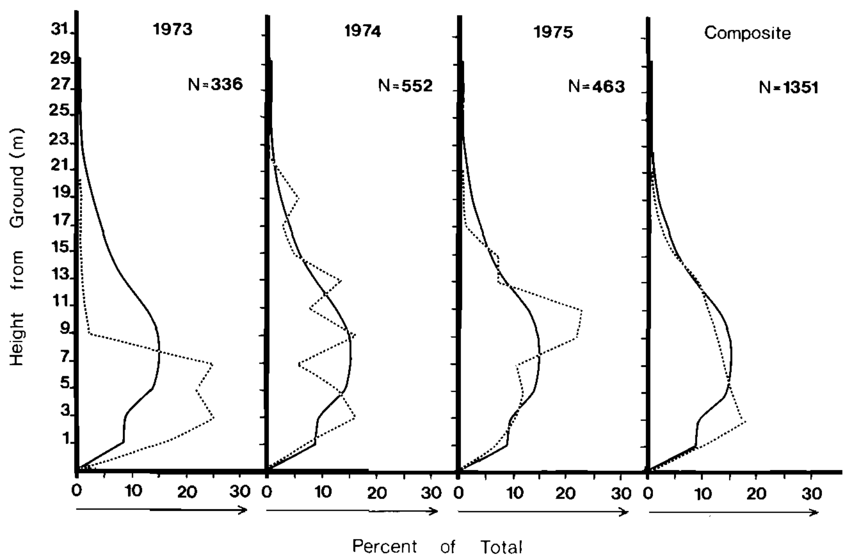

FIGURE 30. Total bird use (dotted line) of the available foliage volume (solid line) by height on the strip cut plot. The composite combines all observations for the study.

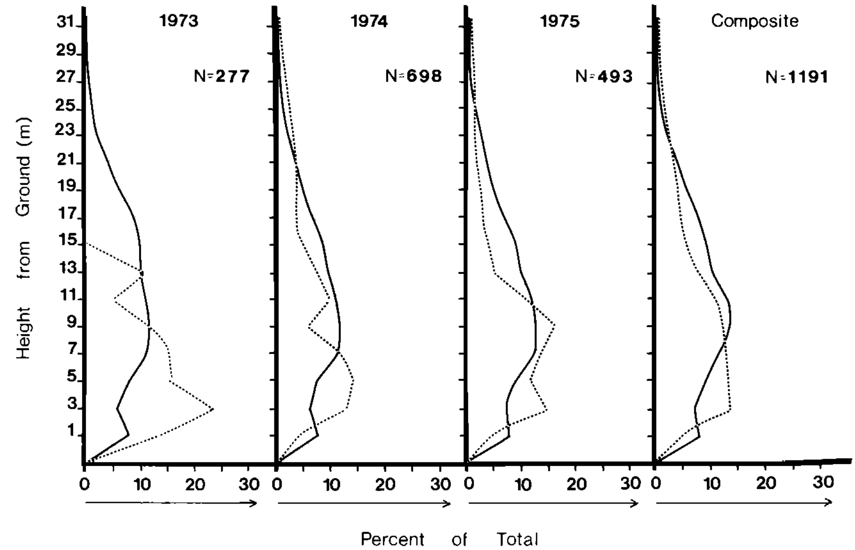

FIGURE 31. Total bird use (dotted line) of the available foliage volume (solid line) by height on the silviculturally cut plot. The composite combines all observations for 1974 and 1975.

munity utilized the foliage on the severely thinned and strip cut plots. These differences, however, averaged out the composite profiles (Figs. 29, 30). On the severely thinned plot, the bird community heavily overused the 3- to 7-m region whereas in 1974 the bird community shifted upward almost using the foliage in relation to its availability. In 1975 the avian community overused the 11- to 13- and 19- to 21-m height classes. The community profile on the strip cut plot showed

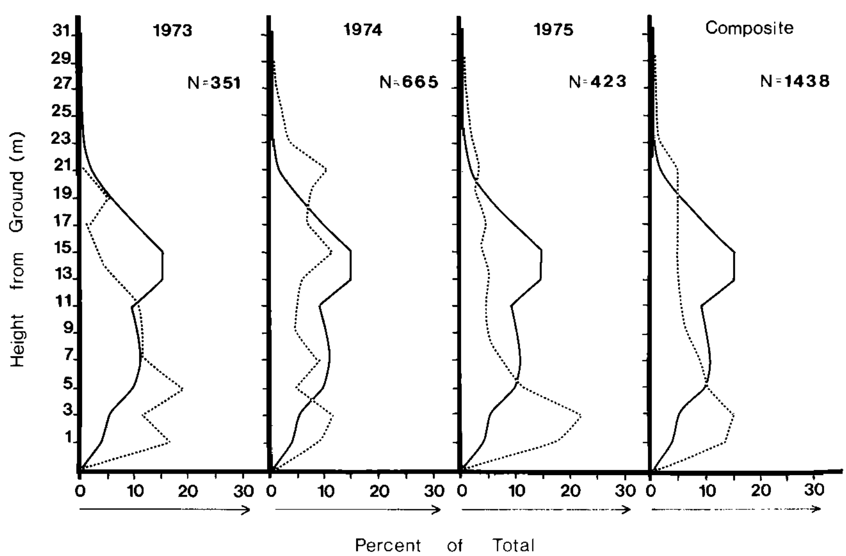

FIGURE 32. Total bird use (dotted line) of the available foliage volume (solid line) by height on the control plot. The composite combines all observations for the study.

TABLE 14
FOLIAGE USE INDICES[a] FOR NINE BIRD SPECIES

Bird species	Plot	1973	1974	1975
Western Wood Pewee	Strip	2.69	2.88	1.93
Mountain Chickadee	Silv.	—	1.15	1.45
	Cntrl.	—	1.65	2.84
White-breasted Nuthatch	S. Thn.	3.54	1.96	2.98
	Strip	4.16	1.54	2.79
	Silv.	2.58	5.44	9.67
	Cntrl.	1.88	2.59	1.54
Pygmy Nuthatch	Silv.	—	2.18	1.69
	Cntrl.	1.63	2.52	1.59
Western Bluebird	S. Thn.	—	4.98	4.11
	Strip	3.26	2.87	3.70
	Silv.	3.29	4.10	3.52
Solitary Vireo	S. Thn.	—	1.51	1.81
	Strip	2.79	1.40	1.81
	Silv.	—	1.96	1.68
	Cntrl.	2.90	3.03	2.97
Yellow-rumped Warbler	Silv.	—	1.52	2.52
Grace's Warbler	S. Thn.	2.64	2.54	1.95
	Strip	2.70	2.75	1.25
	Silv.	2.60	1.54	1.73
	Cntrl.	1.31	1.82	1.53
Gray-headed Junco	Silv.	3.27	9.54	2.22
	Cntrl.	2.19	1.72	2.52

[a] All indices multiplied by 100.

that the birds underused the foliage above 7 m and grossly overused the foliage between 0 and 7 m in 1973. In 1974 the bird community shifted higher into the trees and underused the 7- and 11-m height classes. However, in 1975 the bird community on the strip cut plot greatly overused the 9- to 11-m interval. On the silviculturally cut plot, the bird community profile approximated the foliage profile in 1974 and 1975 (Fig. 31). The bird community on the control plot underused the foliage profile between 7- to 19-m (Fig. 32). The 13- to 17-m region was underused whereas the 0- to 3-m region was overused by the birds all three years of the study. An examination of the avian community profiles on the treated areas showed that although there were yearly fluctuations the composite bird use profiles reasonably approximated the foliage profiles. In contrast, the bird community on the control study plot underused the 7- to 19-m region on the composite profile.

Foliage profile cluster analyses.—The coefficient matrices for the 15 species on the four study plots were subjected to cluster analysis. The species on the study plots clustered according to the distributions of their foliage use profiles. The species on all areas divided into four to seven groups ranging from those that used the lower branches (e.g., Western Wood Pewee, Solitary Vireo) to those that primarily used the upper bulge area and tips of the trees (e.g., Grace's Warbler, Violet-green Swallow).

Foliage use index.—The foliage use index (*FUI*) was used mathematically to

TABLE 15
MEAN TERRITORY SIZES (ha) OF NINE BIRD SPECIES

Species	Plot	1973 *n*	1973 Mean	1973 SD	1974 *n*	1974 Mean	1974 SD	1975 *n*	1975 Mean	1975 SD
Western Wood Pewee	Strip	2	0.28	0.01	3	0.35	0.19	3	0.22	0.12
Mountain Chickadee	Silv.[a]	—	—	—	2	0.27	0.05	1	1.95	0.00
	Cntrl.	—	—	—	2	1.15	0.33	1	1.53	0.00
White-bd. Nuthatch	S. Thn.[a]	2	1.20	0.28	3	0.43	0.11	2	0.55	0.09
	Strip	1	1.38	0.00	4	0.82	0.30	4	1.40	0.48
	Silv.	1	0.43	0.00	3	0.78	0.24	5	1.05	0.36
	Cntrl.	1	0.37	0.00	3	0.56	0.11	1	0.53	0.00
Pygmy Nuthatch	Silv.	—	—	—	5	0.60	0.15	5	0.44	0.19
	Cntrl.[a]	3	0.61	0.11	5	0.84	0.08	4	0.45	0.06
Western Bluebird	S. Thn.[a]	—	—	—	3	0.72	0.05	1	0.57	0.00
	Strip	2	0.74	0.13	4	0.57	0.25	5	0.79	0.33
	Silv.	2	0.56	0.06	3	0.63	0.12	2	0.61	0.15
Solitary Vireo	S. Thn.[a]	—	—	—	2	0.68	0.26	2	1.30	0.09
	Strip	2	0.53	0.21	3	0.37	0.10	2	0.47	0.03
	Silv.[a]	—	—	—	2	0.71	0.17	2	0.33	0.07
	Cntrl.	1	0.48	0.00	2	0.53	0.04	2	0.47	0.02
Yellow-rd. Warbler	Silv.	—	—	—	6	0.39	0.18	3	0.43	0.13
Grace's Warbler	S. Thn.	2	0.75	0.07	2	0.60	0.06	3	0.55	0.10
	Strip	3	0.24	0.10	7	0.30	0.18	3	0.27	0.10
	Silv.	4	0.50	0.11	6	0.40	0.17	6	0.46	0.15
	Cntrl.	2	0.48	0.05	4	0.83	0.25	2	0.43	0.13
Gray-headed Junco	Silv.	3	0.41	0.17	6	0.62	0.20	5	0.53	0.14
	Cntrl.	3	0.65	0.22	6	0.57	0.24	4	0.68	0.11

[a] Differences between years significant ($P \leq 0.05$) by F-test.

express how the bird species used the available foliage. It is the calculation of the Euclidean distance between the composite foliage configuration and the individual species profiles. As the species become specialists, the index number increases. In contrast, the index number decreases when the birds utilize the foliage in closer proportions to its availability. In other words, generalists will have a low index value.

