

BREEDING BIRD USE OF A PINYON-JUNIPER-PONDEROSA PINE ECOTONE

WILLIAM F. LAUDENSLAYER, JR., AND RUSSELL P. BALDA

DIVERSITY of birds in an ecotonal area is usually higher than in the two major communities that contribute plants to it. This is so because specific species are often attracted to ecotones and supplement the birds from each major community that inhabit these edges. Numerous workers have depicted bird populations of ecotones of the central and eastern U.S. (i.e. Beecher 1942, Johnston and Odum 1956) but little work has been done in the mountains of southwestern U.S., where ecotones are very narrow bands because of abrupt elevational changes that cause abrupt vegetational changes. Few if any characteristic "edge" bird species appear to breed in these ecotones, in striking contrast to what occurs in central and eastern U.S. In the western U.S. mountains a clearly distinguishable and easily recognized ecotone exists between the mid-elevation woodlands and higher elevation ponderosa pine (*Pinus ponderosa*) forest.

The purpose of this study was twofold. First we determined the composition and densities of the breeding birds of a pinyon pine (*Pinus edulis*)-juniper (*Juniperus* spp.)-ponderosa pine ecotone to ascertain the contribution made by species from each major community and whether any additional "ecotonal" species inhabited the area. Second we determined how each species used or partitioned the ecotone. This was done to ascertain if species in the ecotone used only the segments of the habitat contributed by the community they normally inhabit, or if they used a combination of the plants from each community.

Partitioning of the habitat can occur by interspecific territoriality (Selander and Giller 1959, Dixon 1961, Orians and Willson 1964). When territories of tree-dwelling birds overlap, partitioning of the habitat may involve the subdivision of the foliage. This can occur by selection of particular tree species (Hartley 1953, Newton 1967, Balda 1969) or division of the vegetation into various horizontal levels (Colquhoun and Morley 1943, MacArthur 1964, MacArthur et al. 1966, Balda 1969). Subdivision may also involve selection of the outer foliage or the inner branches and trunk (Hartley 1953, Morse 1967, Sturman 1968). Also, species may obtain their prey using different foraging behaviors (Sturman 1968, Lack 1971) or may obtain prey of different sizes depending on bill size (Hutchinson 1959, Root 1964, Schoener 1965). Although frequent mention is made in the literature of how species inhabiting

ecotones require habitat components of either major communities contributing to the ecotone, or in the case of "edge" species the combination of components because of their juxtaposition, we know of no studies using the contemporary methods cited above to prove that such is the case. This study attempts to make such an analysis.

METHODS

Vegetative sampling.—The vegetation was sampled using the plotless point quarter method (Cottam and Curtis 1956) for the trees and circular plots for the shrubs and saplings; 144 points containing 576 trees were sampled. Shrubs and saplings were censused and measured in 200 0.016-ha plots.

Data collected from each tree included: tree species, tree shape (either cone, hemisphere, or cylinder), distance from the point to the tree, and tree height (measured with an Abney level). The crown of each tree was measured as an outer area, consisting of green needles and twigs bearing foliage, and an inner area consisting of large twigs, branches, and trunk where little green foliage existed. The distance from the ground to the height where the foliage began was also measured. Trees with a dbh greater than 7.6 cm were classified as trees, except for the junipers, for which a dbh could not be taken because of their shrublike life-form. Junipers with a basal diameter of 15.2 cm or greater were classified as trees. The volume of each tree species was determined using the standard formulas for a cone, cylinder, and hemisphere. In addition, foliage volumes were determined per 1.5 m horizontal height class intervals. Thus total foliage volume and its distribution into horizontal bands was known for the study area. The relative density, dominance, frequency, and importance value for each tree species were also determined.

Measurements of shrubs and saplings included the total height and diameter of each plant. Calculations made for shrubs and saplings, in addition to height class volumes were: relative densities, frequencies, and absolute densities.

Bird sampling.—The spot map method (Williams 1936, Kendeigh 1944) was used to determine the breeding bird densities from April to June 1971; 26 censuses were taken during this period on a surveyed plot of 14 ha. Some aspects of the foraging pattern of the nesting birds were also examined. For each individual seen, the following information was recorded: bird species, tree species, bird height in tree, bird position in tree (inner branches or outer foliage), and the bird's foraging posture (hanging or standing). We analyzed the bird species relationships with the tree species and tree height classes using a modified Chi-square value or use-index value (Balda 1969). The area of each territory (a minimum area) was determined by outlining all known locations of singing males on a map and measuring the area with a compensating planimeter.

Birds collected adjacent to the study area were weighed and the length of the exposed culmen measured.

Description of study area.—The study area was 22 km north of Flagstaff, Arizona at an elevation of 2130 m. This elevation is the upper limit of the pinyon-juniper woodland and the lower limit of the ponderosa pine forest in this area.

