FOLIAGE USE BY BIRDS OF THE OAK-JUNIPER WOODLAND AND PONDEROSA PINE FOREST IN SOUTHEASTERN ARIZONA

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Bird populations obtain their requisites from the resources available to them in a number of different ways. Species within the same community may use different configurations of the habitat, or the same configurations in a different manner or in different proportions. This tends to minimize or eliminate interspecific competition. Habitat utilization by various species of nesting birds is often a main portion of autecological studies (Stenger and Falls 1959), or of studies dealing with the interactions of a few species from a given avian community.

Recent studies by Morse (1967) and MacArthur (1958) have shown that volume of foliage may be an important factor in limiting the density of some species of birds. However, few attempts have been made to quantify the foliage portion of a plant community by species of trees and the height distribution of this foliage on the trees. This information can be of value when correlated with total nesting-bird use. MacArthur (1958) also showed how five species of warblers which overlap in their use of foliage may exploit this feature of the habitat in different ways.

Emlen (1967) has proposed a method for obtaining the canopy cover value of a plant community by recording the presence or absence of foliage above the observer at predetermined points. This method is of value for comparative purposes, but neither gives the absolute volume of foliage nor shows its height distribution above the ground in a plant community. Both aspects of volume of foliage are important in bird utilization.

The objective of this study is to depict the height distribution and volume of foliage in two different plant communities and to show how the total avifauna utilizes this dimension of their habitat during the breeding season. When possible, foliage use by individual bird species is discussed to show their contribution to the overall pattern of use. Data on utilization are expressed in terms of volume of foliage rather than area.

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METHODS

While conducting breeding-bird counts in various plant communities of the Chiricahua Mountains of southeastern Arizona (Balda 1967), two areas were selected for study of foliage use by the nesting birds. In the oak-juniper woodland (36-acre plot) and ponderosa pine forest (38-acre plot) trees and saplings were measured for volume of foliage in conjunction with a sampling plan to obtain relative density, relative frequency, relative dominance, and number of individual trees per acre. I used the plotless point-quarter method of Cottam and Curtis (1956) to sample trees with a DBH of three inches or more in both plots. In each study area a series of points was established and at each point the surrounding area was divided into four quarters. In each quarter the name of the tree closest to the point and its distance from the point were recorded. The DBH was also measured on these four trees per point. Quantitative analysis of these data was made using the standard formulas (Phillips 1959; footnotes, table 1). In addition, the following data were recorded for the four trees sampled at each point: total tree height (from ground to highest point), height from ground to lowest branches, and crown diameter. The shape of the crown for each tree was recorded as being either perfectly conical or perfectly cylindrical. An Abney level was used for height measurements. A total of 30 points (120 trees) in the oak-juniper woodland plot, and 25 points (100 trees) in the ponderosa pine forest plot was sampled.

Saplings were counted within circular plots of 0.01 acre (radius of 3.6 m) and measured for volume as described above for the trees.

The tree and sapling data were expressed in terms of total volume of foliage per species of tree and distribution by height from the ground. These values were then converted to a per acre total for each species of tree for a composite picture of the entire community.

In addition to recording the location of individual singing males by the spot-map method (Kendeigh 1944), the species of tree in which each bird was observed and its height from the ground were recorded. When possible, information was gathered as to behavior of each species. At least 12 complete daylight counts were made on each area. Counts were made during May, June, and July 1965.

I analyzed the interaction of available foliage and observed bird-use in the following two ways. In the first analysis, which yielded the use index value, the per cent of total volume of foliage contributed by each species of tree (including saplings) was calculated from tables 2 and 4. Using this figure, an expected number of bird observations per species of tree, based on percentage of the total foliage, was calculated. For example, if one species of tree contributed 84 per cent of the total volume of foliage in the plant community, then the expected number of bird observations would be 84 per cent of the total observations recorded. This

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FIGURE 1. Oak-juniper woodland study area showing *Quercus* sp., *Pinus leiophylla*, and *Juniperus deppeana*.

expected number of bird observations was then compared with the actual number of bird observations in each species of tree using the standard chi-square procedure and dividing the total obtained by the number of categories used (different species of trees) minus one (degree of freedom). While the procedure described is identical to that used in determining chi-square, the observations were not independent (H. W. Norton, pers. comm.) and the total thus obtained could not be treated for statistical significance. Rather, the values, after modification as shown below, were utilized as the use-index.

There is an inverse linear relationship between the total chi-square figure and the number of observations if the same proportion of the observations occurs in each category. Thus, the larger the number of observations, the lower the chi-square value. Since different numbers of observations were obtained per bird species, it was necessary to adjust the number of observations per species to correspond to the lowest number gathered for any one species. This was done by assigning each observation a number and then randomly removing a number of observations. For example, 45 observations were made on Grace's Warbler and 125 on the Black-throated Gray Warbler. Thus, 80 observations had to be randomly removed from the latter species. The figure obtained from these calculations

$$\left\{\frac{\left(\begin{array}{c}\text{Adjusted Expected}\\ -\text{ Adjusted Observed}\end{array}\right)^2}{\text{Adjusted Expected}} \div \text{Degrees of freedom}\right\}$$

will be referred to hereafter as the use-index value. The lower the use-index value, the better the goodness-of-fit between expected bird use of available foliage and observed use of the foliage.

In the second analysis the total volume of foliage for each species of tree was subdivided by height classes of 5-ft intervals from 0 to 30 ft and 10-ft intervals above 30 ft. The volume of foliage for each species of tree as it was distributed by height was then combined to give a composite picture of the foliage distribution for the entire plant community. The change in scale above 30 ft allowed for the decreased accuracy in determining the height of birds at these elevations. An expected number of bird observations was calculated in the manner described above. The per cent of total bird observations at each height class was then plotted against the per cent of total volume of foliage at each height class, and a use-index value calculated.

RESULTS AND DISCUSSION

OAK-JUNIPER WOODLAND

This study area was located within a large tract of relatively homogeneous vegetation that extended along the south side of Cave Creek about 0.10 miles south of the Southwestern Research Station.

The elevation of this area ranged from 5470 ft at its northern edge up to about 5560 ft at the southern limits. A large rocky outcropping in approximately the center of the plot had an elevation of 5580 ft. The southern two-thirds of the area is on a north-facing slope of about 6°. No grazing or fires have disturbed the area in the past 10 years (fig. 1).

Juniperus deppeana was the most abundant of the eight species of trees present. Its impor-

TABLE 1. Composition of trees in the oak-juniper woodland community.