The indices indicate that foliage utilization by the bird species in the ponderosa pine forest fluctuated between years (Table 14). Seven bird species on three different plots (Western Wood Pewee on the strip cut plot, White-breasted Nuthatch on the control plot, Pygmy Nuthatch on the control plot, Western Bluebird on the silviculturally cut plot, Solitary Vireo on the control plot, Grace's Warbler on the strip cut and control plots, and Gray-headed Junco on the silviculturally cut plot) were more selective of foliage height in 1974 than in 1973 and 1975. In contrast, five bird species on three different study plots (White-breasted Nuthatch on the severely thinned and strip cut plots, Western Bluebird and Solitary Vireo on the strip cut plot, Grace's Warbler and Gray-headed Junco on the silviculturally cut plot) were less selective of specific foliage heights in 1974 than they were in either 1973 or 1975. The White-breasted Nuthatch on the silviculturally cut plot was the only species to increase its *FUI* during the course of the study. The

TABLE 16
MEAN WEIGHT, CONSUMING BIOMASS, AND EXISTENCE ENERGY REQUIREMENTS PER INDIVIDUAL DURING THE BREEDING SEASON

Species	Mean wt. (g) (n = 5)	SD	Con. bio. (g)	Existence energy (kcal/day)		
				1973	1974	1975
Pickers and gleaners						
Grace's Warbler	7.8	0.4	3.7	7.9	7.7	8.1
Red-faced Warbler	9.9[a]	0.8	4.3	8.9	8.7	9.1
House Wren	10.1	0.7	4.3	9.0	8.9	9.2
Pygmy Nuthatch	10.5	0.8	4.4	9.2	9.0	9.4
Mountain Chickadee	11.6	0.9	4.7	9.7	9.5	10.0
Yellow-rumped Warbler	14.1	1.0	5.3	10.8	10.6	11.1
Solitary Vireo	15.6	0.5	5.7	11.5	11.3	11.7
Western Tanager	30.4	1.7	8.7	16.7	16.4	17.0
Hepatic Tanager	37.8[a]	1.2	10.0	18.9	18.6	19.2
Ground feeders						
Chipping Sparrow	12.6	0.3	5.0	10.2	10.0	10.4
Rock Wren	16.9	0.4	6.0	12.0	11.8	12.3
Gray-headed Junco	20.2	1.2	6.7	13.2	13.0	13.5
Hermit Thrush	28.5[a]	2.3	8.3	16.1	15.8	16.4
Robin	81.8	2.3	16.3	29.3	29.0	29.8
Mourning Dove	122.7	11.1	21.0	37.1	36.7	37.7
Aerial feeders						
Broad-tailed Hummingbird	3.5	0.2	2.2	5.1	5.0	5.2
Western Flycatcher	11.8[a]	1.5	4.8	9.8	9.7	10.1
Western Wood Pewee	14.2	1.5	5.4	10.9	10.7	11.1
Violet-green Swallow	14.2	1.0	5.4	10.9	10.7	11.1
Say's Phoebe	21.0[a]	—	6.9	13.5	13.3	13.8
Western Bluebird	25.3	1.3	7.7	15.0	14.8	15.4
Common Nighthawk	51.2	2.8	12.1	22.4	22.1	22.8
Hammerers and tearers						
White-breasted Nuthatch	18.4	0.6	6.3	12.6	12.4	12.9
Black-headed Grosbeak	44.1[a]	1.6	11.0	20.3	20.3	21.0
Hairy Woodpecker	61.8	2.0	13.6	24.6	24.6	25.4
Acorn Woodpecker	65.8[a]	—	14.2	25.6	25.6	26.3
Steller's Jay	102.7	9.6	18.7	33.1	33.1	34.0
Common Flicker	112.8	11.4	19.9	34.9	34.9	35.9

[a] Weights for these species were supplemented from the following sources: Poole (1938), Miller (1951), and Salt (1957).

Grace's Warbler on the severely thinned plot was the only species to decrease its *FUI* during the course of the study. The Mountain Chickadee on the silviculturally cut and control plots became a greater specialist in 1975 than in 1974. The Solitary Vireo increased its *FUI* on the severely thinned plot but decreased on the silviculturally cut plot between 1974 and 1975. The Western Bluebird on the severely thinned plot was more of a generalist in 1975 than in 1974, whereas the Yellow-rumped Warbler was more of a specialist in 1975 than in 1974.

Bulge use.—Concurrently with the changing use profiles, the use of the bulge also shifted. The amount of utilized foliage volume per territory increased with increased utilization of the bulge, all other factors remaining equal. The bulge specifically is that region of the foliage profile which encompasses 70% of the

TABLE 17
STANDING CROP BIOMASS AND CONSUMING BIOMASS OF THE BREEDING BIRDS OF THE STUDY AREAS

Plot	Year	Standing crop biomass (g/ha)	Consuming biomass (g/ha)
Clear cut	1973	17.2	5.0
	1974	21.1	6.1
	1975	32.3	7.9
Severely thinned	1973	91.6	23.9
	1974	171.7	39.8
	1975	131.9	31.9
Strip cut	1973	103.1	27.4
	1974	218.7	59.2
	1975	147.4	42.3
Silviculturally cut	1973	92.2	25.7
	1974	178.5	51.5
	1975	174.1	48.8
Control	1973	67.0	20.2
	1974	182.5	48.5
	1975	139.9	35.4

foliage. Therefore, as species shift upward into the bulge from the spire, the amount of foliage within territories increased. Conversely, foliage volume per territory decreased when the birds moved above or below the bulge. The amount of foliage per territory would decrease even with the increased bulge use either when territory size was greatly reduced or when there was a large contraction of the foliage use range.

TERRITORY SIZE

Territory size was examined for nine species (Table 15). Yearly differences in territory size were statistically significant (F-test, $P \leq 0.05$) in only six of the 23 cases. Territory size varied considerably between years, species, and study plots.

ENERGY REQUIREMENTS

Standing crop biomass and consuming biomass on each of the study sites were calculated using a mean weight (Table 16) and a density (Tables 13–15) for each species. Both standing crop and consuming biomass were the smallest on the clear cut plot (Table 17). In contrast, the largest standing crop and consuming biomass were found on the strip cut plot in 1973 (103.1 g/ha, 27.4 g/ha) and 1974 (218.7 g/ha, 59.2 g/ha) and on the silviculturally cut plot in 1975 (174.1 g/ha, 48.8 g/ha).

Existence energy requirements for individual species varied from a high of 37.7 kcal/day for the Mourning Dove to a low of 5.2 kcal/day for the Broad-tailed Hummingbird in 1973 (Table 16). These two species also had the largest and smallest existence energy requirements in both 1974 and 1975.

Total energy flow in 1973 was highest on the strip cut plot with a value of 52.7 kcal/ha-day and lowest on clear cut plot with a value of 9.6 kcal/ha-day (Table 18). In 1974 the largest energy flow was again on the strip cut (112.8 kcal/ha-day) and the smallest on the clear cut plot (11.6 kcal/ha-day) (Table 19). However, in

TABLE 18
PARTICIPATION OF INDIVIDUAL SPECIES IN ENERGY FLOW THROUGH THE BIRD COMMUNITY IN TERMS OF EXISTENCE ENERGY (kcal/ha-day) IN 1973

	Study plots				
	C. cut	S. Thn.	Strip	Cntrl.	Silv. (PT)
Species (guilds)					
Mountain Chickadee (PG,CD)	—	0.7	—	—	—
Pygmy Nuthatch (PG,CD)	—	—	—	6.2	3.5
House Wren (PG,CD)	—	—	1.0	—	1.0
Solitary Vireo (PG,FN)	—	2.2	3.4	0.9	—
Yellow-rumped Warbler (PG,FN)	—	—	1.6	—	—
Grace's Warbler (PG,FN)	—	1.5	3.0	3.0	4.4
Red-faced Warbler (PG,GN)	—	—	—	1.0	1.3
Western Tanager (PG,FN)	—	1.3	2.5	—	2.5
Rock Wren (GF,GN)	3.0	3.2	2.3	—	—
Robin (GF,FN)	—	9.9	7.7	—	—
Hermit Thrush (GF,GN)	—	—	—	0.6	—
Gray-headed junco (GF,GN)	1.3	6.5	4.0	6.0	8.4
Rufous-sided Towhee (GF,FN)	5.3	—	—	—	—
Chipping Sparrow (GF,FN)	—	3.1	2.3	—	1.5
Common Flicker (HT,CD)	—	5.3	4.0	5.3	5.3
Hairy Woodpecker (HT,CD)	—	2.8	2.8	3.7	3.7
Steller's Jay (HT,FN)	—	—	5.0	—	5.0
White-br. Nuthatch (HT,CD)	—	3.3	2.8	1.9	1.9
Black-headed Grosbeak (HT,FN)	—	—	—	—	1.5
Broad-td. Hummingbird (AF,FN)	—	—	0.8	—	—
Western Flycatcher (AF,CD)	—	—	—	3.0	1.5
Western Wood Pewee (AF,FN)	—	1.6	4.5	—	1.2
Violet-green Swallow (AF,CD)	—	—	—	4.9	3.3
Western Bluebird (AF,CD)	—	4.5	5.1	3.4	4.0
Foraging guilds					
Pickers and gleaners (PG)	—	5.6	11.5	11.0	12.7
Ground feeders (GF)	9.6	22.6	16.2	6.6	10.0
Hammerers and tearers (HT)	—	11.4	14.6	10.9	17.5
Aerial feeders (AF)	—	6.1	10.3	11.2	9.9
Nesting guilds					
Cavity and depression (CD)	—	16.7	15.7	28.4	24.1
Foliage nesters (FN)	5.3	19.4	30.8	3.8	16.2
Ground nesters (GN)	4.3	9.6	6.2	7.5	9.8
Totals	9.6	45.7	52.7	39.7	50.1

1975 the highest energy flow was on the silviculturally cut plot (97.1 kcal/ha-day) whereas the smallest was still on the clear cut plot (15.1 kcal/ha-day) (Table 20).