The area contained five species of trees: ponderosa pine, pinyon pine, rocky mountain juniper (*Juniperus scopulorum*), one-seed juniper (*J. monosperma*), and alligator juniper (*J. deppeana*). The most dominant life-form of tree was the collection of junipers, which when combined had the greatest relative density, dominance, and frequency, and hence the greatest importance value (Tables 1, 2). The junipers

TABLE 1
COMPOSITION OF THE TREE SPECIES

Species	Absolute density (stems/ha)	Relative density	Relative dominance	Relative frequency	Importance value
<i>Juniperus</i> spp.	109.7	38.0	46.2	38.0	122.2
<i>Pinus edulis</i>	115.2	39.8	29.3	37.0	106.1
<i>Pinus ponderosa</i>	64.0	22.2	24.5	25.0	71.7
Total	288.9	100.0	100.0	100.0	300.0

were hemispherical or cylindrical in shape, rarely reached heights of over 7 m, and all had typically small, compressed, scale-shaped leaves. Branches and foliage usually extended to within $\frac{1}{2}$ m of the ground. The pinyon pine was of similar life-form but bore needles about 3 cm long. The ponderosa pines had long needles, distinct straight trunks, a conical life-form, and grew to heights of 19 m (Table 2).

The shrubs and saplings on the area averaged 432 individuals per ha. Horse-brush (*Tetradymia canescens*) was most dense with 208 individuals per ha. The tree sapling densities were much less, with the junipers comprising 96 individuals per ha followed by pinyon pine (89 per ha), and ponderosa pine (7 per ha). The ecotone appears to be relatively permanent.

RESULTS

Breeding bird populations.—The breeding bird community consisted of 5 species representing 3 families: Paridae (3 species), Vireonidae (1 species), and Fringillidae (1 species). The number of species lies between those found by other workers in the pinyon-juniper woodlands.

TABLE 2
FOLIAGE VOLUME (m³) OF EACH TREE SPECIES PER HA

Height (m)	<i>Juniperus</i> spp.		<i>Pinus edulis</i>		<i>Pinus ponderosa</i>		Total
	Trees	Saplings	Trees	Saplings	Trees	Saplings	
0 - 1.5	2172	35	1229	88	272	4	3799
1.6- 3.0	2387	16	1164	48	722	2	4339
3.1- 4.5	1972		808		590		3371
4.6- 6.0	882		459		412		1753
6.1- 7.5	150		176		384		710
7.6- 9.0	3		108		289		400
9.1-10.5			4		192		196
10.6-12.0					143		143
12.1-13.5					101		101
13.6-15.0					87		87
15.1-16.5					78		78
16.6-18.0					69		69
18.1-19.5					1		1
Total	7565	51	3949	136	3340	6	15,047
Percent inner core	25		15		24		

Beidleman (1960) reported 2 species and Hering (1957) 9 breeding species in Colorado per 40 ha. The number of species is low when compared to the diversity of relatively undisturbed ponderosa pine forests. Carothers et al. (1973) report 23 species, Szaro and Balda (MS) 19 species, and Balda (1969) 31 species breeding in southwestern ponderosa pine forests. Thus, the ecotone supports about the usual number of pinyon-juniper species but far fewer ponderosa pine species.

In addition to the five breeding species on the area rare breeding species not on our plot were Broad-tailed Hummingbird (*Selasphorus platycercus*) and Common Flicker (*Colaptes auratus*) from the ponderosa pine forest, and Black-chinned Hummingbird (*Archilochus alexandri*), Piñon Jay (*Gymnorhinus cyanocephalus*), and Black-throated Gray Warbler (*Dendroica nigrescens*) normally found in the pinyon-juniper woodland. The ubiquitous Mourning Dove (*Zenaida macroura*) was also a rare breeder.

The five common breeding species are not usually found together because of their preferences for the major plant communities that contribute to the ecotone. The Mountain Chickadee (*Parus gambeli*) and Solitary Vireo (*Vireo solitarius*) generally inhabit the ponderosa pine forest, whereas the Plain Titmouse (*Parus inornatus*) and Bushtit (*Psaltriparus minimus*) are usually found in the pinyon-juniper woodland. The Chipping Sparrow (*Spizella passerina*) is found in both plant communities in northern Arizona (Phillips et al. 1964). Thus these five species fall into three natural categories: forest species, woodland species, and one ubiquitous species. The six rare species that occasionally breed in the ecotone fall into the same three categories.

The bird species diversity (H') of the area was 1.47. This value falls between various grassland values of 1.51 and 1.62 (Wiens 1969) and 0.65 and 1.34 (Cody 1966). It was much lower than that of an oak-juniper woodland (2.15) and ponderosa pine forest (2.28) (Balda 1969). The avian diversity of this ecotone was therefore closer to that found in grassland regions than it was to that found in other woodland and forest habitats. This particular ecotone does not support an avian community more diverse than the two communities that flank it and contribute the dominant plants to it. This is an interesting contrast to our generally accepted ideas about "edges" and ecotones (e.g. Odum 1971). Reasons for this difference will be discussed later.

Territory.—The mean territory sizes for each species of breeding bird varied from 1.22 ha to 2.78 ha (Table 3). The Chipping Sparrow occupied the largest total area and had the largest mean territory size. This species utilized the ground as its primary foraging stratum, whereas the other four species (all with smaller territories) used an important

TABLE 3
DENSITIES AND TERRITORY SIZES OF THE BIRD SPECIES

Species	Pairs per study area	Pairs per 100 ha	Mean territory size (ha)
<i>Parus inornatus</i>	5.5	39.5	1.2
<i>Parus gambeli</i>	1.5	9.9	1.5
<i>Psaltriparus minimus</i>	2.75	19.8	1.4
<i>Spizella passerina</i>	4.75	34.7	2.8
<i>Vireo solitarius</i>	1.5	9.9	1.7
Total	16.0	113.8	

additional stratum (foliage) to a much greater extent. The heavy use of the foliage probably allowed these four species to subsist on smaller territories.