Species	Relative density[a]	Relative dominance[b]	Relative frequency[c]	Importance value[d]
Juniperus deppeana	38.3	60.1 (60.1)[e]	33.3	131.7
Pinus leiophylla	21.7	17.9 (18.2)	19.4	59.0
Quercus emoryi	20.8	10.7 (10.9)	23.6	55.1
Quercus arizonica	17.4	11.0 (10.4)	20.9	49.3
Pinus cembroides	1.8	0.3 (0.4)	2.8	4.9
Total	100.0	100.0	100.0	300.0

[a] $\frac{\text{Number of individuals of the species}}{\text{Number of individuals of all species}} \times 100.$

[b] $\frac{\text{Total basal area of the species}}{\text{Total basal area of all species}} \times 100.$

[c] $\frac{\text{Number of points of occurrence of the species}}{\text{Number of points of occurrence of all species}} \times 100.$

[d] Sum of relative density, relative dominance, and relative frequency.

[e] Calculated from foliage volume data (table 2).

tance value (sum of relative density, relative dominance, and relative frequency figures) was more than twice that of any other species of tree sampled (table 1). The total density of all trees was 120 trees per acre, with each tree occupying a mean area of 361 ft^2. The mean distance between trees was 19 ft, and the total basal area was 64 ft^2 per acre. The relative dominance figures obtained from the volumes of foliage (table 2) are strikingly similar to the relative dominance figures obtained from the DBH figures. The mean height of the canopy was 23 ft; the tallest tree measured was a 60-ft *Pinus leiophylla*, one of the tallest trees located on the area. Rare trees observed in the study area but not recorded in the sample include: *Juniperus monosperma*, *Pinus engelmannii*, and *Juglans major*.

Juniperus deppeana was the major species contributing to the shrub and sapling strata with a density of 256 individuals per acre. Other species of trees contributed the following sapling densities: *Pinus leiophylla*, 60; *Pinus cembroides*, 48; *Quercus emoryi*, 24; and *Quercus arizonica*, 14. There were 898 shrubs and saplings per acre. A few dead trees, primarily tall pines 60–70 ft in height, were scattered through the area.

The two species of oaks found in the study area were combined for this analysis as they were of similar life-form and profile and probably offered the same requisites. Other tree species used were *Pinus leiophylla* and *Juniperus deppeana*.

This community supported 36 species of birds with a total nesting density of 267 pairs per 100 acres. The most common breeding birds and their respective densities were: Chipping Sparrow (*Spizella passerina*), 30; Black-throated Gray Warbler (*Dendroica nigrescens*), 24; Black-chinned Hummingbird (*Archilochus alexandri*), 21; Bridled Titmouse (*Parus wollweberi*), 18; Ash-throated Flycatcher (*Myiarchus cinerascens*), 12; Rufous-crowned Sparrow (*Aimophila ruficeps*), 11; Plain Titmouse (*Parus inornatus*), 10; Common Bushtit (*Psaltriparus minimus*), 10; Bewick's Wren (*Thryomanes bewickii*), 9; Red-shafted Flicker (*Colaptes cafer*), 8; Acorn Woodpecker (*Melanerpes formicivorus*), 8;

TABLE 2. Foliage volume (ft^3) of trees and saplings in the oak-juniper woodland community.

Height class (ft)	*Juniperus deppeana*		*Pinus leiophylla*		*Quercus* sp.		*Pinus cembroides*		Total (per acre)
	Trees	Saplings	Trees	Saplings	Trees	Saplings	Trees	Saplings	
0– 4	4,952	3,330		636	260	56	352	252	9,838
5– 9	31,012	1,810	1,142	494	9,412	330	328	214	44,742
10–14	28,911		7,188	19	12,939	168	72	6	49,303
15–19	21,484		11,629		9,219		10		42,342
20–24	16,197		8,861		5,304				30,362
25–29	5,852		5,576		1,087				12,515
30–39	3		3,455		211				3,669
40–49			694						694
50–59			255						255
60–69			36						36
Total	108,411	5,140	38,836	1,149	38,432	554	762	472	193,756

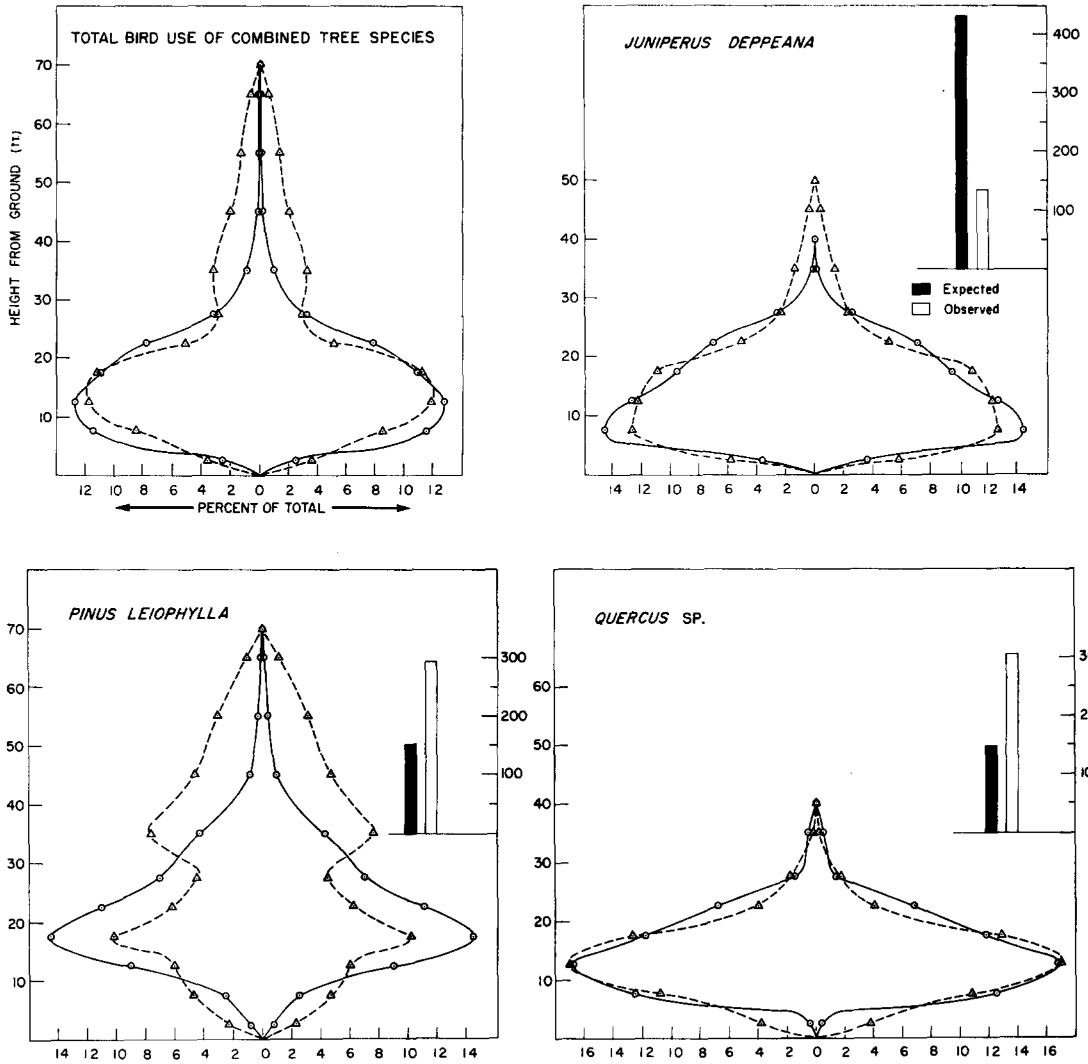

FIGURE 2. Total bird use of tree foliage in the oak-juniper woodland. The shaded bar is the expected bird use in each species of tree based on available foliage volume. The open bar is the actual number of observations. The solid line is the per cent of foliage volume present in each height class. The broken line is the per cent of total observations of birds in each height class.