The birds which comprise the primary energy component in terms of existence energy varied between years and study plots. The analyses of energy flow patterns were based upon the total breeding avifaunas of the study areas. On the severely thinned plot four species (Robin, Gray-headed Junco, Common Flicker, and Western Bluebird) utilized 57% of the total energy flow in 1973. These same four species plus the Steller's Jay and Western Wood Pewee accounted for 57% of the total energy flow on the strip cut plot. On the control plot there were again four species (Common Flicker, Gray-headed Junco, Pygmy Nuthatch, and Violet-

TABLE 19
PARTICIPATION OF INDIVIDUAL SPECIES IN ENERGY FLOW THROUGH THE BIRD COMMUNITY IN TERMS OF EXISTENCE ENERGY (kcal/ha-day) IN 1974

	Study plots				
	C. cut	S. Thn.	Strip	Silv.	Cntrl.
Species (guilds)					
Mountain Chickadee (PG,CD)	—	—	4.3	2.9	3.6
Pygmy Nuthatch (PG,CD)	—	1.0	1.4	6.8	6.8
Solitary Vireo (PG,FN)	—	3.4	6.8	3.4	1.7
Yellow-rumped Warbler (PG,FN)	—	—	1.6	8.0	1.6
Grace's Warbler (PG,FN)	—	2.3	7.2	7.2	4.6
Red-faced Warbler (PG,GN)	—	—	—	—	2.0
Western Tanager (PG,FN)	—	—	2.5	5.6	—
Hepatic Tanager (PG,FN)	—	—	2.8	—	—
Mourning Dove (GF,FN)	—	11.0	—	—	5.5
Rock Wren (GF,GN)	3.2	1.8	4.9	—	—
Robin (GF,FN)	—	6.5	10.9	4.4	—
Hermit Thrush (GF,GN)	—	—	—	0.6	1.2
Gray-headed Junco (GF,FN)	1.3	4.4	6.9	14.6	11.7
Rufous-sided Towhee (GF,FN)	6.2	—	—	—	—
Chipping Sparrow (GF,FN)	—	3.0	6.0	3.7	0.8
Common Flicker (HT,CD)	—	5.2	6.6	5.2	5.2
Hairy Woodpecker (HT,CD)	—	3.7	7.4	3.7	3.7
Steller's Jay (HT,FN)	—	12.4	12.4	10.0	14.9
White-br. Nuthatch (HT,CD)	—	5.6	5.6	14.6	6.6
Black-headed Grosbeak (HT,FN)	—	—	1.5	3.0	4.6
Common Nighthawk (AF,GN)	—	3.3	3.3	—	3.3
Broad-td. Hummingbird (AF,FN)	—	2.6	3.7	1.3	2.2
Say's Phoebe (AF,FN)	—	—	2.0	—	—
Western Flycatcher (AF,CD)	—	—	—	2.5	3.3
Western Wood Pewee (AF,FN)	—	1.6	4.8	1.6	—
Violet-green Swallow (AF,CD)	—	—	1.6	4.8	4.8
Western Bluebird (AF,CD)	—	6.1	8.9	6.1	4.4
Mountain Bluebird (AF,CD)	0.8	—	—	—	—
Foraging guilds					
Pickers and gleaners (PG)	—	6.7	26.5	33.8	20.2
Ground feeders (GF)	10.8	26.7	28.6	23.3	19.2
Hammerers and tearers (HT)	—	26.9	33.4	26.5	34.9
Aerial feeders (AF)	0.8	13.6	24.3	16.3	18.1
Nesting guilds					
Cavity and depression (CD)	0.8	21.6	35.6	36.7	38.3
Foliage nesters (FN)	6.2	42.8	62.2	48.1	35.8
Ground nesters (GN)	4.5	9.5	15.0	15.2	18.2
Totals	11.6	73.9	112.8	100.0	92.3

green Swallow) accounting for 56% of the energy flux (in terms of existence energy). On the silviculturally cut plot (before treatment) the primary energy component consisted of five species (Grace's Warbler, Gray-headed Junco, Common Flicker, Steller's Jay, and Western Bluebird) which accounted for 54% of the total energy flow. Only three species, the Common Flicker, Gray-headed Junco, and Western Bluebird, were members of the primary energy component on all study areas.

TABLE 20
PARTICIPATION OF INDIVIDUAL SPECIES IN ENERGY FLOW THROUGH THE BIRD COMMUNITY IN TERMS OF EXISTENCE ENERGY (kcal/ha-day) IN 1975

	Study plots				
	C. cut	S. Thn.	Strip	Silv.	Cntrl.
Species (guilds)					
Mountain Chickadee (PG,CD)	—	0.8	—	2.2	1.5
Pygmy Nuthatch (PG,CD)	—	0.7	4.2	8.5	6.4
House Wren (PG,CD)	—	—	1.4	—	—
Solitary Vireo (PG,FN)	—	3.5	3.5	3.5	1.8
Yellow-rumped Warbler (PG,FN)	—	1.7	1.7	5.0	—
Grace's Warbler (PG,FN)	—	3.0	4.0	7.9	2.4
Red-faced Warbler (PG,GN)	—	—	—	—	0.7
Western Tanager (PG,FN)	—	—	2.6	3.9	2.6
Mourning Dove (GF,FN)	—	8.5	—	5.7	5.7
Rock Wren (GF,GN)	2.8	3.7	3.7	—	—
Robin (GF,FN)	1.5	4.5	4.5	4.5	—
Hermit Thrush (GF,GN)	—	—	—	—	1.9
Gray-headed Junco (GF,GN)	1.0	4.1	8.1	10.1	8.1
Rufous-sided Towhee (GF,FN)	7.2	—	—	—	—
Chipping Sparrow (GF,FN)	—	1.6	3.1	2.3	1.6
Common Flicker (HT,CD)	2.7	5.4	5.4	5.4	5.4
Acorn Woodpecker (HT,CD)	—	4.0	—	—	—
Hairy Woodpecker (HT,CD)	—	2.0	3.8	3.8	3.8
Steller's Jay (HT,FN)	—	5.1	5.1	5.1	10.2
White-br. Nuthatch (HT,CD)	—	3.9	7.7	9.7	1.9
Black-headed Grosbeak (HT,FN)	—	—	1.6	3.1	3.1
Common Nighthawk (AF,GN)	—	3.4	3.4	3.4	3.4
Broad-td. Hummingbird (AF,FN)	—	2.4	2.4	0.8	0.8
Western Flycatcher (AF,CD)	—	—	—	1.5	1.5
Western Wood Pewee (AF,FN)	—	1.7	5.0	0.8	—
Violet-green Swallow (AF,CD)	—	—	1.7	4.2	4.2
Western Bluebird (AF,CD)	—	2.3	11.5	5.8	2.3
Foraging guilds					
Pickers and gleaners (PG)	—	9.7	17.3	30.9	15.3
Ground feeders (GF)	12.4	22.2	19.4	22.6	17.2
Hammerers and tearers (HT)	2.7	20.2	23.6	27.1	24.5
Aerial feeders (AF)	—	9.8	24.0	16.5	12.2
Nesting guilds					
Cavity and depression (CD)	2.7	18.9	35.7	41.0	27.0
Foliage nesters (FN)	8.7	31.8	33.3	42.5	28.1
Ground nesters (GN)	3.7	11.1	15.2	13.6	14.0
Totals	15.1	61.8	84.2	97.1	69.1

In 1974 the primary energy components consisted of several more species, because of the general increase in density and diversity. The smallest total energy flow was on the clear cut plot and the largest energy flow was on the strip cut plot. On the severely thinned plot the same four species as in 1973, plus the White-breasted Nuthatch, Mourning Dove, and Steller's Jay, accounted for 69% of the total energy flow. On the strip cut plot five of the six species in 1973 (minus the Western Wood Pewee), plus five additional species (White-breasted Nuthatch, Solitary Vireo, Chipping Sparrow, Hairy Woodpecker, and Steller's Jay), accounted for 55% of the total energy flow on the control plot. Four species (Common Flicker, Western Bluebird, Gray-headed Junco, and Steller's Jay) were members of the primary energy components on all the forested plots in 1974.

The primary energy components on all the forested plots in 1975 consisted of between five and seven species of birds. The lowest energy flux in terms of bird communities was on the clear cut plot, whereas the highest energy flux was on the silviculturally cut plot. On the severely thinned plot seven species (White-breasted Nuthatch, Gray-headed Junco, Robin, Mourning Dove, Common Flicker, Steller's Jay, and Acorn Woodpecker) accounted for 57% of the total energy flux. Seven species (White-breasted Nuthatch, Gray-headed Junco, Common Flicker, Steller's Jay, Western Bluebird, Robin, and Western Wood Pewee) accounted for 56% of the energy flow on the strip cut plot. On the control plot five species (Pygmy Nuthatch, Gray-headed Junco, Mourning Dove, Common Flicker, and Steller's Jay) accounted for 52% of the total energy flow and on the silviculturally cut plot the same five species plus the Grace's Warbler, Western Bluebird, and White-breasted Nuthatch comprised 60% of the energy flow. The Gray-headed Junco, Steller's Jay, and Common Flicker were members of the primary energy component on all plots with foliage.

Body Weight

Most of the species (23 of 28) clustered in the lower half of the weight range for each guild (Table 16). The pickers and gleaners and aerial feeders exhibited a fairly contracted body weight range. The pickers and gleaners ranged from 7.8 to 37.8 g, whereas the aerial feeders ranged from 3.5 to 51.2 g. On the other hand, hammerers and tearers and ground feeders have a very wide range of weight. The hammerers and tearers ranged from 18.4 g to 112.8 g, and the ground feeders from 12.6 to 122.8 g.

DISCUSSION

Community Composition

Species numbers and densities.—Comparisons of different bird communities in the ponderosa pine forest in Arizona are limited to those by Haldeman et al. (1973) who reported 27 species in similar areas of northern Arizona, and by Balda (1969) who recorded 31 species of breeding birds in the Chiricahua Mountains of southeastern Arizona. These numbers contrast with the high of 22 species in this study found on the strip cut plot in 1974, and an overall number of 28 breeding species. Balda (1969) recorded eight species in the Chiricahua Mountains found in the present study (Brown Creeper; Whip-poor Will, *Caprimulgus vociferus*; Virginia's Warbler, *Vermivora virginiae*; Band-tailed Pigeon, *Columba fasciata*; Coues' Flycatcher, *Contopus pertinax*; Mexican Junco, *Junco phaeonotus*; Olive Warbler, *Peucedramus taeniatus*; Mexican Chickadee, *Parus sclateri*; and Pygmy Owl, *Glaucidium gnoma*). The Mexican Junco and the Mexican Chickadee are replaced by ecological equivalents, the Gray-headed Junco and the Mountain Chickadee. The Brown Creeper, Virginia's Warbler, and Pygmy Owl are known to breed in the ponderosa pine forest of northern Arizona. The remaining species (Coues' Flycatcher, Olive Warbler, and Band-tailed Pigeon) are found only in the ponderosa pine forests of southern Arizona or in different habitats in northern

Arizona. Thus the species composition of the ponderosa pine forest in Arizona varies from area to area but remains fairly similar in overall species composition.

There are large differences in densities among the studies done by Snyder (1950), Balda (1969), Haldeman et al. (1973) and this study. Balda (1969) reported 336 prs/40 ha whereas Haldeman et al. (1973) reported 232 prs/40 ha. The breeding bird densities on our forested study plots ranged from 57.8 prs/40 ha on the severely thinned plot in 1973 to 162.8 prs/40 ha on the strip cut plot in 1974. On the control plot, the breeding bird densities ranged from 63.0 prs/40 ha in 1973 to 132.8 prs/40 ha in 1974. Snyder (1950) reported a density of 102.0 prs/40 ha in Colorado. These disparities can be attributed to certain species that had high densities in the studies by Balda and Haldeman et al., which were present in lower densities or not present at all in this study. In the Chiricahuas these species were Olive Warbler, Robin, Brown Creeper, Common Flicker, House Wren, Steller's Jay, Pygmy Nuthatch, and Mexican Junco. Haldeman et al. (1973) reported high densities of the Violet-green Swallow, Mountain Chickadee, Robin, Pine Siskin (*Carduelis pinus*), Hermit Thrush, and Brown Creeper. These differences in densities reflect the greater number of species found in the Chiricahuas plus possible differences in productivity between the study sites.