Species could use the ecotone by subdividing it into mutually exclusive territories. The Chi-square test was employed to determine if territories overlapped or were spatially separate. Lack of territory overlap could indicate interspecific territoriality. The expected amount of overlap for each pair of species was determined using set theory, by calculating the probability of two areas overlapping when the probability of their occurrence is known. The null hypothesis, that no spatial segregation existed, was supported by a Chi-square value of 19.74 with 9 df, and was accepted over the alternative hypothesis of spatial exclusion. Comparing the three parids, the Chi-square of 4.71, with 2 df, indicated that they showed no significant amount of segregation at the 99% confidence level. Apparently the five breeding species did not space themselves out in the ecotone to utilize separate territories, but showed a high degree of territorial overlap. Because such is the case, partitioning of the ecotone may have occurred for different components.

Tree species selection.—For statistical purposes we assumed that the number of times a bird species was observed in a certain species of tree was related to the volume of available foliage of that tree species and that the observers were equally competent at finding birds in all tree species. The expected numbers of observations, therefore, were calculated from the total number of bird observations and the percentage of foliage volume contributed to the overstory by each tree species.

The breeding birds used the different tree species in different proportions. In general, pinyon pine was selected more intensely than was expected, whereas the juniper species were selected approximately as often as was expected, but the ponderosa pine was selected much less than was expected (Fig. 1). The extensive use of pinyon pine by all the bird species might be explained by the greater percentage of green

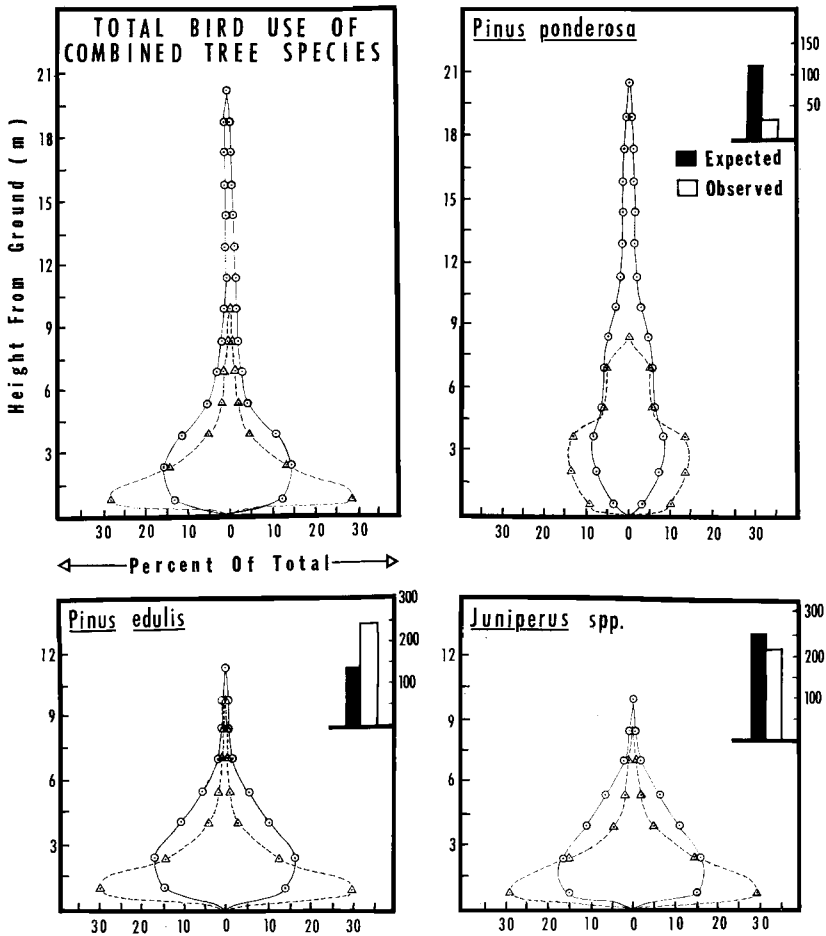


Fig. 1. Total bird use of the foliage. The shaded bar represents the expected bird use of each tree species calculated from the tree species volume. The open bar represents the actual number of observations in a tree species. The solid line represents the percent of foliage volume present in each 1.5-m height interval. The broken line represents the percent of bird observations in each 1.5-m height interval.

foliage per individual tree (see percent inner core figures, Table 2) which may in turn indicate the presence of more foliage insects.