Robin (*Turdus migratorius*), 7; Eastern Bluebird (*Sialia sialis*), 7; and White-breasted Nuthatch (*Sitta carolinensis*), 7. These 14 species contributed 68 per cent of the total breeding pairs present.

A total of 906 height observations was recorded for all birds except hummingbirds, the turkey, and nocturnal species. Of these observations 97 per cent were made between 05:00 and 10:00. Of the total observations, 83 (9.2 per cent) were of various species on the ground, and the same number were made of species on dead trees. Mexican Jays (*Aphelocoma ultramarina*) (6 pairs per 100 acres) and Chipping Sparrows spent 39 and 34 per cent, respectively, of their time on the ground. Neither the above observations nor observations made of species at the nest could be used in the analytical scheme devised for these data.

When the expected number of bird observations, calculated from the volume of foliage of each species of tree (or genus in the case of oak), is compared with the actual number of observations for the entire bird community in a particular species of tree, it is evident that *Pinus leiophylla* and *Quercus* sp. were used much more than would be predicted on the basis of availability, whereas *Juniperus deppeana* was used much less than its volume would seem to indicate (fig. 2).

Volumes were calculated from measurements taken from the tree profile or silhouette rather than actual density of the foliage. The foliage is much denser in juniper than in either pine or oak, and thus there is actually a greater difference between bird use and available foliage than shown above.

During the nesting season, most bird species feed insects to their young. Only 24.7 per cent of all feeding observations were made of birds in juniper while 40.3 per cent and 35 per cent were made of birds in oaks and the pine, respectively (cf. dominance figures, table 1). Insect populations may be lower in juniper than in other species of trees present, offering less food per unit volume of foliage for the birds. Southwood (1961) has shown that of all tree genera in Great Britain, *Juniperus* has the fewest species of insects, whereas *Quercus* has the largest. While a wider range of different insects may live in oak, this does not preclude the possibility of a few insect species with large populations in juniper. Juniper berries, eaten by some species, did not ripen until near the end of the breeding season. Both species of oaks shed their leaves, flowered, and produced new leaves during the nesting season. During the course of study, I observed that the oak flowers and young leaves attracted a large number of insects, which were heavily preyed on by numerous species of birds. At the time of flowering, the oaks do not have a dense canopy, and thus insects may simply be more conspicuous to the birds. Marshall (1957) and Humphrey (1962) state that juniper is presently spreading into new areas and increasing in areas where it was once sparse because of over-grazing, erosion, fire protection, climatic change, or a combination of these factors. If juniper was once unimportant as a member of this plant community, as Marshall (1957) believes, then the birds may have had little exposure to it in the past. Now that juniper has become so prevalent, the birds may not yet have learned to use it as efficiently as the more open foliage of the oaks and pines.

Some species of birds utilize juniper to a greater extent than others (figs. 3, 4). The Black-throated Gray Warbler spent 34 per cent of its time in juniper and three of five nests were located there. The Chipping Sparrow and Bridled Titmouse spent 16 per cent of their time in juniper, while the Common Bushtit was observed there 29 per cent of the time. The Chipping Sparrow and Black-chinned Hummingbird also commonly nested in juniper. Four of seven nests of the former species were in juniper while the latter had three of five nests there. Thus, the three most abundant species in the plant community (Chipping Sparrow, Black-throated Gray Warbler, and Black-chinned Hummingbird) are able to utilize successfully the high foliage density provided by juniper for nest-sites. This ability to use juniper may be an important reason for their relative success in this area. This may not have been true before the spread of juniper. In contrast, two species with low densities, Grace's Warblers (*Dendroica graciae*), three pairs per 100 acres, and Pygmy Nuthatches (*Sitta pygmaea*), two pairs per 100 acres, spent 98 per cent and 78 per cent of their time, respectively, in the low density *Pinus leiophylla*.

For the five species that were observed on 45 or more occasions, use-index values were calculated. The higher the use-index, the greater the discrepancy between availability of all types of trees and the actual use of these trees. The use-index values are as follows: Black-throated Gray Warbler, 9.4; Chipping Sparrow, 15.5; Bridled Titmouse, 16.2; Common Bushtit, 17.4; and Grace's Warbler, 54.6. The correlation (Spearman Rank coefficient) between species abundance on the study area and total foliage use is significant at the five per cent level. However, the most abundant bird, the Chipping Sparrow, may have attained its high population because its ability to utilize the ground for obtaining its requirements is greater than in the other species present. The fit for the Chipping Sparrow would have been better if a method had been used to include nest observations since this species had 60 per cent of the located nests in juniper.

The above analysis deals with total bird use per total volume of foliage for the different species of trees present on the study area, but disregards the height distribution of these bird observations and foliage. The vertical distribution of birds within the community obviously is also important in terms of plant community use and the species interactions which determine how the community is to be subdivided. Figures 2, 3, and 4 show a close fit for bird use and available foliage per height class, and also considerable overlap between bird species. Figure 2 shows the total use of all birds for all trees combined. There is an apparent overuse of the foliage between 30 and 60 ft in both pine and juniper. The bird-use line for juniper extends higher than the volume of foliage line in figure 2 because a few junipers on the area were taller than any recorded in the tree sampling. Since most observations were made during early morning hours, this slight concentration in the upper areas may be due to two factors. First, the majority of singing is done during the early morning hours, and most species sing from the uppermost vegetation in