There are major differences in community composition between the breeding bird communities in eastern and western coniferous forests (Mengel 1970, Wiens 1975). Various warbler species are important constituents of many coniferous forests in eastern North American comprising more than half the individuals present in a stand. In contrast, warblers in most western coniferous forests account for less than 10% of the individuals (Wiens 1975). Only 7–20% of the total breeding bird densities on the silviculturally cut and control plots were contributed by the parulids. Thus both the relative and absolute densities of warblers are generally lower in western coniferous forests than in eastern coniferous forests.

However, the relative paucity of warblers in the West is only partially compensated for by a proportionate increase in other foliage foraging species in these western coniferous forests (Wiens 1975). Part of the difference is made up by other foliage gleaning species such as the Pygmy Nuthatch, Pine Siskin, Golden-crowned Kinglet (*Regulus satrapa*), and Ruby-crowned Kinglet (*Regulus calendula*) in various western coniferous forests, but rarely do more than two of these species occur with relatively high densities in any single forest. Wiens (1975) indicated that 49–61% of the total avian densities in eastern coniferous forests were made up of insectivorous foliage feeding species. In the west the insectivorous foliage feeders account for a much lower proportion of the total breeding bird densities. In the ponderosa pine forest (this study) 16–44% of the total breeding bird densities consisted of this same guild with the Pygmy Nuthatch on the silviculturally cut and control plots accounting for 10–21% of the breeding bird densities on these sites.

The possible reasons for the paucity of warbler species and the lack of a proportionate increase in other picking and gleaning species in the western coniferous forest are twofold. First, part of the reason for the relatively low numbers and densities of warbler species in the west may stem from biogeographic events and speciation processes (Mengel 1964, 1970). Second, the avian data suggest that there may be differences in the availability of prey resources in the different forest regions (Wiens 1975). Insect densities and diversities in the ponderosa pine forest might be expected to be lower because it is a structurally simple plant community. The ponderosa pine forest is a monoculture with its tree foliage located in relatively distinct horizontal strata. Moreover, the ponderosa pine forest is one of the driest coniferous forests in North America (Kuchler 1967). Thus, the paucity of foliage foraging insectivores in the ponderosa pine forest may be due to a combination of biogeographic events as well as a depauperate insect fauna.

Diversities.—Bird species diversities (H') found on all forested sites varied from 2.23 on the control plot in 1973 to 2.89 on the strip cut plot in 1974. The 1974 diversities (2.67–2.89) are similar to those reported by Balda (1969) and Haldeman et al. (1973) in other ponderosa pine forests inArizona (3.10 and 2.83, respectively).

The bird species diversities on the forested sites were relatively high because of the high degree of evenness (E) found in these bird communities (.91–.97). Evenness was high probably because of the relatively simple structure of the ponderosa pine forest. Those species which were able to survive in the ponderosa pine forest did so in relatively low numbers. Certain species (Grace's Warbler, Pygmy Nuthatch, and Gray-headed Junco) did reach high densities on certain study plots, but the vast majority of species had densities between 2.0 and 9.0 prs/40 ha. The fairly equal densities of most species were probably brought about by the relatively few successful life styles available to the bird species in the ponderosa pine forest, with its limited number of microhabitats.

Bird Species Diversity vs. Vegetational Complexity

The structure of avian communities and its relation to vegetational complexity has been studied by many investigators. Since birds are known actively to select their habitat on the basis of such proximate factors as features of the landscape, terrain, substrate, vegetative structure, or the arrangement of the vegetation (Hilden 1965, Wiens 1969), it is probable that foliage complexity is associated with structure of the avian community. Plant species composition is highly significant in regulating the composition of breeding bird communities in desert scrub habitats (Tomoff 1974). Bird species diversity (BSD) in deciduous forests has been correlated with foliage height diversity (MacArthur and MacArthur 1961, MacArthur et al. 1962, MacArthur et al. 1966, Recher 1969, Karr 1971, Karr and Roth 1971, Willson 1974). Other investigators have found little or no correlation between foliage height diversity and BSD (Balda 1969, Lovejoy 1972, Carothers et al. 1974, Pearson 1975). No correlation was evident between BSD and foliage height diversity, plant species diversity, or plant volume diversity in this study, except in 1974 when BSD was correlated (r = 0.95) with plant volume diversity, and in 1975 when BSD was correlated (r = 0.95) with plant species diversity. Willson (1974) showed that among forested areas no correlation of BSD with foliage height diversity was apparent. A significant correlation between BSD and a heterogeneity index (derived from the coefficient of variation of the distances between tree or shrubs and the central point of the point-quarter technique), was found in Texas, Illinois, and Delaware habitats (Roth 1976). There was no significant correlation between BSD and this parameter in the ponderosa pine forest. Perhaps such correlations are possible in dissimilar habitats because the between-

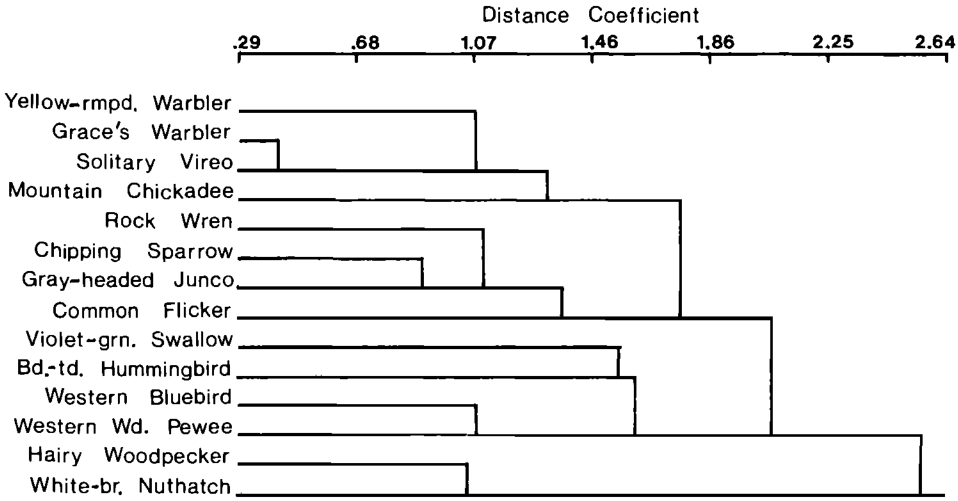

FIGURE 33. Dendrogram resulting from cluster analysis of the Euclidean distance matrix of composite behavior for the breeding birds of the severely thinned plot.

habitat effects are so great that differences in methodology and sample size are overshadowed. However, when comparing more homogeneous areas, the methodological differences are enough to influence the results. In this study, where all observations were made by a single observer, the methodological techniques were at least consistent. Moreover, BSD was very similar on all the forested plots in 1974 and 1975 (2.67–2.83) as were the heterogeneity indices (64.3–78.0). This similarity produced a fairly tight cluster of points which fit a little above the regression line presented by Roth (1976). In fact, his regression equation predicts that BSD in the ponderosa pine forest should range from 2.35 on the severely thinned plot to 2.61 on the control plot. We feel that significant correlations between BSD and habitat parameters in such similar habitats as we examined in the ponderosa pine forest are not possible because even after treatment the ponderosa pine forest is very homogeneous in plant species composition and in physiognomy. Needle bundles, twig configuration, bark pattern, and branch pattern are very similar from top to bottom of the foliage (Balda 1975). Thus factors such as intraspecific and interspecific competition rather than foliage configuration were probably of overriding importance in determining bird species diversity in the ponderosa pine forest.

Resource Partitioning and the Niche

Ecological isolation is particularly orderly and precise and especially noticeable in groups of ecologically related species (guilds) which commonly show nonoverlapping ranges on a resource span (Cody 1974). However, the coexistence of guild members may be achieved by the evolution of some minimal degree of difference in resource use. It is clear that most guild members differ from other species in the same guild by differences along a number of resource spans. In fact, in this study shifts along resource spans are evident in activity patterns, foraging methods, tree species selection, trunk position, perch selection, stance selection and particularly along foliage height use spans.

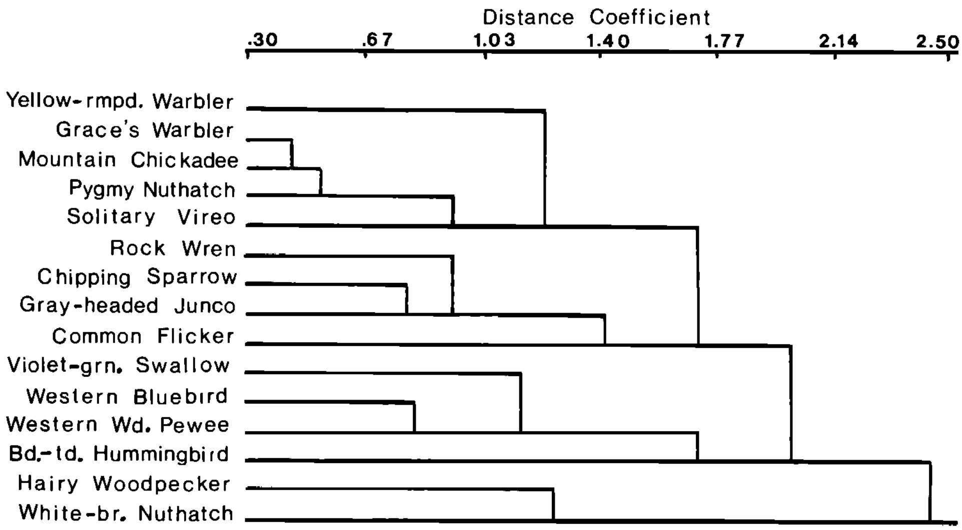

FIGURE 34. Dendrogram resulting from cluster analysis of the Euclidean distance matrix of composite behavior for the breeding birds of the strip cut plot.

Composite cluster analyses.—Before discussing differences between guild members it is necessary to verify that guild members are closer to each other than to members of other guilds. All seven factors (activities, foraging methods, tree species selection, horizontal tree positions, perch selection, stance, and foliage profile) are combined by taking the square root of the sum of the squares of the Euclidean distances of all the factors. The coefficient matrices are then subjected to cluster analysis in order to determine the actual ecological groupings present on the different study plots. Basically the bird species on all four study plots cluster into foraging guilds (Figs. 33–36). The only switch from one guild to another was that of the Common Flicker, which was a ground feeder on the severely thinned and strip cut plots but an exclusive hammerer and tearer on the silviculturally cut and control plots.