The pinyon pine had a needle configuration similar to that of the low density ponderosa pine. The ponderosa pine birds (Mountain Chickadee and Solitary Vireo) foraged in pinyon pines 45.5% of the time compared to 9.0% usage of the ponderosa pine. This latter figure is surprisingly low for species that normally reach their highest densities in the pon-

TABLE 4
FORAGING CHARACTERISTICS OF THE FIVE BREEDING SPECIES

	Bushtit	Mountain Chickadee	Plain Titmouse	Solitary Vireo	Chipping Sparrow
Tree species selection ¹	24.3	32.5	39.1	9.8	47.5
Tree height selection ¹	66.9	72.0	65.9	23.5	100.0
Inner tree selection ²	4.5	3.6	7.5	17.6	16.0
Foraging strategy ³	55.5	41.1	2.7	0.0	0.0
Bill length ⁴	58.7	75.8	90.1	100.0	76.5

¹ Use-index value.

² Percent use of the inner core.

³ Percent of time spent hanging.

⁴ Percent of longest bill.

derosa pine forest. The ubiquitous Chipping Sparrow used pinyon pines far more often (69%) than did the other birds. Thus all the breeding birds preferred pinyon pine over ponderosa pine. All the nests we located (three Chipping Sparrow and two Plain Titmouse) were in pinyon pines.

The tree species selection was measured as goodness-of-fit to the foliage volumes of each species of tree. The breeding bird species ranked from the best to the poorest fit as follows: Solitary Vireo, Bushtit, Mountain Chickadee, Plain Titmouse, and Chipping Sparrow (Table 4).

Pinyon pine was the most important source of requisites for the breeding birds as indicated by its high use (Fig. 1). The junipers provided a moderate amount of the birds' requirements, whereas the ponderosa pine contributed surprisingly little, even to the species that normally inhabit the ponderosa pine forest.

Tree height class selection.—The birds utilized the lower portions of the foliage to a greater extent than the higher portions. The birds spent 84% of their time foraging in the lowest 3 m of the trees that contained 56% of the total foliage volume (Fig. 1). This occurred in all the tree species examined, even though the observers spent a much higher proportion of their time searching the higher reaches of the trees. The Plain Titmouse (Fig. 2), Mountain Chickadee, and Chipping Sparrow (Fig. 3) followed this general trend with minor variations. The extensive use of the ground (52%) by the Chipping Sparrow was not included in Fig. 3. The graph would be even more skewed to the lower areas if ground foraging were included.

The goodness-of-fit to the height class volume (Table 4) was closest for the Solitary Vireo, followed by the Plain Titmouse, Bushtit, Mountain Chickadee, and Chipping Sparrow. These data suggest that most of the needed requirements for the breeding birds were found in the lower levels of the canopy.

Inner tree partitioning.—The inner tree volume consisted of 22% of

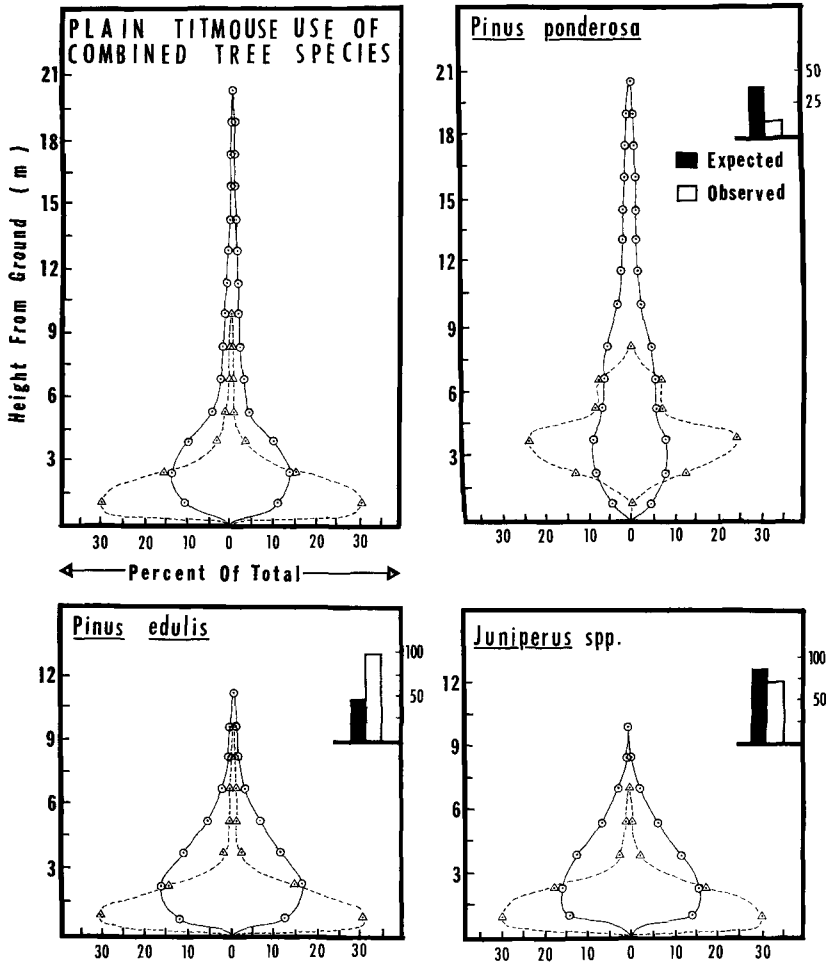


Fig. 2. Plain Titmouse usage of the foliage. The bar graphs and line areas as in Fig. 1.

the total vegetation available (Table 2). The pinyon pine contained the smallest amount of inner core per tree, thus providing the birds with the greatest amount of green foliage per total volume. The utilization of the inner tree (twigs, branches, and trunk) varied considerably with the species of bird. The three parids utilized the inner core of the trees to a very small extent, whereas the Solitary Vireo and the Chipping Sparrow spent a much greater proportion of their time there (Table 4). Hence, it appears that the requirements of these two groups of species were found in different portions of the trees.