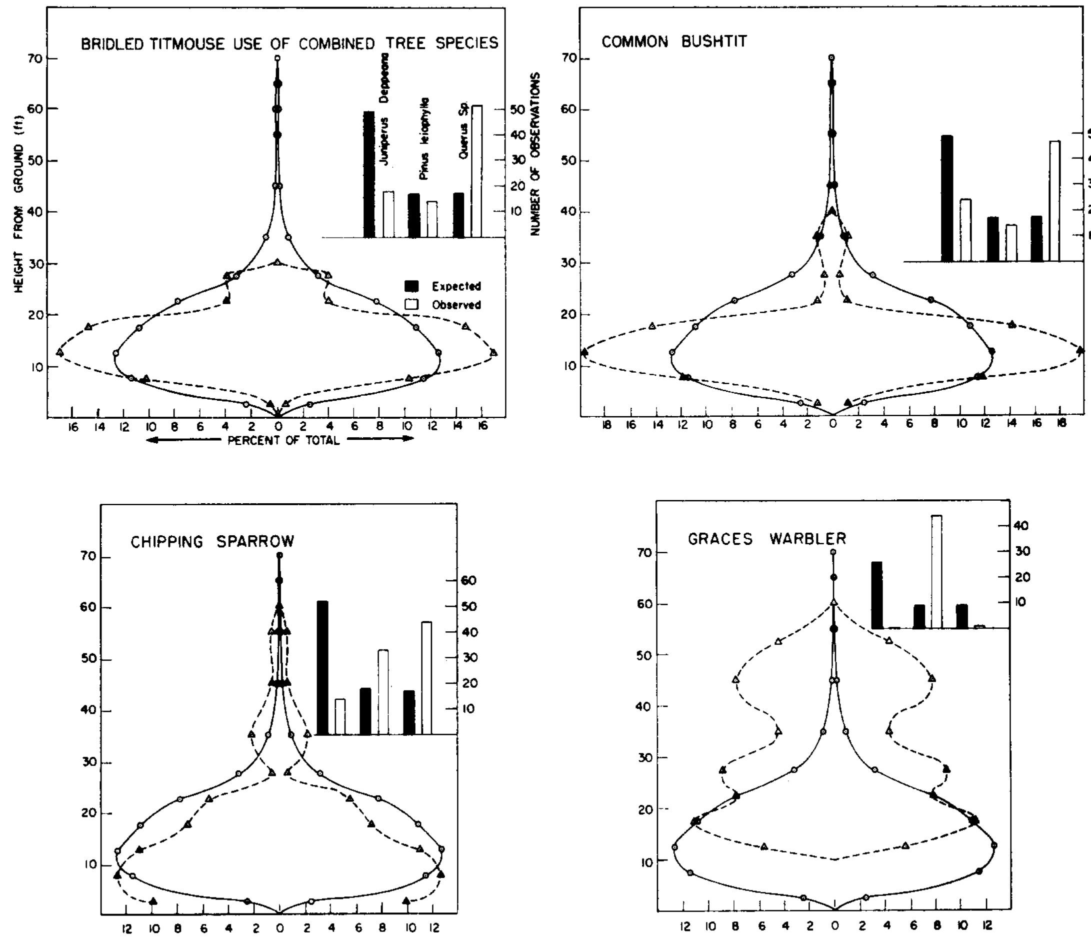

FIGURE 3. Use of the available foliage volume of all tree species combined by four common bird species in the oak-juniper study plot. The open bottom of the broken line signifies the species was observed on the ground. The bar graph represents expected and observed use of the three tree species.

their territories (Martin 1960). Second, as the sun rises, it illuminates and warms the upper portions of the trees first; consequently, insects at these levels may become active before those at lower levels, thus attracting foraging birds to these heights for a brief period in the morning. When observations were divided into singing and feeding, this same pattern of overuse persisted for both activities.

Total bird use in the oaks and juniper showed a height distribution expected if volume of foliage as measured in this study is an important factor in the height distribution of birds. The fit for pine, however, was not as good. The higher portions were overused, whereas a large volume of little use existed between 15 and 30 ft. The overuse of the upper heights may be explained as above, since the pines stood somewhat higher than the oaks and juniper.

The Black-throated Gray Warbler was commonly found at heights of 15 to 20 ft in oak and juniper and from 10 to 15 ft in the pine (fig. 4). Grace's Warbler was found almost exclusively in pines at heights above 15 ft (fig. 3). Thus, these two warblers divide the pines in such a way that there is little chance for interaction. No conflicts were observed between these species. The Bridled Titmouse was commonly found between 10 and 20 ft, ranging up to 35 ft, while the Common Bushtit spent the majority of its time at the same height but ranged up to 40 ft (fig. 3). On three occasions Bridled Titmice chased Common Bushtits from trees.

For the five species of birds observed more than 45 times, the use-index value for foliage height are as follows: Black-throated Gray Warbler, 0.9; Bridled Titmouse, 1.1; Common Bushtit, 2.4; Chipping Sparrow, 4.5; and Grace's Warbler, 20.4. The Chipping Sparrow has a lower rank in this analysis than in the last because of its habit of spending so much of its time low in the foliage. The other four species