Species segregation.—Species that occur together in the habitat can most effectively separate their activities by the vertical segregation of foliage-use zones. Species which use different heights above the ground will come into competition only to the extent that these foliage-use zones overlap (Cody 1974). Competition in these zones of overlap will be reduced when there are differences in other resource dimensions. The number of coexisting species is greatly influenced by the vegetational diversity within a given area. Moreover, in a finite ecological space there is a presumed advantage in reducing the degree of overlap among species in resource use or habitat preference (MacArthur and Levins 1967).

Vertical stratification within avian communities has received much previous attention (Colquhoun and Morley 1943, Balda 1969, Pearson 1971, 1975). Species of woodland birds apparently occupy a definite vertical niche in the vegetation and this niche only partially overlaps that of its closest neighbor in the community (Colquhoun 1941). Three separate vertical communities exist in British oak woods (Colquhoun and Morley 1943). Pearson (1971) suggested that there is a limited vertical distribution of some species. MacArthur (1958), Morse (1971), and others

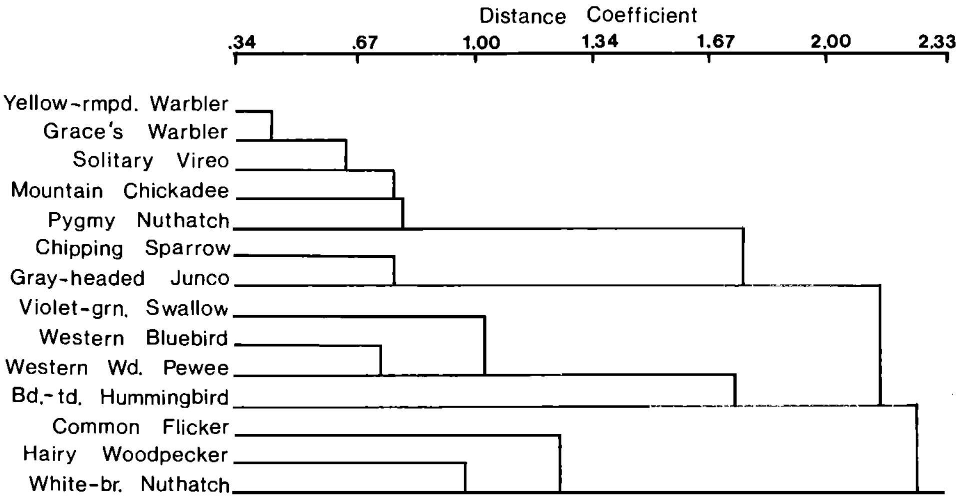

FIGURE 35. Dendrogram resulting from cluster analysis of the Euclidean distance matrix of composite behavior for the breeding birds of the silviculturally cut plot.

report that differences in foraging heights are important factors in the segregation of species' feeding activities in habitats other than grasslands. In a forest in New Guinea the foraging ranges of most bird species are vertically restricted with little overlap (Diamond 1970a). Thus, one way by which bird species reduce niche overlap between themselves and other species is by vertical segregation.

The pickers and gleaners exhibited vertical stratification by using different portions of the trees on all study plots. On the control plot the Solitary Vireo remained in the smaller shrub-like pines and lower reaches of the taller pines (mean height = 3.9 m), whereas the Mountain Chickadee was found at a mean height of 9.8 m. In contrast, Grace's Warbler utilized mainly the bulge region (mean height = 13.7 m) and the Pygmy Nuthatch was found at the tops of the trees

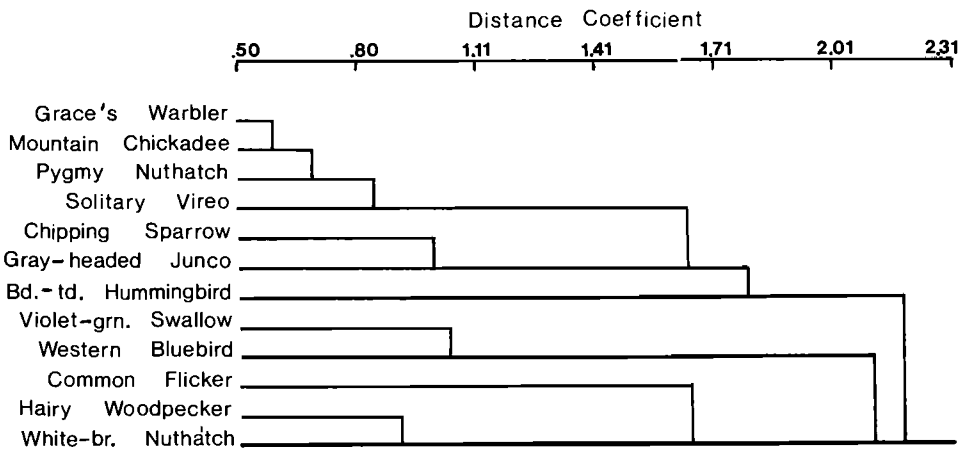

FIGURE 36. Dendrogram resulting from cluster analysis of the Euclidean distance matrix of composite behavior for the breeding birds of the control plot.

(mean height = 17.0 m). On the silviculturally cut plot the picker and gleaner species segregated by mean height in the following order: Yellow-rumped Warbler (6.8 m), Solitary Vireo (8.8 m), Mountain Chickadee (11.2 m), Pygmy Nuthatch (13.3 m), and Grace's Warbler (16.4 m). The same type of vertical separation occurred on the strip cut and severely thinned plots although the differences in mean height were somewhat smaller. Furthermore, there were shifts in distribution by the species, with the Solitary Vireo using the highest portions of the severely thinned plot but the lowest portions on the control plot. The Grace's Warbler and Pygmy Nuthatch reversed positions on the silviculturally cut and control plots. The Grace's Warbler and Yellow-rumped Warbler markedly segregated from one another on the basis of vertical segregation, with the latter utilizing the lower reaches and lower bulge and the former utilizing the upper bulge and spire on all study plots where they coexist. Diamond (1970b) showed that among southwest Pacific birds which were relieved of competition as a result of invading a species poor area, spatial expansion with change in foraging technique was often a prompt response requiring little or no evolutionary change in the genotype. Thus, on the control plot, where the Yellow-rumped Warbler was absent and only the Grace's Warbler was present, the latter made a shift downward into the lower portions of the trees.

In addition to vertical stratification, the pickers and gleaners segregated from each other along many other resource spans. The Yellow-rumped Warbler differed from Grace's Warbler by spending more time probing (4–32 vs. 0%) and in gambel oak (16–62 vs. 3–27%), but less time perched on twigs (45–86 vs. 89–90%). The Grace's Warbler differed from the Solitary Vireo by spending more time in the outer foliage (94–100 vs. 64–87%) and on twigs (85–90 vs. 53–78%), but spent less time on branches (1–6 vs. 20–46%). The Grace's Warbler differed from the Pygmy Nuthatch by spending less time hanging (2–7 vs. 13–23%) and perched in the needle clusters and buds (4–7 vs. 15–23%). The Grace's Warbler segregated from the Mountain Chickadee by spending less time perched on branches (1–6 vs. 7–18%) and in the ponderosa pine on severely thinned, strip cut, and control plots (72–88 vs. 91–100%), but more time in ponderosa pine on the silviculturally cut plot (97 vs. 63%). The Yellow-rumped Warbler separated from the Pygmy Nuthatch by spending less time hanging (4.5 vs. 13–20%) and in the needle clusters (6–11 vs. 15–20%). The Solitary Vireo differed from the Pygmy Nuthatch by spending less time hanging (1–6 vs. 13–23%) and in the needle clusters (1–2 vs. 15–23%), but more time in the inner trunk and branches (13–36 vs. 2–15%). The Solitary Vireo separated from the Mountain Chickadee by making greater use of the branches (20–46 vs. 7–18%) but lesser use of the needle clusters (1–2 vs. 4–33%) and hanging (1–6 vs. 7–18%). The Yellow-rumped Warbler segregated from the Solitary Vireo by probing more (4–32 vs. 0%), but using the pine (35–87 vs. 71–100%) and inner branch region (0–6 vs. 13–36%) less. The Mountain Chickadee differed from the Pygmy Nuthatch by spending less time hanging (7–11 vs. 13–23%) and perched on the trunk (0 vs. 2–9%). Thus pickers and gleaners segregated along a number of resource spans, but primarily on a vertical basis.

The situation is not as clear in the other foraging guilds. There was no vertical segregation by the ground feeders and the aerial feeders and only a slight vertical segregation on the part of the hammerers and tearers. In these cases where vertical segregation was slight, the species segregated by differences in other niche dimensions.

Bird species that find themselves at the same point in space can segregate by using different food items (Cody 1974). Hespenheide (1971) showed that both body size and bill size of some insectivorous birds were well correlated with mean prey size, but in general the correlation was higher for body size. Other workers have suggested the possibility that body size is a more accurate predictor of prey size than is bill size in birds (Schoener 1965, Lack 1971, Cody 1974). An examination of the body sizes of these species may therefore further illustrate how species in the same guild can coexist in the same space.

The hammerers and tearers certainly separated on the basis of body size. Mean weight of the three species ranged from 113 g for the Common Flicker to 62 g for the Hairy Woodpecker and to 18 g for the White-breasted Nuthatch. Thus, these species were probably selecting greatly different prey sizes.

Hammerers and tearers also separated in many other niche dimensions. The Common Flicker differed from the Hairy Woodpecker by foraging less (20–46 vs. 55–100%), spending less time moving and foraging vertically upward (6–46 vs. 57–100%), but more time perching on the ground (31–46 vs. 0–2%) on the severely thinned and strip cut plots. This contrasts with Stallcup's (1968) findings in a ponderosa pine forest in Colorado where the Common Flicker was confined to the ground. In this study, the Common Flicker was observed on the ground only on the treated study plots. On the control plot the Common Flicker was confined to the trees. The Common Flicker and White-breasted Nuthatch differed in that the latter species spent more time picking and gleaning (1–16 vs. 0%), in gambel oak (15–33 vs. 0–10%), moving vertically down the trunk (23–44 vs. 0%), and perching on the trunk (71–97 vs. 14–46%) on all study plots. The White-breasted Nuthatch and Hairy Woodpecker differed in that the nuthatch spent more time in oak (15–33 vs. 0%), hanging (2–14 vs. 0%), and moving vertically downward (23–45 vs. 0%).

The three ground feeders segregated on the basis of body size as well as on other niche dimension differences. The Chipping Sparrow weighed 12.5 g whereas the Rock Wren weighed 16.9 g. The largest of these three ground feeders was the Gray-headed Junco at 20.1 g (Table 17). The Rock Wren differed from the other two species by foraging less and spending more time on the ground and in the slash piles. The Chipping Sparrow separated from the Gray-headed Junco by resting (7–28 vs. 0–13%) and singing (40–100 vs. 34–69%) more on all four study plots. The Chipping Sparrow also probed 100% of the time while foraging whereas the Gray-headed Junco picked and gleaned 10–28% of the time. The Common Flicker, which was a ground feeder on the severely thinned and strip cut plots, spent less time probing but more time on the trunk than any of the other ground feeders.