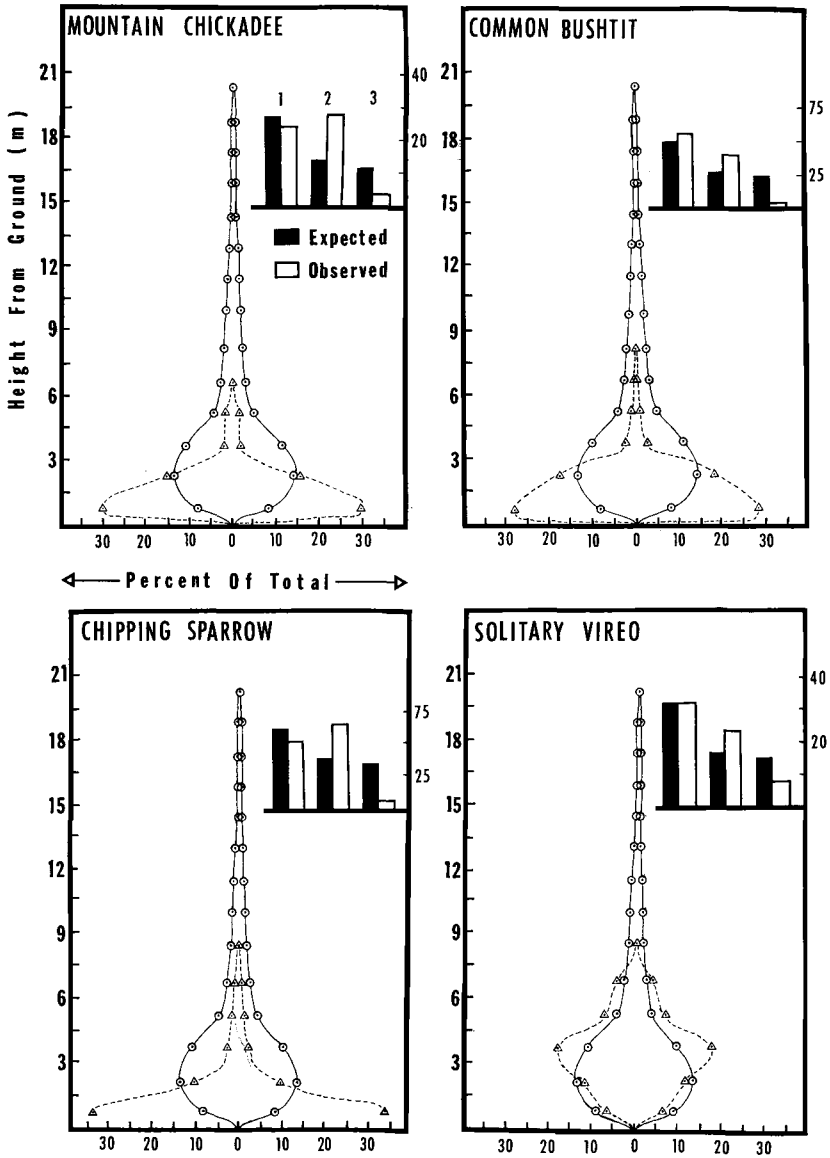


Fig. 3. Other bird usage of the foliage. The use of each tree species is contained in the bar graphs with: 1, *Juniperus* spp.; 2, *Pinus edulis*; 3, *Pinus ponderosa*. The open bottom of the broken line indicates that the species was observed on the ground. The other variables are as in Fig. 1.

Foraging strategy.—Knowledge of the foraging stance of the breeding birds was helpful in discerning the means these bird species used to locate their food. The Chipping Sparrow and Solitary Vireo foraged exclusively by standing. The Plain Titmouse, Mountain Chickadee, and Bushtit used the hanging posture in addition to standing (Table 4). We assume the differences shown in Table 4 indicate crudely the location of the preferred food items of each species.

The proportion of time spent hanging was related to use of the outer portions of the tree. Birds that spent the majority of their time exploiting the outer foliage tended to utilize the hanging stance to a greater extent than those using the inner core (Table 4). If the food item is found among the dense needles and leaves, the bird may need to use the hanging position to glean insects from the foliage. In contrast, if the prey is found on the twigs and branches, it is probably not necessary to use the hanging stance.

The amount of hanging done by a particular bird species was also inversely correlated with the weight of the bird. The Plain Titmouse was the heaviest species ($\bar{x} = 15.7$ g, $n = 4$) followed by the Mountain Chickadee ($\bar{x} = 10.5$ g, $n = 6$) and the Bushtit ($\bar{x} = 5.8$ g, $n = 4$). These lighter birds are probably more agile than the heavier species and consequently can maneuver with relative ease among dense foliage. The heavier species may be more restricted to the sparsely vegetated inner core because of reduced mobility.