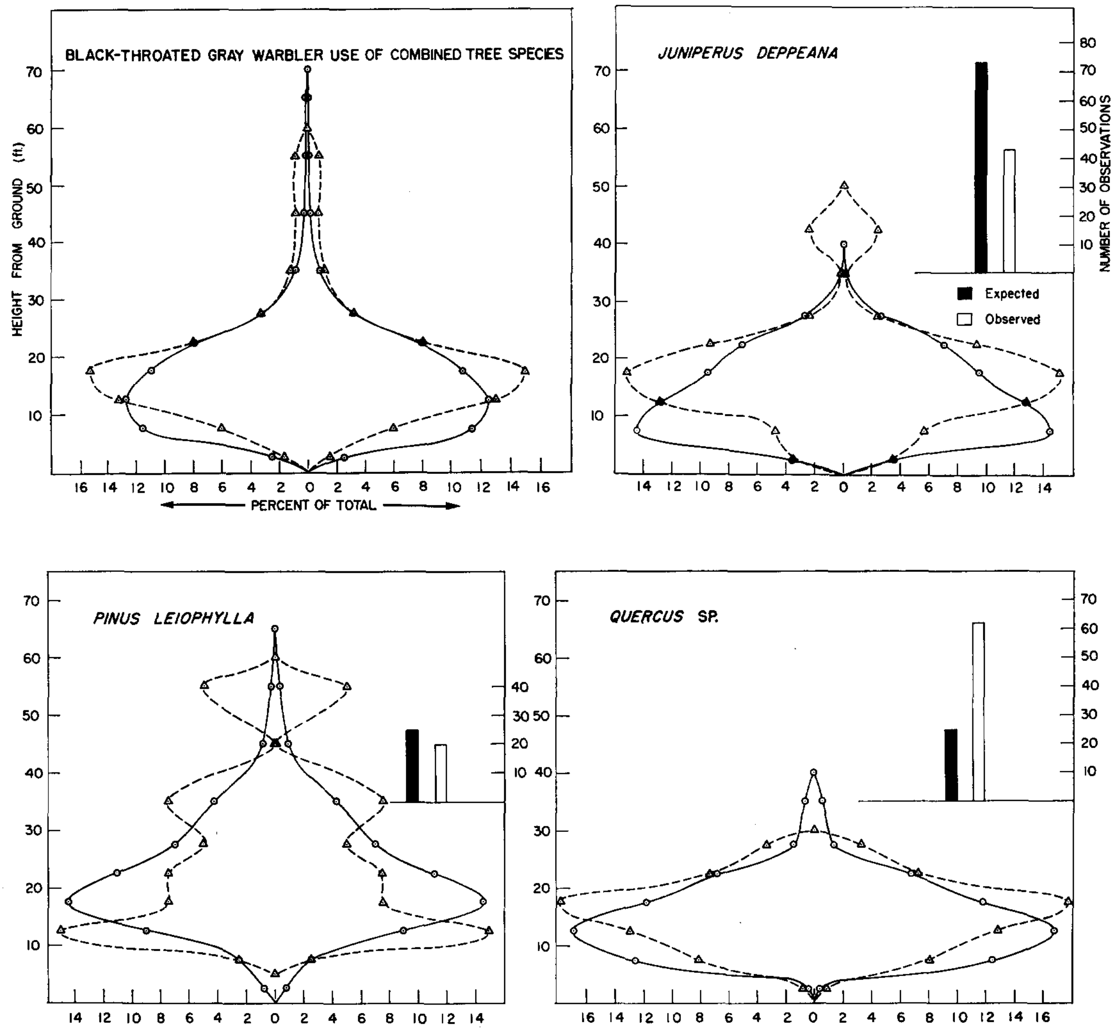

FIGURE 4. Black-throated Gray Warbler use of the available foliage volume in each height class and by tree species (bar graph).

attain the same rank order in this analysis as they did for total volume of foliage use per tree species.

These two measures of foliage use (volume of foliage by height class, and volume of foliage for each species of tree) are related and a poor fit in one would seem to indicate a poor fit in the other. Thus, if a bird is highly selective as to the species of tree it utilizes, as is the case for Grace's Warbler, the foliage distribution of that tree will then be a determining factor as to the heights at which the bird is found throughout the community.

The total use-index value for all birds is 165.0 when bird use is compared with total volume of foliage per species of tree and 123.4 when bird use is compared with the total volume of foliage by height class. Thus, the selection or avoidance which is apparent for use of a particular tree species is greater than the selectiveness for particular heights in the tree itself. Requirements provided by the sparsely-used juniper are probably found throughout the entire foliage of the tree. Escape cover would be a likely requisite provided by juniper uniformly throughout its foliage.

PONDEROSA PINE FOREST

This study plot was located within one of the only accessible areas of mature ponderosa pine in the mountain where the terrain was relatively flat. The plot was established at the intersection of the road to Barfoot Park and the Cave Creek Canyon road to Rustler's Park. Elevation ranged from a low of 8100 ft on the northeast edge to 8500 ft along the northwest side. The southeast one-third of the area sloped 3° downward to the south. A steep east-facing incline of about 40° was encountered from

FIGURE 5. Ponderosa pine forest study area showing *Pinus ponderosa* and *Pseudotsuga menziesii.*

near the center of the plot to the west boundary (fig. 5).

Of the seven species of trees present *Pinus ponderosa* was the major dominant, followed by *Pinus strobiformis* and *Pseudotsuga menziesii* (table 3). Rare tree species present but not included in the sample included *Quercus gambelii* and *Quercus rugosa.* There were about 100 trees per acre; each individual tree occupied a mean area of 436 ft^2, with a mean distance between trees of 21 ft. The canopy volume of foliage totaled 211,325 ft^3 per acre (table 4). The total basal area for all tree species was 89 ft^2 per acre. The mean height of the canopy was 37 ft; the tallest tree sampled was a 92-ft ponderosa pine, but a few Douglas fir were over 100 ft tall. The ponderosa pine were segregated into two groups: old trees between 60 and 90 ft tall, and young second-growth trees between 10 and 40 ft tall. Most *Pinus strobiformis* were under 40 ft.

Pinus ponderosa, with a density of 188 individuals per acre, was the most abundant constituent of the shrub and sapling understory, with the other tree species contributing the following numbers of saplings per acre: *Pinus strobiformis*, 40; *Pseudotsuga menziesii*, 46; *Quercus hypoleucoides*, 28; and *Juniperus deppeana*, 4.

The vegetation had a park-like appearance, with the canopy open and the larger ponderosa pines spread well apart. The smaller second-growth pines were located in scattered dense clumps throughout the study area. Few young trees had become established on the steeper

TABLE 3. Composition of trees in the ponderosa pine forest community.

Species	Relative density[a]	Relative dominance[a]	Relative frequency[a]	Importance value[a]
Pinus ponderosa	81.8	89.4 (84.2)[b]	61.9	233.1
Pinus strobiformis	6.3	4.2 (5.3)	15.9	26.4
Pseudotsuga menziesii	6.8	4.2 (7.6)	12.7	23.7
Quercus hypoleucoides	3.8	1.2 (0.8)	6.3	11.3
Juniperus deppeana	1.3	1.0 (2.1)	3.2	5.5
Total	100.0	100.0	100.0	300.0

[a] As in table 1.
[b] Calculated from foliage volume data (table 4).

TABLE 4. Foliage volume (ft^3) of trees and saplings in the ponderosa pine forest community.

Height class (ft)	Species										Total (per acre)
	Pinus ponderosa		*Pseudotsuga menziesii*		*Pinus strobiformis*		*Quercus hypoleucoides*		*Juniperus deppeana*		
	Trees	Saplings	Trees	Saplings	Trees	Saplings	Trees	Saplings	Trees	Saplings	
0–4	675	1,496	536	692	1,687	700	322	335			6,443
5–9	5,319	1,873	3,887	663	2,263	418	1,190	2,212	825		18,650
10–14	7,848	658	4,192	246	1,977	12	219	237	1,650		17,039
15–19	9,345	27	2,961	84	952				1,650		15,019
20–24	19,403		1,864	9	212				347		21,835
25–29	20,594		1,150		26						21,770
30–39	33,589		1,070		1,909						36,568
40–49	38,997		316		2,265						41,578
50–59	28,493		26								28,519
60–69	9,669										9,669
70–79	3,737										3,737
80–89	497										497
90–99	1										1
Total	178,167	4,054	16,002	1,694	11,291	1,130	1,731	2,784	4,472		221,325

slopes where very tall ponderosa pines dominated.

This plant community supported 31 species of breeding birds with a total nesting density of 336 nesting pairs per 100 acres. The number of breeding species and the size of their populations are much higher than those reported by Snyder (1950) from a ponderosa pine forest in the Colorado Rocky Mountains. The most common breeding species, with their densities, were: Pygmy Nuthatch, 43; Mexican Junco (*Junco phaeonotus*), 40; Olive Warbler (*Peucedramus taeniatus*), 23; Grace's Warbler, 20; Western Bluebird (*Sialia mexicana*), 20; Robin, 17; Brown Creeper (*Certhia familiaris*), 16; Broad-tailed Hummingbird (*Selasphorus platycercus*), 15; Solitary Vireo (*Vireo solitarius*), 14; Red-shafted Flicker, 13; White-breasted Nuthatch, 10; House Wren (*Troglodytes aedon*), 10; Audubon's Warbler (*Dendroica auduboni*), 10; and Steller's Jay (*Cyanocitta stelleri*), 10. These 14 species contributed 78 per cent of the total nesting pairs present.