Segregation of the aerial feeders was more complicated. The Violet-green Swallow and Western Wood Pewee had the same body size (14.2 g). However, there was a significant vertical segregation between the two on the silviculturally cut plot (14.1 vs. 5.3 m). On the strip cut plot, where no vertical segregation existed between the two species, they separated on the basis of the Western Wood Pewee's greater use of oaks and of twigs of the outer foliage. The pewee was primarily a hawker whereas the swallow was mainly an aerial feeder. The Broad-tailed Hummingbird was the smallest bird in the study (3.5 g) whereas the Western Bluebird was the largest hawker (25.3 g). Cody (1974) suggested that the chief means of ecological segregation among flycatching species, at least in temperate areas, are body size differences (and hence prey size differences) and foraging height differences. This was exactly the case in this study.

Segregation in vertical height and prey size inferred from differences in body sizes were the most important factors in potentially reducing intraspecific and interspecific competition. Vertical segregation was more important in the pickers and gleaners where differences in body weights were less than those of the other guilds. The hammerers and tearers and the ground feeders separated primarily on a weight basis and thereby differences in prey size selection. These two guilds also segregated by differences in perch selection and foraging methods. The aerial feeders segregated primarily on a weight basis except for the Western Wood Pewee and Violet-green Swallow. These species separated on a vertical basis on the silviculturally cut plot and by differences in foraging methods (hawking vs. aerial feeding) on all study plots. Thus, in these groups of ecologically similar species there were various differences in several niche dimensions which allowed them to coexist.

Foliage Utilization

There was great variability in the foliage-use profiles of the individual species and of the entire bird communities from year to year as well as from study plot to study plot. The composite profiles of the avian communities on the treated study plots closely approximated the foliage profiles of these areas (Figs. 29–32). Use profiles of many species showed great yearly variation which averaged out on the composite profiles. These fluctuations may be in response to differences in yearly food abundance and distribution as suggested by Hartley (1953). Severe winter weather conditions may differentially affect the insects at different heights in the trees, thereby causing the birds to respond to areas of differential abundance. Heavy foraging in a particular zone one year may deplete the insect population for the following year. The cyclic patterns of foliage utilization may therefore be in response to a changing food supply. Such fluctuations were shown on a diurnal basis in tropical environments (Pearson 1971), whereas Hartley (1953) has reported them in titmice on a seasonal basis.

On the control plot, cyclic changes were also evident but the upper bulge region was consistently underutilized even on the three year composite profile (Fig. 32). This secondary upper bulge, which was not present on the treated study plots, may be characteristic of an aging forest. However, the secondary bulge may not be utilized fully simply because there is an overabundance of foliage on the control plot, whereas on the other study plots the community is forced to make better use of all the foliage because of its more limited availability.

The tendency for many species was to overutilize the lower reaches and lower bulge regions of the foliage profile on all plots. Some of this is undoubtedly due to sampling error, as the birds were more readily visible closer to the ground. The Western Wood Pewee, Western Bluebird, and Gray-headed Junco used primarily the lower portions of the trees as resting, foraging, and singing posts. These species overutilized the lower reaches because much of their food was obtained either on the ground or in the air space close to the ground. The White-breasted Nuthatch heavily utilized the lower trunks on the severely thinned and control plots. The Yellow-rumped Warbler was commonly seen in the lower reaches and lower bulge on all plots, whereas the Grace's Warbler used the upper bulge and spires. In response to the denser foliage on the contol plot, the Solitary Vireo greatly overutilized the lower reaches and shrubs. On the other plots the vireo overutilized the bulge region. This is in contrast to Balda's (1969) findings which showed that the Solitary Vireo had a better fit with the foliage profile than any other species in the ponderosa pine forest in southeastern Arizona. The vireo might be expected to respond differently on the control plot where there were 646 trees/ha than on the treated plots where tree densities ranged from 69 trees/ha on the severely thinned plot to 236 trees/ha on the silviculturally cut plot. Balda (1969) reported 242 trees/ha in southeastern Arizona. Therefore, even though tree densities were similar on the silviculturally cut plot and in southeastern Arizona, the Solitary Vireo has responded differently in northern Arizona than in southern Arizona.

Grace's Warbler and Pygmy Nuthatch, the two species that heavily utilized the upper bulge and spire were both foliage gleaners. Similarly, Balda (1969) showed that foliage inhabiting birds, such as the Grace's Warbler and Pygmy Nuthatch, showed a definite overuse of the upper portions of the trees.

Thus, the fluctuations in foliage utilization patterns by individual species and by the entire bird community seem to indicate that there is a cyclic pattern in bird use possibly resulting from fluctuations in food availability.

Territory Size

Mean territory sizes of individual species varied from year to year (Table 16). One might expect territory size to exhibit an inverse relationship with density. However, this was not the case in the ponderosa pine forest. Territory was not predictable with changes in bird density, indicating that territory size is not defined by bird density in the ponderosa pine forest, and can expand and contract without regard for bird density. This is in direct contrast to Kendeigh's (1947) findings in the eastern spruce-fir forest where a direct relationship between territory size and density existed. This direct relationship between territory size and density in the eastern coniferous forest might reflect the abundance of warblers and other foliage gleaning species. The warblers are ecologically and systematically very similar to one another and there may therefore be a large amount of potential intraspecific and interspecific competition occurring among them in the eastern coniferous forest. The amount of interspecific competition is probably much lower in the west than in the east due to the paucity of warblers and a lack of proportionate increase in other insectivorous picker and gleaner species. Again, generalizations made in the eastern coniferous forest do not necessarily apply to the western coniferous forest and must be used with caution.

On the other hand, territory size in the ponderosa pine forest appears to be related to how the birds use the available foliage and the amount of utilized foliage volume per territory. In 19 cases from all forested plots, as territory size became larger, the fit with the available foliage decreased; that is, the birds became more selective of specific strata of foliage. In contrast, in 20 cases, as territory size decreased, the fit with the available foliage increased. It must be stressed that even though the changes in mean territory size were statistically significant in

TABLE 21
RELATIONSHIP BETWEEN MEAN TERRITORY SIZE, USE OF THE BULGE, AND FIT WITH THE FOLIAGE PROFILE

Species	Plot	Years	Bulge use	Fit	Terr. size
Western Wood Pewee	Strip	73–74	I[a]	D	I
		74–75	I	I	D
Mountain Chickadee	Silv.	74–75	I	D	I
	Cntrl.	74–75	D	D	I
White-breasted Nuthatch	S. Thn.	73–74	I	I	D
		74–75	D	D	I
	Strip	73–74	I	I	D
		74–75	D	D	I
	Silv.	73–74	D	D	I
		74–75	D	D	I
	Cntrl.	73–74	I	D	I
		74–75	D	I	D
Pygmy Nuthatch	Silv.	74–75	I	I	D
	Cntrl.	73–74	D	D	I
		74–75	I	I	D
Western Bluebird	S. Thn.	74–75	D	D	I
	Strip	73–74	I	I	D
		74–75	S	D	I
	Silv.	73–74	D	D	I
		74–75	I	I	D
Solitary Vireo	S. Thn.	74–75	D	D	I
	Strip	73–74	I	I	D
		74–75	S	D	I
	Silv.	74–75	D	I	D
	Cntrl.	73–74	S	D	I
Yellow-rumped Warbler	Silv.	74–75	D	D	I
Grace's Warbler	S. Thn.	73–74	I	I	D
		74–75	D	I	D
	Strip	73–74	D	D	I
		74–75	I	I	D
	Silv.	73–74	D	I	D
		74–75	D	D	I
	Cntrl.	73–74	D	D	I
		74–75	I	I	D
Gray-headed Junco	Silv.	73–74	I	D	I
		74–75	D	I	D
	Cntrl.	73–74	I	I	D
		74–75	D	D	I

[a] I = increased; D = decreased; S = stable.

only six cases ($P \leq 0.05$), this trend between the foliage use index and territory size holds in all 39 cases. The changes in mean territory size were not significant probably because of the small sample sizes. Because the change in territory size can be predicted in all cases, the following model is suggested. A combination of bulge use and foliage fit and, thereby utilized foliage volume per territory, can be used to predict the direction of territory size change in all cases (Table 21). As the foliage use index decreases (i.e., becomes smaller), the bird use profile better approximates the foliage profile. All species examined either increased or decreased foliage fit betewen years and, in conjunction, changed territory size. There are six options open to the birds in terms of changing territory size (percentages indicate the proportion of the 39 cases examined that used a particular option): 1) increase bulge use, increase fit with the available foliage, and decrease territory size (33%), 2) decrease bulge use, decrease fit, and increase territory size (33%), 3) decrease bulge use, increase fit, and decrease territory size (13%), 4) increase bulge use, decrease fit, and increase territory size (10%), 5) stable bulge use, decrease fit, and decrease territory size (8%), and 6) stable bulge use, increase fit, and decrease territory size (3%).

A bird can increase the amount of foliage volume it uses by increasing its use of the bulge, by increasing its fit with the foliage, by increasing its territory size or by any combination of these. Since foliage volume is probably directly related to the insect food supply, an increase in utilized foliage volume by a bird should indicate an increase in its resource base. In this manner, if a bird increases its resource base by more efficiently utilizing the foliage on its territory, it should not need as large a territory. In contrast, a bird should need a larger territory when it makes relatively inefficient use of the foliage on its territory. There were 13 samples of birds on a particular study plot increasing their bulge use and their foliage fit between years. These same species also reduced their territory size between years (option 1). In contrast, there were 13 samples of birds on a particular study plot decreasing their bulge use and foliage fit. These species also increased their territory sizes between years (option 2). A bird can still increase its resource base, even with decreased bulge use, as long as it uses the foliage more efficiently than it did the year before (option 3). There were five samples of birds decreasing territory size using option 3. In contrast, a bird can increase its bulge use but decrease its fit with the available foliage by becoming highly selective of specific strata of foliage. This stenotypic selection of foliage strata by a bird was coupled with an increase in territory size (option 4). The final two options revolve around increased or decreased fit with the foliage profile and stable bulge use. Only the Solitary Vireo on the control plot from 1974 to 1975 increased its fit with the foliage, had stable bulge use, and thereby decreased its territory size. The commoner option with stable bulge use was to become more selective of specific strata, thereby necessitating a larger territory. Thus, a bird can decrease its territory size by increasing its use of the bulge, using more total foliage volume and, most importantly, by more effectively using the foliage strata (Fig. 37).