Bill size.—The bill size of a particular bird species provides a crude estimate of the size of the prey items. Hutchinson (1959) showed that if the ratio of the larger to the smaller bill is between 1.1 and 1.4 to 1 in closely related species, then the two organisms are selecting different sizes of prey items. Using the exposed culmen, the ranking from the smallest to the largest bill was: Bushtit ($\bar{x} = 8.12$ mm, $n = 15$), Mountain Chickadee ($\bar{x} = 10.8$ mm, $n = 13$), Chipping Sparrow ($\bar{x} = 10.8$ mm, $n = 15$), Plain Titmouse ($\bar{x} = 12.7$ mm, $n = 8$), and Solitary Vireo ($\bar{x} = 14.4$ mm, $n = 14$). The percentage of each bill compared to the length of the longest bill, that of the Solitary Vireo, is given in Table 4.

The ratios of bill lengths of all species pairs were calculated and compared with Hutchinson's (1959) ratio to determine if overlap existed in the size of potential prey selected by some of the species. The only pair of species that did not fall into the interval between 1.4 and 1 were the Mountain Chickadee and the Chipping Sparrow, which had a 1:1 ratio. But the sparrow is graminivorous whereas the chickadee is insectivorous. These differences suggest selection of different sized prey by each species of breeding bird on the study area.

DISCUSSION

The breeding bird species diversity of the ecotone was lower than what is usually found in the adjacent plant communities that contribute plant species to it. No species occupied the ecotone that did not occupy the adjacent contributing communities. This suggests there are no typical edge species available to breed in this ecotone. Balda (pers. obs.) has also found this to be true in ecotonal areas between the pinyon-juniper woodland and the grassland in the Southwest. Marshall (1957) considered the pine-oak woodland of southeastern Arizona and Mexico as a permanent "self-perpetuating" ecotone consisting of a mixture of elements from two biomes. Yet only a small portion of the bird species appeared to require a combination of oaks and pines.

One must question the reason for this apparent lack of strictly ecotonal species in our area. Two possible explanations are available. First, the ecotone we studied had no plants that can be considered edge species. Ecotones are merely a simple blending of plant species from the adjacent communities. Thus no additional habitat parameters are available for use save those that may occur because of a unique combination of plant species. Second, ecotones are usually very narrow because of the abrupt elevational changes that often occur on rugged terrain. These areas may be too small to support other species than those from the surrounding communities.

Because of the mixture of pines and junipers the plant species diversity and structural complexity of the ecotone under study was much higher than that found in the contributing plant communities, but bird species diversity did not reflect this added habitat diversity. The low bird species diversity was probably the result of the reduced utilization of the ponderosa pine. Apparently some minimum threshold of pine density (or pine foliage volume) exists below which it is not economical for species to depend on it for requisites. The Solitary Vireo and Mountain Chickadee, which elsewhere occupy ponderosa pine, used it only seldom on the study tract. By using the pinyons and junipers these species avoided making the long flights between trees that foraging exclusively in ponderosa pines would necessitate, as the pinyons and junipers were relatively close together compared to the ponderosa pines. If the birds can procure adequate energy in the junipers and pinyons, it is more economical in terms of flight time and energy to forage there. This may also explain why the birds did not make use of the higher reaches of the pines. It is probably more economical to forage at those heights where the horizontal band of vegetation is continuous rather than higher in a sparsely distributed tree species.

The Solitary Vireo may inhabit the ecotone because of its habit of foraging on the larger limbs and branches, so that it could use the pinyon pine and junipers in much the same fashion it uses ponderosa pine. The dense crowns of these latter two species afford adequate foraging substrate. The Bushtit and Plain Titmouse probably foraged in the same manner in the ecotone that they use in the woodland, but no data are available to substantiate this suggestion. The factors responsible for the inclusion of the chickadee are unknown to us at this time. The Chipping Sparrow is ubiquitous to both major communities and the ecotone possibly because it can use the inner areas (branches) of trees and make extensive use of the ground. The use of the ground may also account for the presence of the Common Flicker and Mourning Dove and the use of flowers for the inclusion of the Broad-tailed and Black-chinned Hummingbirds in the ecotone. Until detailed studies are conducted on the habitat use of the excluded species it is difficult if not impossible to explain why other species did not inhabit the area. Balda (1969) suggested that two common ponderosa pine birds, the Pygmy Nuthatch (*Sitta pygmaea*) and Grace's Warbler (*Dendroica graciae*) may be limited in density by the amount of foliage volume available to them. It is possible that other ponderosa pine birds are excluded from this ecotone for similar reasons.

MacArthur et al. (1962), Karr (1968), Recher (1969), Karr and Roth (1971), and others demonstrated a relationship between the structural complexity of the habitat and bird species diversity. This relationship assumed that the birds were utilizing the entire habitat, which did not occur in this habitat. As the complexity of the habitat is reduced as a result of minimal use of one tree species and the use of only the lower portions of all tree species, the bird species diversity would be expected to be relatively low. Thus, one must measure the structure and complexity of the utilized habitat in addition to the total habitat potentially available. Balda (1969) found a similar pattern of bird use in oak-juniper woodland in southeastern Arizona.