A total of 1430 observations was made of individual birds using various dimensions of this plant community. Of these, 71 per cent were made between 05:00 and 10:00. Twelve per cent of these observations were made of birds on the ground. The Robin was found on the ground 48 per cent of the time, while the Mexican Junco and Red-shafted Flicker used the ground 46 and 38 per cent of the time, respectively. No sampling was done of the dead trees and stumps present in this area, but birds observed using them were recorded. Seven per cent of the total number of observations were of birds utilizing these dead trees and stumps. The Western Wood Pewee (*Contopus sordidulus*), 3 pairs per 100 acres, and Coues' Flycatcher (*Contopus pertinax*), 8 pairs per 100 acres, sang and fed from dead trees 33 and 19 per cent of the time, respectively. The House Wren spent 67 per cent of its time feeding and singing from fallen logs. Seven observations were made in miscellaneous saplings which were too rare to be present in the vegetation data. The above observations, comprising 19 per cent of the total number of observations, were not included in the analysis of bird use and available foliage volume.

When the expected number of bird observations calculated from the foliage volume of each species of tree is compared with the actual number of observations for the entire bird community there is an exceptionally good fit. Figure 6 shows this fit for total bird use for the combined tree species and separately for *Pinus ponderosa* and *Pseudotsuga menziesii* in which 95 per cent of the usable observations were made. Only 37 observations were made in *Pinus strobiformis*, while the expected number was 64. The use-index value calculated from these data is a low 6.7 for the total bird community. Feeding observations in the four most abundant tree species yield per cent values similar to those of total use. Of all feeding behavior, 90 per cent was observed in *Pinus ponderosa*, six per cent in *Pseudotsuga menziesii*, three per cent in *Pinus strobiformis*, and one per cent in *Quercus hypoleucoides* (see dominance values, table 3). Non-feeding activities within a tree species yields similar percentages: *Pinus ponderosa*, 89; *Pseudotsuga menziesii*, 6; *Pinus strobiformis*, 4; and *Quercus hypoleucoides*, 1.

The use-index value for birds in the total foliage of the various trees present was calculated for the six species of birds which were observed at least 70 times. These values are as

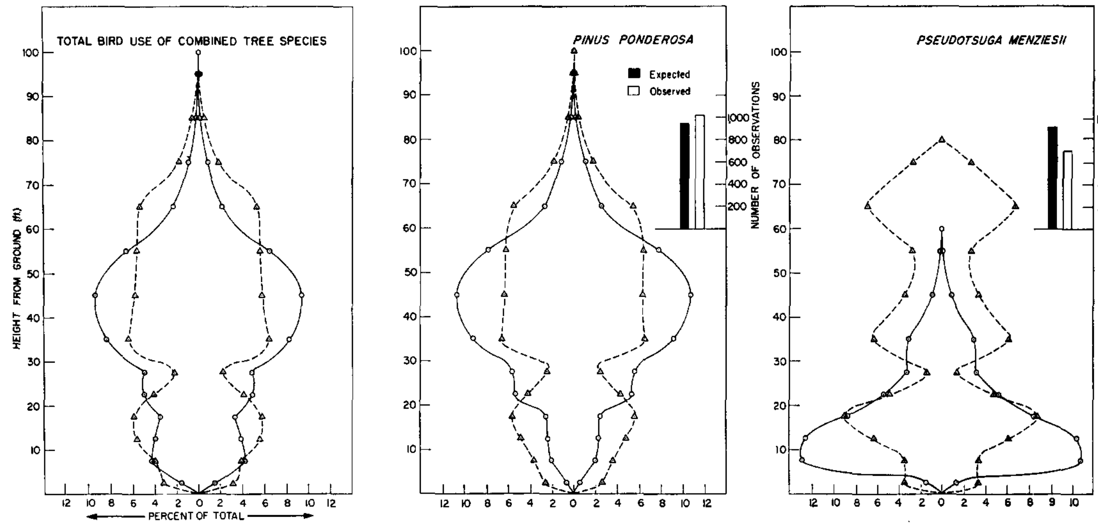

FIGURE 6. The total bird use of tree foliage in the ponderosa pine forest. The shaded bar is the expected bird use in each species of tree based on available foliage volume of that tree species. The open bar is the actual number of observations. The solid line is the per cent of total foliage volume in each height class. The broken line is the per cent of total observations of birds in each height class. The middle and right figure show total bird use and available foliage volume in the two most abundant tree species.

follows: Pygmy Nuthatch, 1.0; Mexican Junco, 1.1; Olive Warbler, 1.3; Grace's Warbler, 1.4; Western Bluebird, 4.3; and Solitary Vireo, 4.4. The correlation (Spearman Rank coefficient) between species abundance and total foliage use is significant at the one per cent level.

The greatest amount of foliage for all trees and saplings combined was found between 40 and 49 ft, where 41,578 ft^3 of foliage per acre was present (fig. 6; table 4). Since there were two definite height classes of trees in the study area (tall old trees and smaller second growth trees), the plotted foliage profiles are somewhat irregular. The taller, older trees with a large diameter at the lower edge of the canopy contributed most of the foliage volume above 30 ft. The lower edge of the canopy of these trees lies between between 30 and 40 ft from the ground. However, 50 per cent of the trees measured were less than 35 ft tall. Most of the Douglas fir in this study area were less than 50 ft tall, although a few larger firs were present in the plot but were not sampled.

As can be seen from figure 6, there is a slight concentration of bird activity in the foliage at the lower heights, less use than expected in the median heights, and some overuse at the top of the forest canopy. A very apparent restriction of use exists between 25 and 30 ft. This is the height at which the second-growth trees peak and is just below the height at which the canopy of many of the older trees begins. The foliage volume diagrams (figs. 6, 7, 8) do not show a restriction at this height because there were a few trees of intermediate height with a wide crown diameter.

The use of ponderosa pine by all species of birds is very similar to that shown for the entire community (fig. 6) because this pine predominates, contributing 82 per cent of the tree and sapling foliage and 89 per cent of the bird observations.

The fit of total bird use of Douglas fir foliage by height class is not close, as there is a large section of low foliage which is underused while the upper heights show a heavy concentration of bird activity. Thus, the few very tall Douglas firs in the area, which do not appear in the vegetation sample, were used greatly out of proportion to their availability. When bird observations at the various height classes in this tree species are classified as feeding or non-feeding, 26 per cent of all feeding observations occur above 60 ft and 21 per cent of all non-feeding activities occur there. Thus, both feeding and other activities are performed at this height more often than expected on the basis of available volume of foliage. This may be due to the heavy concentration of cones and very dense foliage near the very tips of these trees. Many of the smaller firs had few or no cones.