Energy Flow

The standing crop biomass of the bird communities on all the study areas was much lower than those reported by many previous workers. The standing crop varied from 67.0 to 218.6 g/ha on the forested areas (Table 17). Haldeman et al. (1973) reported 399.8 g/ha in similar areas of northern Arizona. Holmes and Sturges (1973) reported a standing crop of 653.8 g/ha in an eastern hardwood forest whereas Karr and Roth (1971) reported 335.3 g/ha in a coniferous forest in the Bahamas. On bare ground in Illinois the standing crop was 80.5 g/ha versus 782.1 g/ha in the early shrub layer (Karr 1971). Wiens and Nussbaum (1975)

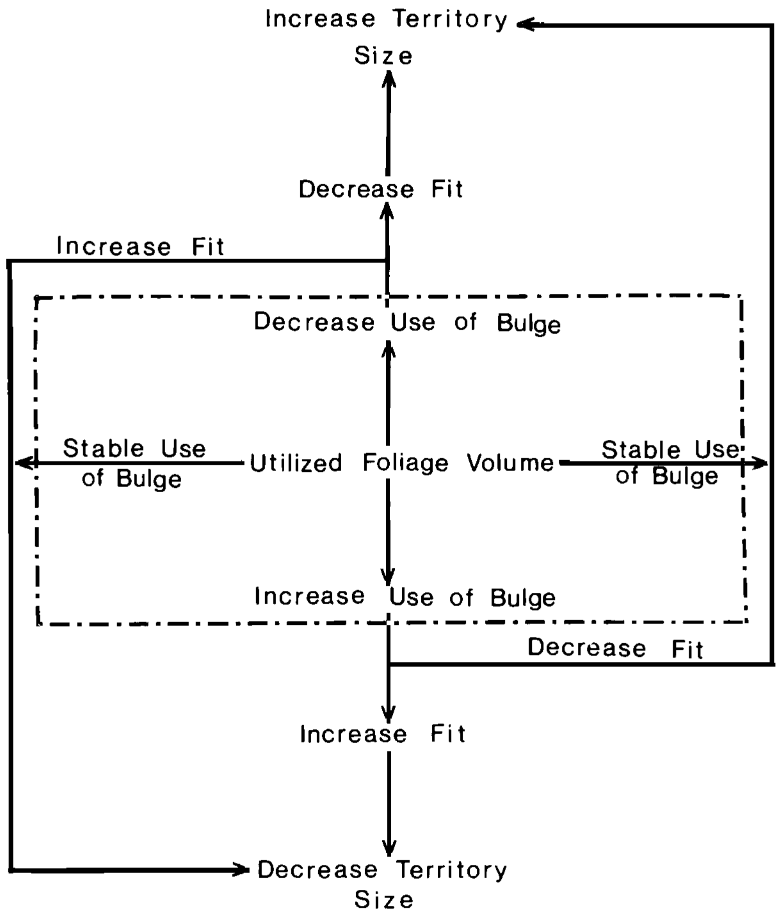

FIGURE 37. Relationship between mean territory size, utilized foliage volume, bulge use, and foliage fit.

reported standing crops of 223.3 to 526.1 g/ha in six coniferous forests in the Oregon Cascades. Thus, the standing crop biomass of the birds in the ponderosa pine forest is closer to that in an Illinois grassland than to that in any other forest.

Similarly, the consuming biomasses of the bird communities on all study areas were much lower than those reported in other forested areas by previous workers. The consuming biomass on the forested areas varied from 20.1 to 59.2 g/ha, whereas the consuming biomass in a similar area in northern Arizona was 95.9 g/ha (Haldeman et al. 1973), and in a coniferous forest in the Bahamas, 104.2 g/ha (Karr and Roth 1971). A consuming biomass of 18.0 g/ha was found on the bare ground area and 161.7 g/ha in the early shrub area in Illinois (Karr 1971). The consuming biomass of the bird community in a wet grazed grassland in Illinois was 30.0 g/ha (Karr 1971).

The low standing crops and consuming biomasses of the bird communities in this study were attributable to the low breeding bird densities. Higher values for standing crop and consuming biomass were found in other similar areas of northern Arizona because of the higher densities of the Violet-green Swallow, Mountain Chickadee, Pine Siskin, and Brown Creeper (Haldeman et al. 1973). The higher values of standing crops and consuming biomasses in spruce-fir forests in Oregon (Wiens and Nussbaum 1975) were attributable to high densities of Chestnut-backed Chickadees (*Parus rufescens*), Brown Creeper, Golden-crowned Kinglets, and Hermit Warblers, (*Dendroica occidentalis*). Karr and Roth (1971) report that the breeding bird community in the Bahamas has a high proportion of warblers (42% on a density basis). The values of standing crop and consuming biomass in the Bahamas were greater than those reported in this study because of the lack in the ponderosa pine forest of proportionate compensation by other foliage feeding species for the paucity of warbler densities.

In terms of the primary energy component (based on existence energy), small birds (19-g body weight or less) only became important when their densities became very high. This contrasts with the finding of Wiens and Nussbaum (1975) that foliage gleaning bird species accounted for the greatest proportion of the energy intake in most stands of spruce-fir forest in Oregon. In their study, small species (10-g body weight or less) numerically dominated the bird communities at all stands. In this study, however, only five species weighed less than 10 g (Broad-tailed Hummingbird, Pygmy Nuthatch, Grace's Warbler, Red-faced Warbler, and House Wren). The species composition in this study was closer to that of shrub-steppe habitats in Oregon where 11–25-g species tended to predominate (Wiens 1974).

The total energy intake of the avian community was much lower than that reported by Weiner and Glowacinski (1975) and Karr (1971). The energy flow on the forested study plots varied from 39.7 to 112.8 kcal/ha-day (Tables 18–20). The total energy flow on bare ground in Illinois was 29.5 kcal/ha-day, whereas in the early shrub area it was 313.8 kcal/ha-day (Karr 1971). Weiner and Glowacinski (1975) reported a total energy flow of 232.9 kcal/ha-day in a deciduous forest in Poland, whereas Karr (1971) recorded a total energy flow of 411.3 kcal/ha-day in a mature bottomland deciduous forest in Illinois. The total energy flow of the wet grazed grassland in Illinois was 47.3 kcal/ha-day (Karr 1971). The energy flow in the ponderosa pine forest was similar to the energy flow of a bird community in a pine forest on Great Abaco Island, Bahamas (116.75 kcal/ha-day, Karr and Roth 1971).

The permanent residents were the primary energy component on all the forested areas (52–74%). Permanent residents accounted for 68–92% of the total energy flow in a coniferous forest in Oregon (Wiens and Nussbaum 1975). Thus, although the proportion of the total energy flow contributed by the permanent residents in the ponderosa pine forest was lower than that reported in an Oregon coniferous forest, the permanent residents were of great importance to the total energy flux in both communities.

Overall energy flow (in terms of existence energy) appears to be very low in the ponderosa pine forest bird community. The energy flux was higher on the strip cut and silviculturally cut plots than on the natural area, reflecting the higher densities on the former plots. The low energy flux of the bird community in the ponderosa pine forest reflects the low breeding bird densities. Other studies (Haldeman et al. 1973, Wiens and Nussbaum 1975) reported greater energy flows because of the higher densities on their areas. In general, the energy flux through the avian community is small compared with the total system energy flow (Holmes and Sturges 1975), and it is highly probable that this generalization holds for the ponderosa pine forest. However, the avian community probably had a substantial effect on the overwintering insect population when its density was most likely at its low point, thereby affecting insect densities throughout the year.

Species Substitutions

Potential competitive pressures were probably greatest in the closely clumped groups of species, on a weight basis, within each guild (Table 16). Interestingly, species substitutions (the replacement of a species on a natural or near natural area by another species) on the heavily treated areas occurred in these closely clustered groups of species. The Western Flycatcher, which prefers dense foliage and a nearly closed canopy, bred only on the control plot and some areas of the silviculturally cut plot, whereas the Western Wood Pewee, which prefers more open habitat, bred on the severely thinned and strip cut plots and in an open area on the silviculturally cut plot. Similarly, the Red-faced Warbler, which was only present on the control and silviculturally cut (before treatment) plots, was replaced on the treated areas by the Yellow-rumped Warbler.

The possibility exists that further niche exploitations could occur in those guilds with large gaps between bird sizes. Additional species probably could be accommodated between the following pairs of species: Solitary Vireo and Western Tanager, Broad-tailed Hummingbird and Common Nighthawk, Hermit Thrush and Robin, and White-breasted Nuthatch and Black-headed Grosbeak (Table 16). Haldeman et al. (1973) and Balda (1969) failed to find any intermediate species that could fill these gaps in their studies of bird communities in the ponderosa pine forest. The addition of potential competitors in the gaps between the larger species may be limited by food resources (Schoener 1971). The larger prey selected by the larger birds may be in short supply, whereas there may be large numbers of small prey species in the ponderosa pine forest. The commonest insect species in a lowland deciduous-conifer forest in Massachusetts are in the 2- to 4-mm class (Schoener and Janzen 1968). The majority of insects in temperate forests are between 2 and 8 mm in length (Schoener 1971). Since insect prey items are distributed log normally in size (a normal distribution on a log scale), large prey species are less abundant than are medium-sized prey species (Schoener and Janzen 1968, Price 1975). This suggests the possibility of greater specialization being possible on the smaller end of the weight spectrum. In the ponderosa pine forest, 23 of the 28 species examined were at the lower ends of the weight spectrums in their respective guilds.

Species Dominance

In conclusion, one might hypothesize on the basis of the bulk of the data of this study that those species able to alter their habitat requirements and niche dimensions in response to treatment should be the most dominant bird species in the ponderosa pine forest. As defined by McNaughton and Wolf (1970), generalists are able to maintain themselves over a broader environmental range then specialists. One hypothesis suggested by Järvinen and Väisänen (1976) is that behavioral flexibility with respect to habitat tolerance may account for the dif-

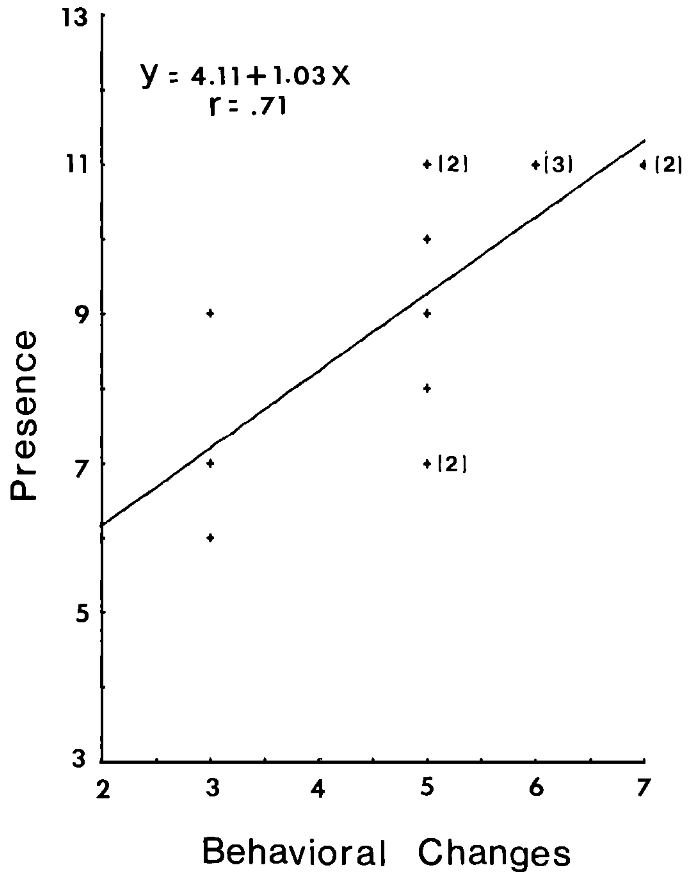

FIGURE 38. Relation between the number of behavioral changes (from Table 6) and overall presence. Overall presence is the sum of the number of times a species was present on the four forested study areas for the three-year period. The maximum value is 11 as the pre-treatment silviculturally cut plot was not used in the calculation.