To determine how each species used the trees in the ecotone, we measured three variables, foraging height, tree species selected, and use of the inner core and outer tree foliage. The bird species separated out into three groups: (1) Plain Titmouse, Mountain Chickadee, and Bushtit; (2) Chipping Sparrow; and (3) Solitary Vireo (Fig. 4). The use-index values of the Solitary Vireo, for the tree species selection and the tree height selection, fit the expected values more closely than did the use-index values of any of the other species. This occurred because of the vireo's slightly greater use of ponderosa pine and of higher portions of all tree species. It also utilized the inner core of all of the trees to the

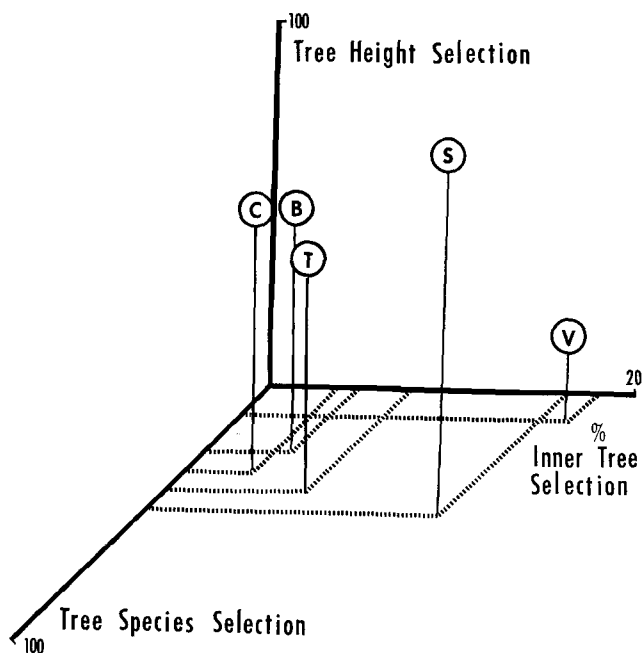


Fig. 4. Patterns of tree utilization by the breeding birds. The variables measured are: tree species selection (χ^2), tree height selection (χ^2), and tree inner core selection (percent of observations). The various letters represent the different bird species as follows B, Bushtit; C, Mountain Chickadee; S, Chipping Sparrow; T, Plain Titmouse; V, Solitary Vireo.

greatest degree (about 18% of the total observations). This indicates that, in the habitat studied, the vireo was more of a generalist than any of the other species.

The use-index values of the tree species and the tree height intervals for the Chipping Sparrow were the poorest fits to the expected values, but it had the second best fit in its use of the inner cores of the trees. The Chipping Sparrow's habit of foraging on the ground separated it from the other species and also affected its tree height use-index value. The high use of the pinyon pine by Chipping Sparrows may be accounted for by their preference for pinyon pines as nest sites.

The three parids were closely clustered together in all three tree selection variables (Fig. 4). Because these variables differed but little, other mechanisms may have operated to allow economical coexistence. These similarities are even more enlightening when the preferred habitat of the three species is compared. In ponderosa pine forests the Mountain

Chickadee prefer the ponderosa pine, whereas the Plain Titmouse and Bushtit prefer the pinyons and junipers (Bent 1946). Dixon (1961) found that when two members of the family Paridae coexisted and utilized their environment in a similar manner, they evolved other mechanisms to allow coexistence.

Although the three parids studied used very similar foraging substrates they foraged differently in them. The Bushtit spent over 50% of its time foraging by hanging, whereas the Plain Titmouse foraged in this manner only 2.7% of its time. Thus these two species are easily separated by this factor. The Mountain Chickadee only differs from the Bushtit by 14% in this factor, but the bill lengths of these two species are different enough to warrant the conclusion that they are selecting different sizes of prey. These latter two factors are the only ones measured in this study that suggest ecological partitioning of the habitat by the chickadee and Bushtit, even though the two normally inhabit different plant communities.

ACKNOWLEDGMENTS

We are extremely grateful for the field help of R. A. Lightfoot and R. Cooms, as well as W. S. Gaud, W. J. Rozema, and R. L. Hutto for their aid in the mathematical analysis. We also appreciate the aid of J. T. Emlen, K. Franzreb, R. H. Hevly, C. D. Johnson, R. D. Ohmart, and T. A. Vaughan for their valuable comments on an earlier draft of this manuscript. J. Balda is thanked for her careful preparation of the typescript.

SUMMARY

The densities, foliage preferences, and foraging habits of five species of breeding birds in a pinyon pine, juniper, ponderosa pine ecotone were examined and compared during one breeding season. The bird species separated into three natural groups: Mountain Chickadee and Solitary Vireo from the ponderosa pine forest; Bushtit and Plain Titmouse from the pinyon-juniper woodland; and the ubiquitous Chipping Sparrow.

We conclude that few if any truly "edge" species exist to use this ecotone in the southwestern mountains. The species that do inhabit this narrow, permanent ecotone appear to partition the habitat in different ways. The few species of ponderosa pine birds that breed in the ecotone make use of the pinyon and juniper trees far more than they do the sparsely distributed ponderosa pine. The birds that are usual breeding residents of the pinyon-juniper woodland appeared to forage in their usual substrates. The Chipping Sparrow and Solitary Vireo utilized different foraging substrates from each other, whereas the three species of parids utilized the same foraging substrates to the same degree but used different means of foraging and possibly different prey sizes.