Figures 7 and 8 show bird use of the foliage present by height class for six species of birds that appear in the sample at least 70 times. The Solitary Vireo has the best fit, with a use-index value of 0.8, even though it was not observed above 70 ft. It was observed more often on the

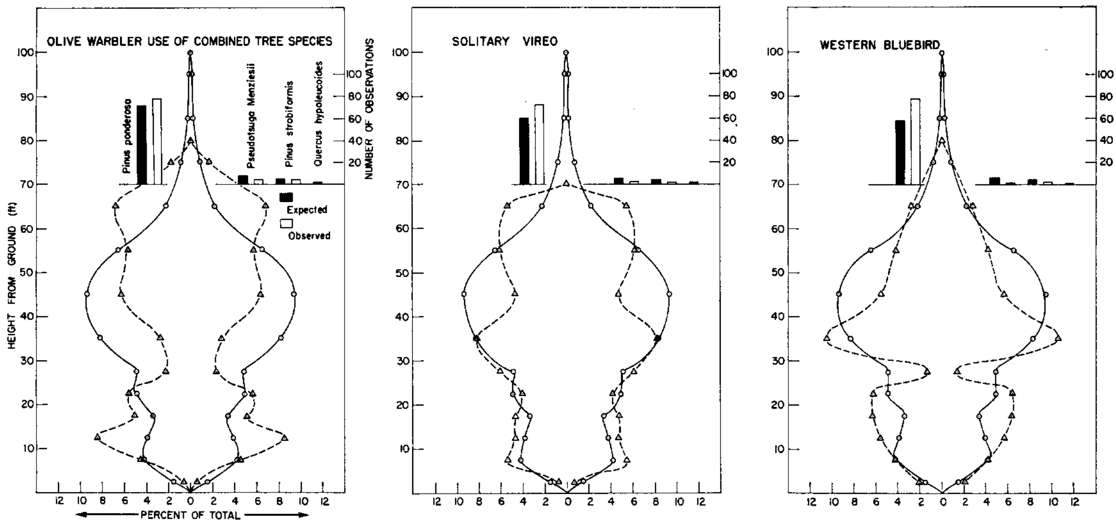

FIGURE 7. The use of available foliage volume of all tree species combined by three common birds in the ponderosa pine study plot. The bar graph represents expected and observed use of the four tree species.

branches and twigs than in the actual green foliage. The Western Bluebird had a use-index value of 1.6. This species was often observed in the lower branches of the large ponderosa pines, from which it flew out to catch flying insects; as a result of this foraging habit, there was a concentration of use between 30 and 40 ft. The Pygmy Nuthatch, which had a use-index value of 2.7, spent more time in the foliage and cones than on the branches and twigs. The Olive Warbler spent nearly equal time at all height classes, ranging up to 80 ft, and had a use-index value of 3.9. This species spent about equal time in the foliage and on the branches and twigs. The Mexican Junco had a use-index value of 9.1 and ranged from the ground to 70 ft, although it spent the majority of its time below 40 ft. Singing males in the tips of pines and firs accounted for 81 per cent of the higher observations. The poorest fit of the six species was found for Grace's Warbler, which had a use-index value of 12.3. This species spent the majority of its time high in the foliage of pines and firs.

The use-index for the total bird community for the total foliage volume arranged by height classes was 20.3. Thus there is a somewhat better fit for total tree species use (6.7) than for use of foliage per height class, or just the opposite of what was observed in the oak-

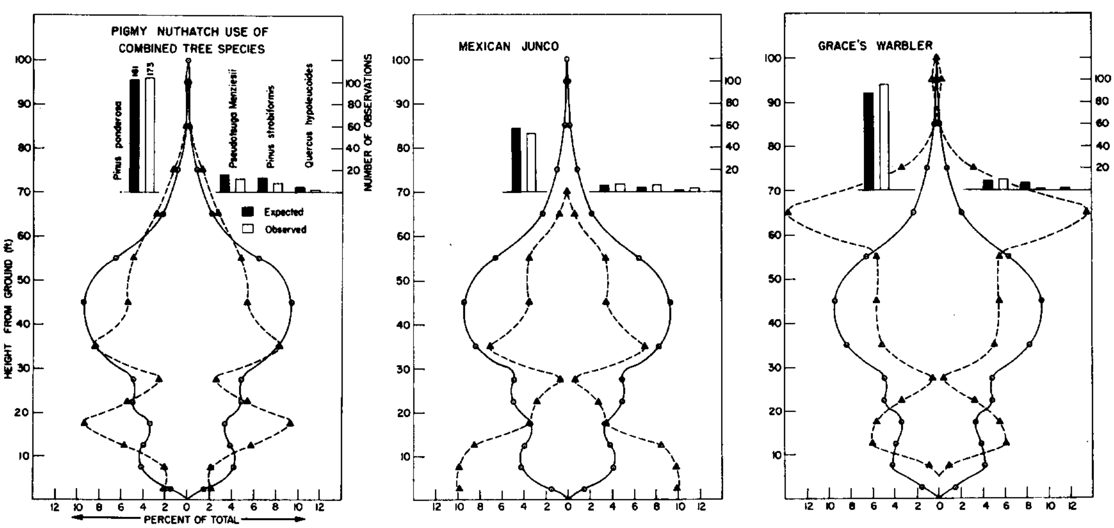

FIGURE 8. The use of available foliage volume of all tree species combined by three common birds in the ponderosa pine study plot. The bar graph represents expected and observed use of the four tree species.

juniper woodland plot. Since all tree species except the oak are coniferous, there may be little selection among them.

The reason for the slightly poorer fit for foliage volume when subdivided into height classes may be the differential insect abundance and activity during different times of day. It was also observed that during rainy and windy weather, common in July and August, the birds often descended to lower heights, increasing the use of the denser, smaller, second-growth trees. Also, when young of most species left the nest, they descended to heights below those normally inhabited by the adults and the latter in turn moved downward. It is common knowledge that areal territories often break down once the young leave the nest, and this suggests that the height boundaries may break down as well. This shift may also reflect higher insect abundance in the shrub and herbaceous layers because of increased soil moisture and plant growth during the rainy season. Root (1967) demonstrated a similar shift in foraging height of the Blue-gray Gnatcatcher (*Polioptila caerulea*) while feeding young, but this downward shift did not correspond to the onset of inclement weather.

The foliage volume measurements are based solely on tree shape profile and not the true inner density of the foliage. This would not be critical if the foliage were evenly distributed throughout the tree and if the foliage distribution were the same for all species and for all trees of the same species, regardless of size class. The foliage of the young, second-growth trees was much denser than that of the taller, older trees. In tall trees, the central area around the trunk consists almost entirely of branches, twigs, and dead needles, whereas the green foliage is limited to the outer edges. Also, as the top of a cone-shaped tree is approached, the inner, more barren, portion of the tree decreases more rapidly as foliage moves inward, so that near the tip there is uniform foliage throughout the profile. This discrepancy between actual foliage and profile volume of the foliage may be another reason for the higher bird use in the upper and lower areas and the underuse of the middle areas of the trees. The birds are probably, therefore, using the foliage in even closer agreement to its availability than the figures show.