ferences between successful (that is, a species which has occupied a large number of biotopes) and unsuccessful species. If this is the case, the most flexible species in the ponderosa pine forest should be present on more study plots during more years and with greater standing crops than relatively inflexible species. Behavioral plasticity was greatest in five species (Solitary Vireo, Gray-headed Junco, Western Bluebird, Common Flicker, and White-breased Nuthatch). In response to habitat modification, these species significantly altered at least six of the seven behavioral characteristics examined (Table 6). If the suggested hypothesis is correct, then these five species should have been present on more study plots during more years and with greater standing crops than any other of the 15 species examined in detail. Indeed, these five species were present on all study plots in all years during the course of the study. The Grace's Warbler and Hairy Woodpecker were also present on all study plots in all years, and both species altered five behavioral characteristics in response to habitat alteration, indicating that they were also fairly resilient. Overall, there was a positive correlation (r = 0.71,

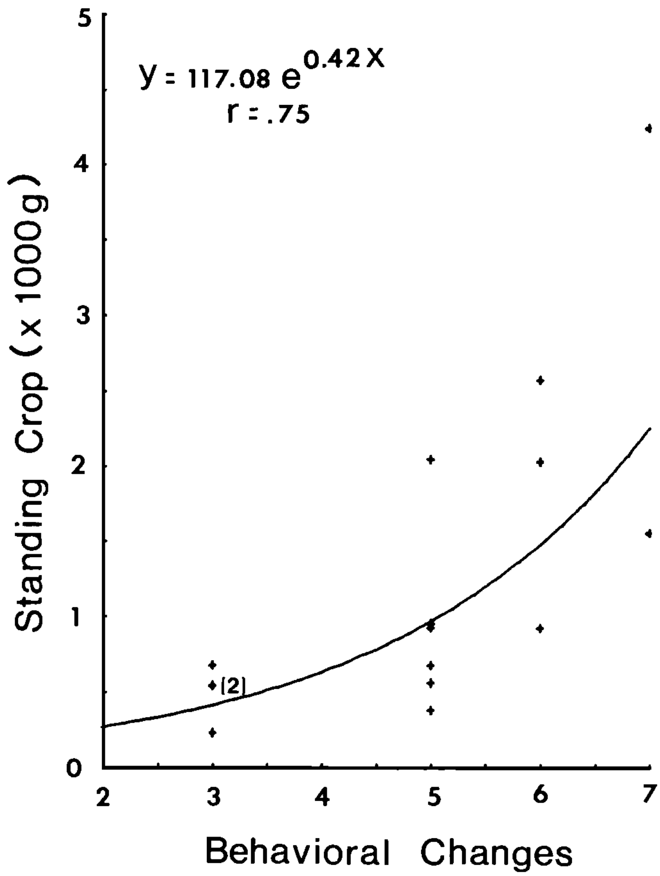

FIGURE 39. Relation between the number of behavioral changes (from Table 6) and overall standing crop. Overall standing crop is the sum of the total standing crop for a given species on the four forested study areas for the three-year period (exclusive of the pre-treatment silviculturally cut plot).

$P \leq 0.05$) between the number of behavioral changes and species presence over the three years on the study areas (Fig. 38).

In terms of standing crop (calculated for the overall study) the five most plastic species ranked first, second, fourth, fifth, and seventh out of the 15 breeding species examined in detail. The Hairy Woodpecker ranked third; Pygmy Nuthatch, sixth; and the Grace's Warbler, eighth. The Pygmy Nuthatch altered five behavioral characteristics and was important in terms of standing crop because of its high densities on the silviculturally cut and control plots. These high densities of Pygmy Nuthatches were due to the high availability of its typical habitat on these plots. There was a positive correlation ($r = 0.75$, $P \leq 0.05$) between the number of behavioral changes and standing crop of the bird species (Fig. 39). The most inflexible species (Violet-green Swallow, Rock Wren, and Broad-tailed Hummingbird) ranked ninth, thirteenth, and fifteenth in terms of standing crop and were not present on all study plots in all years. The Rock Wren was absent on the silviculturally cut and control plots whereas the Violet-green Swallow was absent on the severely thinned plot. The Broad-tailed Hummingbird was a breeding species on all plots but was missing from most plots in 1973. Thus, those species which exhibited the greatest behavioral flexibility were also the most successful breeding species in the ponderosa pine forest.

An examination of how the most successful species related to the other species in their foraging guilds in terms of body weight may help explain why these species were able to be ecologically resilient. These five species (Solitary Vireo, Gray-headed Junco, Western Bluebird, Common Flicker, and White-breasted Nuthatch) plus the Grace's Warbler, Pygmy Nuthatch, and the Hairy Woodpecker, tended to be on the extremes of the weight ranges of each guild (Table 16). The Grace's Warbler was the smallest picker and gleaner, whereas the Solitary Vireo was the heaviest picker and gleaner except for the tanagers, which, besides being present in very low densities, were twice the size of the Solitary Vireo. The Western Bluebird was the largest aerial feeder except for the Common Nighthawk. However, not only was the nighthawk a crepuscular species, but it was twice the size of the Western Bluebird. The most successful hammerers and tearers were the Common Flicker and the White-breasted Nuthatch, which were the largest and smallest members of that guild. The Hairy Woodpecker, which was present all years and on all study plots, also faced potentially reduced competitor pressure by being three times as large as the White-breasted Nuthatch but half the size of the Common Flicker. The most successful ground feeder was the Gray-headed Junco. Its nearest potential competitors were the Rock Wren and Hermit Thrush. However, the Hermit Thrush was present only on the silviculturally cut and control plots in very low densities. The next heaviest species, the Robin, was four times the size of the junco. The Rock Wren, which was smaller than the junco, was present only on the severely thinned and strip cut plots. Competition between species of different size probably occurs only over a relatively narrow intermediate range of resource size classes (Ricklefs 1972). Indeed, Hespenheide (1971) showed that flycatchers exhibited a strong positive correlation of average prey size with body weight. Therefore, those species at the extremes or situated in the large gaps of the weight range of a particular guild probably have reduced competitive pressures when compared with those species of similar body weights in the same guild. Potential competition between species of different guilds is probably minimal as guild members use different foraging substrates. Broadening of habitat selection made possible by reduced competition has been observed in island situations (Crowell 1962, MacArthur and Wilson 1967, Williams 1969, Diamond 1970a). Thus, the behavioral plasticity observed in the five most successful species in the ponderosa pine forest was possible probably because of reduced competitive pressure. The Grace's Warbler and Hairy Woodpecker were successful for the same reason.

We conclude from this evidence that the most dominant species in the ponderosa pine forest community, when dominance is based on presence and standing crop biomass, are those species that have one or both of the following attributes: 1) behavioral plasticity, and 2) occupation of the extremes or occurrence in large gaps in the guild weight spectrum. One or both of these factors may be of prime concern in defining "niche dominance" in such a way that it will aid in understanding community composition. This is obviously an oversimplification of the constellation of factors that affects community organization but it does account for a large proportion of the variability present in avian community organization in this study.

SUMMARY

This study was undertaken to measure and evaluate 1) the effects of differing foliage volume, foliage patterns, and densities of trees on the diversity, density, and behavior patterns of the breeding birds of ponderosa pine forest, and 2) the standing crop biomass, consuming biomass, and existence energy requirements of the breeding birds on each plot. Five study plots were chosen in relatively homogeneous stands on ponderosa pine. Plots were selected in clear cut, strip cut, severely thinned, silviculturally cut, and natural areas. The trees on each study site were analyzed to determine the relative density, relative frequency, importance value, absolute density, and foliage volume in 2-m height classes for each tree species. Breeding bird behavior was examined in detail in seven different categories: activity pattern, foraging method, tree species selection, position from the trunk, perch selection, stance, and foliage use profile. The following major points were evident.

1. Breeding bird populations varied from a low of 12.5 prs/40 ha on the clear cut area in 1973 to a high of 162.8 prs/40 ha on the strip cut area in 1974. Bird densities on the natural area varied from a low of 63.0 prs/40 ha in 1973 to a high of 132.8 prs/40 ha in 1974. The number of nesting species was highest on the strip cut area where 22 species nested in 1974 and lowest on the clear cut area where three species nested in 1973.
2. When bird species diversity is related to plant species diversity, foliage height diversity, and plant volume diversity for the forested areas, it is evident that these factors are not significantly correlated with breeding bird diversity. Other factors such as territoriality, food supply, and the openness of the habitat or other foliage configurations are more important in determining breeding bird diversity than the above three factors.
3. The behavior patterns of most bird species were influenced by habitat alteration. Foraging method and stance were the two types of behavior least affected by habitat manipulation. Perch selection, tree species selection, and mean height were most affected by treatment.
4. Bird species in the ponderosa pine forest segregated primarily on a vertical basis by using different portions of the trees, or on a body weight basis. Pickers and gleaners separated primarily on a vertical basis, whereas the other three guilds (hammerers and tearers, ground feeders, and aerial feeders) segregated primarily by body weight. Species in the same guild also separated on the basis of differences in several other niche dimensions.
5. Comparisons between the foliage profiles and bird use profiles illustrated a cyclic pattern of bird use during the course of the study, perhaps in reponse to fluctuations in the resource base.
6. No correlation existed between territory size and breeding bird density for individual species or community densities. Territory size did vary directly with changes in the fit between the bird use profile and the foliage profile. Territory size decreased with (1) increased use of the foliage profile bulge, (2) increased utilized foliage volume per territory, and, most importantly, (3) an increased fit of the bird use profile and the foliage profile, or a combination of these.

7. The standing crop biomass on the forested study plots varied from a low of 67.0 g/ha on the control plot in 1973 to a high of 218.6 g/ha on the strip cut plot in 1974.

8. The consuming biomass on the forested study plots varied from a low of 20.2 g/ha on the natural area in 1973 to a high of 59.2 g/ha on the strip cut area in 1974.

9. The total energy flux (in terms of existence energy) on the forested areas varied from a low of 39.7 kcal/ha-day on the natural area in 1973 to a high of 112.8 kcal/ha-day on the strip cut area in 1974.

10. The most behaviorally plastic species (Solitary Vireo, Gray-headed Junco, Western Bluebird, Common Flicker, and White-breasted Nuthatch) were also the most successful species in the ponderosa pine forest in terms of overall standing crop and presence. These same five species were also located at the extremes or in gaps of their guild weight ranges.

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