LITERATURE CITED

- BALDA, R. P. 1969. Foliage use by birds of the oak-juniper woodland and ponderosa pine forest in southeastern Arizona. *Condor* 71: 399-412.
- BEECHER, W. J. 1942. Nesting birds and the vegetative substrate. Chicago, Chicago Ornithological Soc.
- BEIDLEMAN, R. G. 1960. Breeding bird census. Pinyon pine-Rocky Mountain juniper forest. *Audubon Field Notes* 14: 495-496.
- BENT, A. C. 1946. Life histories of North American jays, crows and titmice. U.S. Natl. Mus. Bull. No. 191.
- CAROTHERS, S. W., J. R. HALDEMAN, AND R. P. BALDA. 1973. Breeding birds of the San Francisco Mountain area and the White Mountains, Arizona. *Mus. Northern Ariz. Tech. Ser.* 12.
- CODY, M. L. 1966. The consistency of intra- and inter-continental grassland bird species counts. *Amer. Naturalist* 100: 371-376.
- COLQUHOUN, M. K., AND A. MORLEY. 1943. Vertical zonation in woodland bird communities. *J. Anim. Ecol.* 12: 75-81.
- COTTAM, G., AND J. T. CURTIS. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37: 451-460.
- DIXON, K. L. 1961. Habitat distribution and niche relationships in North American species of *Parus*. Pp. 179-216 in *Vertebrate speciation* (W. F. Blair, Ed.). Austin, Univ. Texas Press.
- HARTLEY, P. H. T. 1953. An ecological study of the feeding habits of English titmice. *J. Anim. Ecol.* 22: 261-288.
- HERING, L. 1957. Breeding bird census. Pinyon-juniper forest. *Audubon Field Notes* 11: 448-449.
- HUTCHINSON, G. E. 1959. Homage to Santa Rosalia, or why are there so many animals? *Amer. Naturalist* 93:145-159.
- JOHNSTON, D. W., AND E. P. ODUM. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. *Ecology* 37: 50-62.
- KARR, J. R. 1968. Habitat and avian diversity on strip-mined land in east-central Illinois. *Condor* 70: 348-357.
- KARR, J. R., AND R. R. ROTH. 1971. Vegetation structures and avian diversity in several New World areas. *Amer. Naturalist* 105: 423-435.
- KENDEIGH, S. C. 1944. Measurements of bird populations. *Ecol. Monogr.* 14: 67-106.
- LACK, D. 1971. *Ecological isolation in birds*. Oxford, Blackwell Scientific Publ.
- MACARTHUR, R. H. 1964. Environmental factors affecting bird species diversity. *Amer. Naturalist* 98: 387-397.
- MACARTHUR, R. H., J. W. MACARTHUR, AND J. PREER. 1962. On bird species diversity. 2. Prediction of bird census from habitat measurements. *Amer. Naturalist* 96: 167-174.
- MACARTHUR, R. H., H. F. RECHER, AND M. L. CODY. 1966. On the relation between habitat selection and species diversity. *Amer. Naturalist* 100: 319-332.
- MARSHALL, J. T., JR. 1957. Birds of pine-oak woodland in southern Arizona and adjacent Mexico. *Pacific Coast Avifauna* No. 32.
- MORSE, D. H. 1967. Competitive relationships between *Parula* Warblers and other species during the breeding season. *Auk* 84: 490-502.
- NEWTON, I. 1967. The adaptive radiation and feeding ecology of some British finches. *Ibis* 109: 33-98.

- ODUM, E. P. 1971. Fundamentals of ecology, third ed. Philadelphia, W. B. Saunders Co.
- ORIAN, G. H., AND M. F. WILLSON. 1964. Interspecific territories of birds. *Ecology* 45: 736-745.
- PHILLIPS, A. R., J. T. MARSHALL, AND G. MONSON. 1964. The birds of Arizona. Tucson, Univ. Arizona Press.
- RECHER, H. F. 1969. Bird species diversity and habitat diversity in Australia and North America. *Amer. Naturalist* 103: 75-80.
- ROOT, R. B. 1964. Ecological interactions of the Chestnut-backed Chickadee following a range extension. *Condor* 66: 229-238.
- SCHOENER, T. W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. *Evolution* 19: 189-213.
- SELANDER, R. K., AND D. R. GILLER. 1959. Interspecific relations of woodpeckers in Texas. *Wilson Bull.* 71: 107-124.
- STURMAN, W. A. 1968. The foraging ecology of *Parus atricapillus* and *P. rufescens* in the breeding season, with comparisons with other species of *Parus*. *Condor* 70: 309-322.
- WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornithol. Monogr.* 8.
- WILLIAMS, A. B. 1936. The composition and dynamics of a beech-maple climax community. *Ecol. Monogr.* 6: 317-408.

Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86001. Present address of first author: Department of Zoology, Arizona State University, Tempe, Arizona 85281. Accepted 20 March 1975.