In the oak-juniper woodland study area, bird use of the total volume of foliage per species of tree and use of the foliage by height class are not independent. A close fit of bird use with total foliage for a species of tree dictates a close fit for bird use of foliage as it is distributed by height class. This relationship does not occur in this community because of the above mentioned discrepancy between true foliage volume and foliage volume measured by profile. The Solitary Vireo has the best fit for use of foliage volume by height class, but the worst fit for total use of available foliage per tree species. This species spent the majority of its time on branches and twigs, while Grace's Warbler, which had the worst fit for volume of foliage by height class, spent the majority of its time in the actual foliage. Thus, foliage-inhabiting birds, such as Grace's Warbler and Pygmy Nuthatch, show a definite overuse of tree heights where the density of foliage is highest.

CONCLUSIONS

An avian community existing in a particular plant community utilizes the habitat so that each species obtains its requirements in an efficient manner. The morphological, physiological, and behavioral adjustments necessary to avoid or minimize competition within a community probably play a major role in determining how the requisites are to be obtained. Some species show a very close adherence to a specific resource present in the habitat, while others are able to use the overall habitat indiscriminately (MacArthur and Levins 1964). It is important to know how much of a resource is present in a given community, its horizontal and vertical distribution, and how it is used. MacArthur et al. (1962) have demonstrated how important the spatial mosaic or "patchiness" of the vegetation is in determining the presence and abundance of bird species. Data presented earlier depict two ways in which avian exploitation of the available vegetation takes place. First, a bird species may be restricted to a species or life-form of tree. The Pygmy Nuthatch, which appears partial to conifers, is such a species. Second, a bird species may utilize a particular height in the canopy and make use of all trees with foliage at that height. The Chipping Sparrow appears to do this. Grace's Warbler appears partial to both aspects, being somewhat restricted to upper reaches of pines. The foliage volume figures for pines strongly suggest that foliage volume may be an imporant factor in limiting the densities of the Pygmy Nuthatch and Grace's Warbler, even though the former species is a cavity nester.

There is a great deal of overlap in heights at which bird species exist. Presence of two or more species at a particular height does not necessarily mean competition is occurring, since each species may be selecting a different kind or size of food and may obtain it in a different manner. A species may also select a different vegetational configuration for a songpost or nest site (MacArthur 1958). The vertical distributions of the Bridled Titmouse and the Common Bushtit are very similar, but the latter species spends a greater share of its time feeding out at the tips of branches and twigs, picking small insects off the foliage, while the Bridled Titmouse spends more time foraging in crevices on trunks and branches.

Avian use of oak, juniper, and Douglas fir illustrates some striking differences, which may reflect the role of these trees in providing basic requirements for the avian community. The very heavily used oak shows an exceptionally good fit for bird use according to the height distribution of the foliage. This is also true for the sparsely used juniper. Thus, the entire tree is exploited in both cases, even though there is a large discrepancy in bird use of the two trees compared with their availability. In contrast, the bird community used Douglas fir in proportion to its overall availability in the community, but the upper portions show a heavy concentration of bird activity in comparison to foliage available at these heights. This suggests a concentration of some requirement at these heights.

These three patterns of tree use by the bird community may provide an index of the relative desirability of a given species of tree, which may be reflected in the overall density of the breeding birds. On the basis of these three patterns of use, oak would be the most desirable tree, while juniper would be the least desirable.

The bird aggregation of the ponderosa pine forest shows some major differences in foliage use when compared with the bird aggregation of the oak-juniper woodland. The use-index value for the oak-juniper woodland community is 123.4 for foliage use by height class and 165.0 for use of the total foliage of all species of trees. The ponderosa pine forest avifauna has the following values: total foliage use of all species of trees, 6.7 and foliage use by height class, 20.3. Since the lower the use-index value the better the fit of bird use with available foliage, the ponderosa pine avifauna appears to utilize all tree species and all tree heights more in proportion to their availability than does the avifauna of the oak-juniper woodland community. This appears to indicate a greater efficiency on the part of the ponderosa pine avifauna. There was also a slightly higher use of the ground (three per cent) in the ponderosa pine forest, which may account for a small portion of the higher population densities.

The difference between the two areas in use of the total foliage of a tree without regard to its distribution has been ascribed to the low bird use of juniper. This may explain why in the oak-juniper woodland, the use of foliage by height class gives a better fit than bird use of the total foliage. Just the opposite appears true for the ponderosa pine avifauna. There is a better fit of bird use in total foliage of each tree than in foliage distributed by height classes. This reversal seems to reflect the high concentration of activities in the tips of Douglas fir and the difference between measured and actual foliage volume, a discrepancy not observed for the oaks or junipers. Also, the birds of the ponderosa pine forest showed a definite movement into the lower strata during inclement weather, and such weather was much more common in the pine forest than in the oak-juniper woodland.

The greater efficiency of the ponderosa pine forest avifauna is also indicated by the total number of nesting pairs on both areas. The ponderosa pine forest supports about 69, or 21 per cent, more breeding pairs than the oak-juniper woodland. This pine forest also contained 27,569 ft^3 per acre, or 12 per cent, more foliage than the oak-juniper woodland.

If the foliage were equally divided among all nesting pairs, the mean volume of foliage per bird territory would be 72.567 ft^3 in the oak-juniper woodland and 65,871 ft^3 in the ponderosa pine forest. Thus, the 12 per cent more foliage available within the territories of the former bird community may be accounted for by the low use of juniper.

The lower nesting bird populations in the oak-juniper woodland may not be a result solely of available habitat, but may also be partly determined by the unique plant species composition of this area. As Marshall (1957) points out, this area contains a heterogeneous mixture of plant life forms, but only a small percentage of the nesting species requires this combination to exist. Those that do use the existing plant complex have relatively high populations. Some bird species are partial to pines, others to oaks, and few if any to juniper. Thus there are few jack-of-all-trades species present in the oak-juniper woodland.

MacArthur and MacArthur (1961) have demonstrated that foliage height diversity may be an important factor in determining bird species diversity. The methods used in this study provide foliage information by height classes. Using the percentage of foliage present in each height class, it is possible to calculate a diversity index (H′) as did the above authors. This value is 2.25 for the ponderosa pine forest and 1.73 for the oak-juniper woodland. This diversity index (H′) for the oak-juniper birds is 3.29 and for the ponderosa pine birds, 3.10. The lack of correlation between bird species diversity and foliage height diversity may well reflect the differential use of some portions of the foliage as demonstrated herein.

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